# CHARACTERIZATION OF *MYRIOGRAMME LIVIDA,* MYRIOGRAMMEAE TRIB. NOV. (DELESSERIACEAE, RHODOPHYTA)[1]

*Max H. Hommersand*[2] *and Suzanne Fredericq*[3]

Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599-3280

### ABSTRACT

*The Myriogramme group of Kylin was found to contain two distinct clusters of genera that merit recognition at the tribal level. In this paper, we establish the tribe Myriogrammeae based on a study of the type species of Myriogramme, M. livida, from the Southern Hemisphere. The Myriogrammeae is characterized by 1) marginal and diffuse intercalary meristems; 2) nuclei arranged in a ring bordering the side walls of vegetative cells; 3) microscopic veins absent; 4) procarps scattered, formed opposite one another on both sides of the blade posterior to one or more vegetative pericentral cells (cover cells) and consisting of a carpogonial branch, a one-/to two-celled lateral sterile group and a one-celled basal sterile group; 5) auxiliary cell diploidized by a connecting cell cut off posteriolaterally from the fertilized carpogonium; 6) gonimoblast initial cut off distally from the auxiliary cell, generating one distal and one to two lateral gonimoblast filaments that branch in the plane of the expanding cystocarp cavity and later fuse to form an extensive, branched fusion cell; 7) spermatangial and tetrasporangial sori formed inside the margin on both sides of the blade by resumption of meristematic activity; and 8) tetrasporangia produced primarily from the central cells. The Myriogrammeae currently includes Myriogramme Kylin, Gonimocolax Kylin, Haraldiophyllum A. Zinova, Hideophyllum A. Zinova, and a possible undescribed genus from Pacific North and South America. Genera are separated based primarily on features of gonimoblast and carposporangial development.*

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

In 1923, Kylin investigated the vegetative and reproductive development of the type species of each of five prominent European genera of Delesseriaceae using material stained with hematoxylin. He divided the Delesseriaceae into two subfamilies based on the position of procarps and cystocarps (pre-/and postfertilization stages of the female reproductive apparatus): along the midrib of a fertile blade in Delesserioideae versus scattered randomly over the blade surface in Nitophylloideae. The following year, Kylin (1924) published a comprehensive taxonomic revision of the Delesseriaceae in which he divided the family into 11 "Gruppen" (groups), 5 in Delesserioideae and 6 in Nitophyllo-

ideae, and 40 genera, many of them new. Most generic names proposed by Kylin had been used previously by J. Agardh (1876, 1898) for subgenera or "tribes" (sections) in *Nitophyllum* or *Delesseria.* *Myriogramme* Kylin (1924:55), type of the Myriogramme group Kylin (1924:53), for example, was based on Tribus III *Myriogramma* of subgenus II *Aglaophyllum* in *Nitophyllum* (J. Agardh 1898:42). Kylin designated *Nitophyllum lividum* J. D. Hooker et Harvey 1845 as the type species of *Myriogramme* because, in his opinion, it included *Nitophyllum grayanum* J. Agardh (1876:449), the first species listed by J. Agardh (1898) under *Myriogramma.* An element of confusion was introduced from the beginning in that, although Kylin selected *M. livida* as the type species, he based his concept of *Myriogramme* primarily on a study of *M. minuta* Kylin (1924:56), a new species from Naples, Italy. Subsequent investigations of related taxa placed in *Nitophyllum* Greville 1830 (nom cons.), *Myriogramme* Kylin 1924, *Haraldiophyllum* Zinova 1981, or *Hideophyllum* Zinova 1981 have not resolved the many ambiguities arising from Kylin's original characterization of *Myriogramme* based on nontype material (Kylin 1925, 1929, 1934, 1956, Hollenberg and Abbott 1965, Abbott 1969, Norris and Wynne 1969, Mikami 1972, Zinova 1981, Wynne 1983, 1986, 1996, Millar 1990, 1994, Millar and Huisman 1996).

We began our study of *Myriogramme* by surveying procarp and cystocarp development in type and field-collected material of potentially interesting species placed in the Nitophyllum group, the Cryptopleura group, and the Myriogramme group in the North Atlantic Ocean, Pacific North and South America, Australia, and New Zealand. Our preliminary observations indicated that the Myriogramme group requires systematic revision. In this paper, we describe the developmental morphology of type and field-collected material of *M. livida,* the type species of *Myriogramme,* and propose a new tribe Myriogrammeae trib. nov., to contain *Myriogramme, Gonimocolax, Haraldiophyllum, Hideophyllum,* and a few species currently placed in *Nitophyllum.*

### MATERIALS AND METHODS

Type collections of *Myriogramme livida* and *M. crozieri* used in this study were kindly loaned by The Natural History Museum (London). Morphological observations were largely made on material fixed in 8–10% formalin–seawater and preserved in 5% formalin–seawater. Whole-mount and sectioned material either was stained with aniline blue and mounted in Karo® syrup or glycerine or was treated with Wittmann's aceto-iron–hematoxylin–chloral hydrate (Wittmann 1965) and mounted in 50% Hoyer's mounting medium, as described in Hommersand et al. (1992).

Whole-mount preparations were sometimes cleared for critical observations. Slides were placed in an alcohol chamber for 12–24 h after destaining in 45% glacial acetic acid, transferred by stages (⅔ absolute ethanol, ⅓ xylene; ⅓ absolute ethanol, ⅔ xylene) into xylene, and mounted in Piccolyte® (Ward's Natural Science Establishment, Inc., Rochester, New York). Drawings were made with a camera lucida, and photographs were taken with a Zeiss Photomicroscope III. Herbarium abbreviations follow Holmgren et al. (1990).

## OBSERVATIONS

### *Myriogramme* Kylin (1924:55)

Description: Plant body foliose, erect and basally attached, or repent and attached secondarily by rhizoids; entire, sinuous, lobed, lacerate, or deeply divided; membranous above, thickening toward the base, sometimes with a basal nerve, or the nerves subdichotomously branched in lower parts; estipitate or with a compressed to cylindrical stipe. Blade monostromatic or tristromatic at margin, polystromatic toward base and in basal thickenings, nerves and stipes. Microscopic veins absent. Cells polygonal in surface view and rectangular in sectional view, arranged in horizontal tiers and vertical rows in polystromatic parts. Growth diffuse, by marginal and intercalary meristems, the divisions often perpendicular to one another, producing clusters of rectangular cells that later become polygonal in shape. Chloroplasts parietal, simple or dissected in marginal cells, later breaking into small units of defined size and shape linked initially by fine strands. Nuclei one to many in meristematic cells, at first arranged in a median plate or ring alongside lateral walls, later forming two rings bordering side walls on either side of plane passing through middle of blade, ultimately lying in a broad band bordering side walls between chloroplasts. Primary and secondary pit connections initially median, usually one between each adjoining cell, sometimes with finer secondary pit connections formed later near cell surfaces. Spermatangia produced in small circular to elliptical sori formed at random in upper parts of blade by renewed meristematic activity within thallus margin. Sori initially solitary, sometimes becoming partly confluent. Procarps scattered, formed simultaneously on both sides of thallus from meristematic tissues near margin, the fertile central cell first cutting off a vegetative pericentral cell (cover cell) on each side from the anterior end, followed by a posterior fertile pericentral cell (= supporting cell). Functional procarps consisting of a one-/to two-celled lateral sterile group, a four-celled carpogonial branch, and a one-celled basal sterile group. Carpogonium cutting off two connecting cells after fertilization, the auxiliary cell diploidized by the second, posteriolateral connecting cell. After diploidization, the auxiliary cell dividing into an anterior gonimoblast initial containing a diploid nucleus, and a posterior residual auxiliary cell containing a diploid and one or two haploid nuclei. Gonimoblast filaments developing monopodially in an arc encircling the supporting cell, afterward radiating upwardly and bearing primary carposporangia either terminally or in chains; secondary carposporangia, where present, developing sympodially from inner gonimoblast cells and either terminal and solitary, or forming clusters or branched chains. Fusion cell formed progressively, incorporating the supporting cell, central cell, residual auxiliary cell, and primary gonimoblast cell and extending to include inner gonimoblast cells and cells in floor of cystocarp. Sterile groups either excluded from, or included within, fusion cell. Cystocarp cavity formed schizogenously, covered by a multilayered pericarp with a single ostiole overlying sterile group 1. Tetrasporangia borne in small circular, elliptical, or rectangular sori scattered randomly bordered by a sterile margin in upper parts of blade. Sori formed by renewal of meristematic activity, mostly five cell layers thick at maturity. Primary tetrasporangia arising two (to four) per cell from central cells. Secondary tetrasporangia also cut off from central cells and possibly from inner cortical cells. Division of tetrasporangia tetrahedral.

### *Myriogramme livida* (J. D. Hooker et Harvey) Kylin (1924:58)
#### (Figs. 1–55)

Description: Thalli erect from a compact basal rhizoidal system to 40 cm high, bluish red to rose red or reddish brown, foliose with acute to rounded tips and smooth or ruffled margins, undivided, laciniate, lobed or deeply dissected; blade mostly monostromatic, polystromatic toward base, estipitate or with a compressed to cylindrical stipe and basal nerve, or the nerves subdichotomously branched below. Central cell layer of stipes and polystromatic parts typically broader than the cells on either side, or with several cell layers in the center distended forming a central core of larger diameter cells. Spermatangia borne in elliptical to irregularly shaped, separate or confluent sori on both sides of blade. Procarps initiated inside margins. Cystocarps low, circular with a central ostiole, scattered on both sides in monostromatic portions of blade. Gonimoblasts initially bearing carposporangia in open, monopodially branched chains, subsequently producing secondary carposporangia sympodially in small clusters of tightly branched chains. Fusion cell initially small, basal, later candelabra-like through progressive fusions of inner gonimoblast cells concomitant with the formation of secondary carposporangia. Tetrasporangia in small circular, elliptical or oblong sori distributed uniformly over monostromatic portions of blade.

Lectotype: BM; cystocarpic specimen corresponding to the reverse image of a habit drawing in J. D. Hooker 1847:plate CLXXIX, upper right-hand figure; Port William, East Falkland I., July 1842, Capt Cr[ozier] (Fig. 1). (Selected from among the syntypes in BM by J. Price; see Ricker 1987.)

Nomenclatural synonyms: *Nitophyllum lividum* J. D.
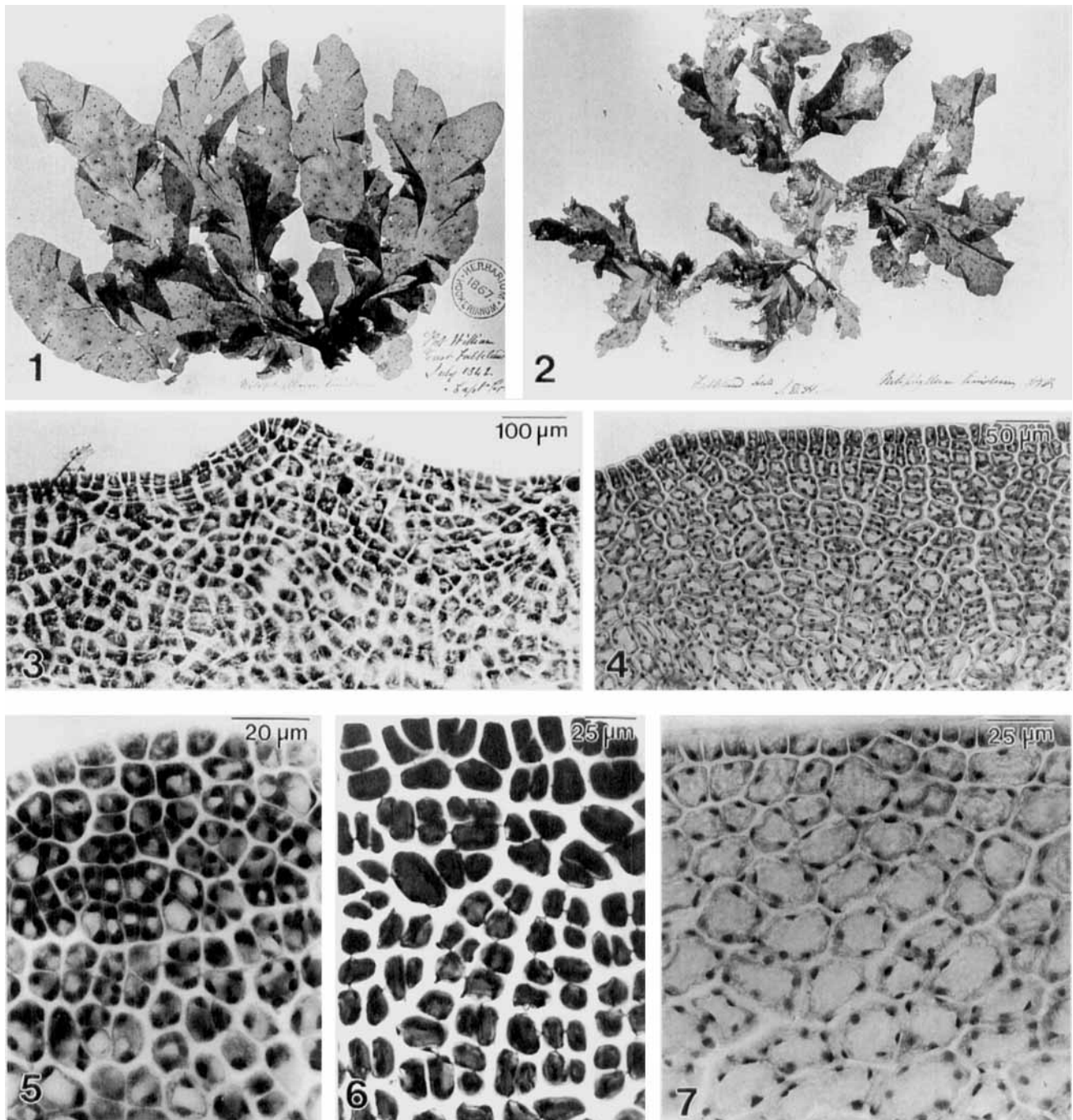
FIGS. 1–7. *Myriogramme livida.* FIG. 1. Habit of lectotype (Port William, Falkland Islands). FIG. 2. Habit of specimen collected by J. D. Hooker (Falkland Islands). FIG. 3. Meristematic margin. Specimen from type sheet of *M. crozieri* (Hermite Island, Cape Horn). FIG. 4. Meristematic margin of rapidly growing blade. FIG. 5. Meristematic margin showing patterns of intercalary cell divisions. FIG. 6. Meristematic margin showing enlarged marginal cells and dividing intercalary cells linked by primary pit connections. FIG. 7. Margin in slowly growing region of thallus. Figures 4, 5, 7, hematoxylin; Figures 3, 6, aniline blue.

Hooker et Harvey 1845:253. *Cryptopleura livida* (J. D. Hooker et Harvey) Kützing 1866:12, plate 31.

Taxonomic synonyms: *Nitophyllum crozieri* J. D. Hooker et Harvey 1845:254, 1847:472, plate CLXXVII. *Cryptopleura crozieri* (J. D. Hooker et Harvey) Kützing 1866:11, plate 27. *Myriogramme crozieri*

(J. D. Hooker et Harvey) Kylin 1924:59. *Nitophyllum grayanum* J. Agardh 1876:449, 1898:42.

Ricker (1987) questioned whether or not *Myriogramme crozieri* is distinct from *M. livida.* Here we place it in synonymy under *M. livida* for the first time. Another species, *Myriogramme smithii* (J. D.

Hooker et Harvey) Kylin 1924, with strongly developed macroscopic nerves that extend almost to the margins (J. D. Hooker 1847:plate CLXXVIII, central figure; see Cotton 1915), has sometimes been regarded as being closely related to *M. livida* (Kylin 1924). Pending further studies, we concur with the opinion of Mendoza (1969) that *M. smithii* represents a separate species.

Distribution: Southern South America, Antarctic Penninsula and Scotia Sea, Falkland Island, South Georgia, Isles Kerguelen, Macquarie Island. (For more complete distribution records and synonymy, see Papenfuss [1964], Mendoza [1969], and Ricker [1987].)

Specimens examined: *Myriogramme livida* (J. D. Hooker et Harvey) Kylin: lectotype of *Nitophyllum lividum* Port William, East Falkland, female, coll. Capt. Crozier, vii:1842, BM (Fig. 1); Falkland Island, female, coll. J. D. Hooker, BM (Fig. 2); on the beach, Berkeley Sound, Falkland Island, tetrasporic, vi: 1842, BM; additional tetrasporic or sterile specimens, Berkeley Sound or undesignated localities, BM; (no specimen was found that corresponded to the habit of the tetrasporic plant on the left in J. D. Hooker 1847: plate CLXXIX); lectotype of *Nitophyllum crozieri* in deep water, St. Martin's Cove, Hermite Island, Cape Horn, tetrasporic, BM, J. D. Hooker 1847:472–3, plate CLXVII (right-hand side of composite figure), Levring 1960:68–9, figure 18; other tetrasporic and sterile specimens from the same locality, BM; 8 km northeast of Punta Arenas, Strait of Magellan, Chile, male, female, and tetrasporic, coll. M. H. Hommersand, 9:i:1979, NCU.

Specimens of other taxa examined: *Myriogramme denticulata* (Harvey) Kylin 1924: 1 km south of The Kaik, Akaroa Harbor, South Island, New Zealand, male, female, and tetrasporic; coll. M. H. & F. C. Hommersand, 13:x:1974, NCU. *Myriogramme crispata* (J. D. Hooker et Harvey) Kylin 1929: drift, Ringa Ringa, Stewart Island, New Zealand, female and tetrasporic, coll. M. H. Hommersand, 3:xii:1974, NCU. *Haraldiophyllum bonnemaisonii* (Kylin) A. Zinova 1981: on kelp stipe, Skomer, North Wales, female, coll. S. Hiscock, 5:xi:1984, NCU; Carrickadda spit, Finavarra, Co. Clare, Ireland, male, female, and tetrasporic; coll. M. H. Hommersand, 1:vii:1985, NCU. *Hideophyllum yezoensis* (Yamada et Tokida) Zinova 1981: Urakawa, Hidaka Province, Hokkaido, Japan, female and tetrasporic, coll. Mikami, 23:xii:1971, US 070559. *Haraldiophyllum mirabile* (Kylin) A. Zinova 1981: isosyntypes, Canoe Island, near Friday Harbor, Washington, female and tetrasporic, coll. H. Kylin, 24:vi:1924, UC 279580. *Haraldiophyllum nottii* (R. E. Norris et Wynne) Wynne 1983: holotype, Hood Canal, 10-m depth, 1 mi south of Eldon, Mason Co., Washington, female and tetrsporic, coll. D. Russell, 18:xi:1967, WTU 238051. *Myriogramme spectabilis* (Eaton) Kylin 1924: syntypes, Santa Cruz, California, female and tetrsporic, coll. C. L. Anderson, 1874, FH; reef, 1 km south of Jalama Beach State Beach Park,

Santa Barbara Co., California, male, female, and tetrasporic, coll. M. H. Hommersand, 21:vii:1966, NCU. *Nitophyllum northii* Hollenberg et Abbott 1965: holotype, on *Prionitis* at 100 ft, Carmel Submarine Canyon, Monterey Co., California, male and female, coll. Wheeler J. North, 1962, US 077797. *Nitophyllum hollenbergii* (Kylin) Abbott 1969: syntypes, on piling, municipal wharf, Monterey, Monterey Co., California, female and tetrasporic, coll. G. J. Hollenberg, 20:vii:1939, US 077788. *Myriogramme* sp.: Dichato, Bahía de Coliumo, 40 km north of Concepción, Chile, female and tetrasporic, coll. M. H. Hommersand, 31:xii:1978, NCU.

*Vegetative morphology.* Juvenile thalli were not seen in this study. Growth of the adult thallus involved the activity of both marginal and intercalary meristems. Meristematic cells may be uninucleate, binucleate, or multinucleate, with few to many nuclei. Marginal meristematic cells were mostly rectangular in shape, with cell divisions taking place either at right angles or parallel to the thallus margin. Occasionally, marginal growth was initiated by triangular cells that divided obliquely, forming files of cells oriented parallel to the thallus margin. Intercalary cell divisions often occurred successively at right angles, forming patches in which the cells were grouped in twos, fours, or eights, similar to patterns seen in *Porphyra*.

Rapid marginal growth is particularly well illustrated in type material of *Myriogramme crozieri*, in which the pattern of periclinal and anticlinal divisions near the margin gives the appearance of dichotomously branched cell rows emanating from clusters of cells in the interior (Fig. 3). This feature had already been noted by J. Agardh (1898) and Cotton (1915) in the type of *M. crozieri* (as *Platyclinia crozieri*) and is seen in rapidly growing margins in our material of *M. livida* (Fig. 4). Often, cells in the outermost one to three layers at the margin appear to be growing slowly, while those in the interior divide more rapidly, forming distinct meristematic patches (Figs. 5, 6). Occasionally, marginal files overgrow one another to the left and right, forming distinct marginal layers (Fig. 6). In slower growing tissues, cell enlargement keeps pace with cell divisions, both along the margin and in the thallus interior, and cell shapes and sizes grade more or less uniformly from inside to outside (Fig. 7). The range of growth patterns described here were seen in different parts of the same thallus and in different thalli.

Cytokinesis takes place perpendicular to the plane of the blade. Primary pit connections are median when viewed optically in periclinal section (Figs. 5, 6). Rapidly dividing cells tend to be small and contain few (one to six) nuclei (Figs. 4, 5, 9). The number of nuclei is closely correlated with cell volume: the larger the cell the more nuclei, with up to 40–60 nuclei in the largest cells. Nuclei aggregate in a ring of cytoplasm along the side walls, such that mer-
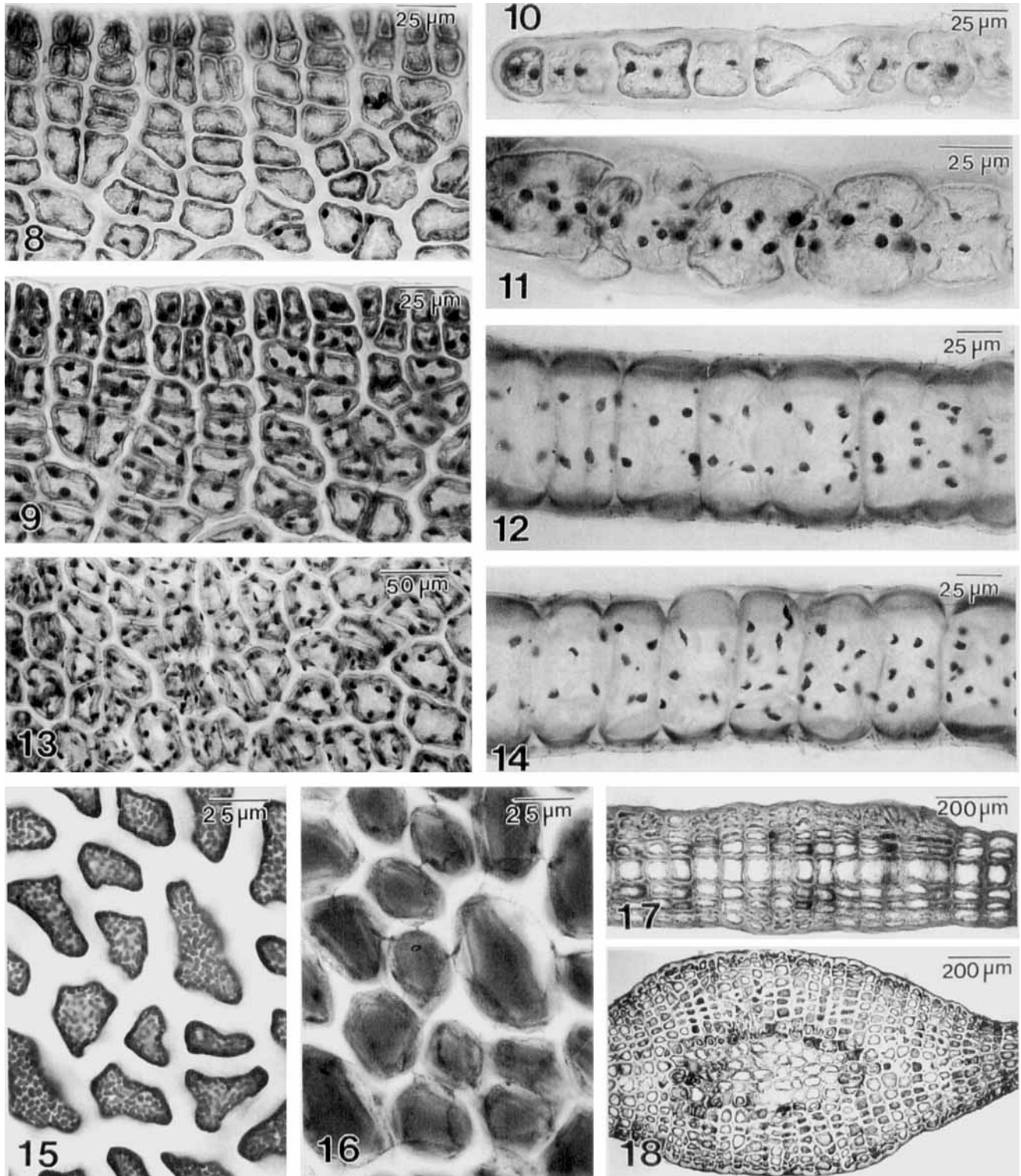
FIGS. 8–18.  *Myriogramme livida.* FIGS. 8–14. Distribution of nuclei. FIGS. 8, 9. Meristematic margin seen in surface and median focal planes. FIG. 10. Cross-section of meristematic margin showing nuclei in single, medial band. FIGS. 11, 12. Cross-sections of meristematic and mature tissues showing nuclei in two bands. FIG. 13. Meristematic tissue in median optical section showing medial pit connections and nuclei in two bands. FIG. 14. Cross-section of older monostromatic tissue showing nuclei dispersed in a broad peripheral band. FIGS. 15, 16. Surface and median optical section of mature tissue. FIG. 17. Cross-section of a nerve. FIG. 18. Cross-section of stipe. Figures 8–14, 17, hematoxylin; Figures 15, 16, 18, aniline blue.

istematic and mature cells present a window in surface view (Fig. 8), framed by a border of nuclei when seen in median optical section (Figs. 4, 7, 9). Nuclei are aligned in a single plane in dividing cells near the margin of the thallus (Fig. 10). Further in the interior, the nuclei divide and separate into two distinct rings disposed along side walls on either side of the plane passing through the middle of the blade in both meristematic and mature cells (Figs. 11, 12). These are resolved as two rings of nuclei lying in different planes around the periphery inside the cell wall when viewed in a median optical section under conditions of low resolution and high contrast (Fig. 13). Still older cells may have many nuclei distributed in a broad circular band around the central vacuole and between the chloroplasts that face outward on either side (Fig. 14). Nuclei were variable in size in dividing cells, ranging from 3 to 6 μm in diameter, but were relatively constant at a 5–6 μm diameter in mature, nonmeristematic cells. Larger meristematic and young mature vegetative cells tended to have 12–16 nuclei per cell, or six to eight in each circular ring, with greater numbers in larger cells.

Young marginal cells may contain parietal laminate chloroplasts; however, the chloroplasts are soon dissected into minute discoid elements approximately 3–4 μm wide and 4–8 μm long, as seen in older meristematic and mature cells (Fig. 15). Secondary pit connections appeared to be formed at a steady rate over time, with the result that there were fewer secondary pit connections per unit area in rapidly dividing patches of meristematic tissue, and recently formed secondary pit connections were more abundant near the margin in slower growing regions. Initially, they were median to submedian in position and only rarely, if ever, were they produced adjacent to external cell walls. At maturity, each adjoining cell was connected by either a primary or a secondary pit connection, or a pit connection was absent. Seldom was there more than one pit connection between adjacent cells. The arrangement of cell walls, protoplasts, and pit connections is readily seen in material stained with aniline blue and mounted in Karo® syrup, a medium that tends to expand cell walls and the intercellular matrix and shrink protoplasts (Fig. 16).

The vegetative thallus of *Myriogramme livida* was monostromatic except for the stipe, central midrib, and subdichotomously branched nerves that were usually restricted to the base or lower portion of a blade. Reproductive structures were also polystromatic. Midribs and nerves were formed by a periclinal division of primary cells or surface cortical cells on both sides of the thallus, such that the cells are arranged in tiers and rows. The residual primary cells form a central row that is distinctly broader in young nerves (Fig. 17) but that may be variously modified in older, thicker ribs and stipes, often as a result of differential cell expansion (Fig. 18).

*Female reproduction.* Procarps are formed on both surfaces of the thallus in growing regions near the margin. A fertile central cell is either binucleate or multinucleate. It first elongates in the prevailing direction of growth, usually toward the thallus apex or margin, and cuts off four pericentral cells, two anterior and two posterior on either side. Cytoplasm and nuclei first migrate toward the anterior end of the fertile central cell, the nuclei divide, and the cytoplasm divides twice obliquely, cutting off anterior pericentral cells on both sides that remain sterile and do not contribute further to the development of the procarps (Fig. 19). An anterior pericentral cell was either uninucleate or multinucleate at inception but became multinucleate and vacuolate and elongated transversely and divided once or twice as the procarp enlarged and matured. Kylin (1934, 1956) called such vegetative pericentral cells and their derivatives "cover cells." They resemble ordinary vegetative cells but can usually be distinguished by the presence of a single primary pit connection linking the innermost cover cell to the central cell (Fig. 20), even at late stages. Only rarely did a fertile central cell divide transversely and then the cover cells were absent.

Once the cover cells have been cut off, the cytoplasm is reorganized toward the posterior end of the fertile central cell, and a single, uninucleate pericentral cell is cut off on both sides that form procarps (Fig. 20). A fertile pericentral cell divides obliquely, cutting off the first sterile group initial outwardly and to one side (Fig. 21). It then divides longitudinally by a concavo-convex wall to form the initial of the carpogonial branch, which divides transversely to form first a two-celled and then a three-celled carpogonial filament (Fig. 22). At this stage, the supporting cell cuts off a second sterile group initial. Finally, the third cell of the carpogonial filament divides obliquely, cutting off the carpogonium, which lies partly beneath the third cell of the carpogonial branch. The tip of the carpogonium elongates into a trichogyne that emerges from the thallus surface directly behind the cover cells (Fig. 23). Sterile groups normally remained one-celled and uninucleate in functional procarps before fertilization. Unfertilized procarps in which the sterile groups were divided had usually started to degenerate and were nonfunctional. The second and sometimes the third cell of the carpogonial branch becomes binucleate before fertilization, whereas the first cell usually remains uninucleate (Fig. 23). The carpogonium is uninucleate.

The carpogonium divides twice after presumed fertilization, cutting off two connecting cells, the first distal and the second proximal on the side facing the supporting cell (Fig. 24). Each connecting cell contains a highly condensed nucleus surrounded by a hyaline region and an outer membrane or thin cell wall (Fig. 29). At the same time, the supporting cell cuts off a large auxiliary cell distally, and
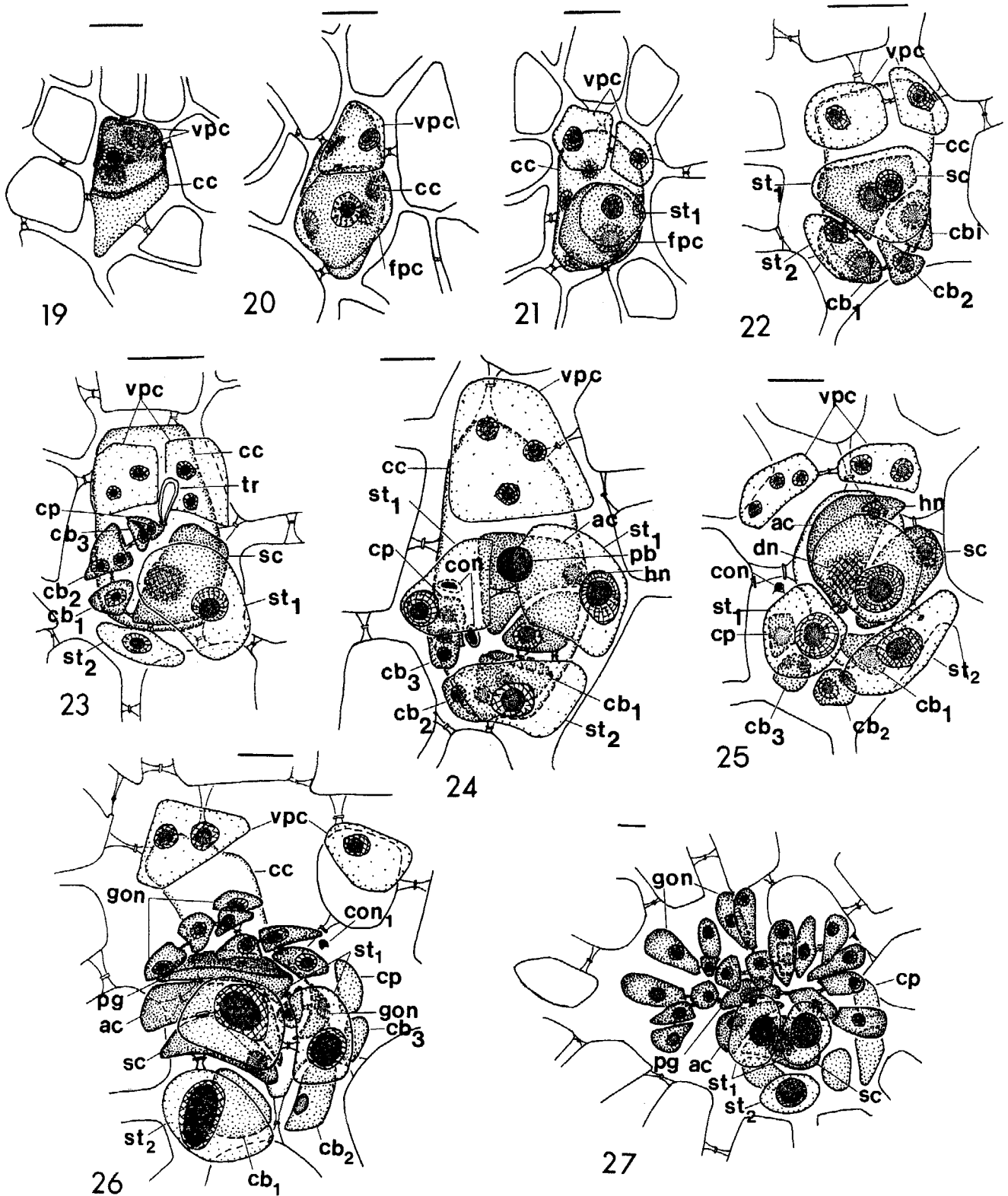
Figs. 19–27.   Procarp and cystocarp development in *Myriogramme livida*. Bars = 10 μm. Abbreviations: ac = auxiliary cell, $cb_1$, $cb_2$, $cb_3$, cbi = cells of the carpogonial branch, cc = central cell, $con_1$, $con_2$ = connecting cells, cp = carpogonium, dn = diploid nucleus, fpc = fertile pericentral cell, gon = gonimoblasts, hn = haploid nucleus, pb = protein body, pg = primary gonimoblast cell, sc = supporting cell, $st_1$, $st_2$ = sterile groups, tr = trichogyne, vpc = vegetative pericentral cell (= cover cell). Fig. 19. Central cell with two nuclei and two opposite anterior vegetative pericentral cells with one nucleus each. Fig. 20. Anterior vegetative pericentral cell and posterior fertile pericentral cell. Fig. 21. Sterile group 1 cut off from the fertile pericentral cell. Fig. 22. Stage with a three-celled carpogonial branch and sterile group 2. Fig. 23. Stage with a four-celled carpogonial branch and trichogyne. Fig. 24. Postfertilization stage. Carpogonium with two connecting cells, auxiliary cell with a haploid nucleus and protein body. Fig. 25. Auxiliary cell containing a diploid and a haploid

the first and second sterile groups sometimes also divide (Figs. 24, 28). The auxiliary cell becomes densely filled with cytoplasm, one or more protein bodies form, and the haploid nucleus is situated in the lower corner on the side away from the carpogonial branch (Fig. 24). The distal connecting cell is nonfunctional whereas the proximal connecting cell fuses onto the lower side of the auxiliary cell, and the diploid nucleus migrates toward the center of the auxiliary cell (Fig. 25). The diploidized auxiliary cell enlarges and divides, forming a small distal gonimoblast initial and a larger proximal remnant auxiliary cell. Figure 30 illustrates the position of the gonimoblast initial in relation to the remnant auxiliary cell, supporting cell, central cell, and the two sterile cell groups in an unstained preparation.

The gonimoblast initial divides apically (Fig. 31) and laterally, usually producing three initials that branch radially, arching forward and backward around the auxiliary cell (Figs. 26, 27). Fusions take place early during gonimoblast formation, starting with the supporting cell, which fuses with the remnant of the auxiliary cell (Fig. 31) and later includes the central cell and its pericentral cell on the opposite side, the primary gonimoblast cell, and basal cells of the gonimoblast filaments (Figs. 32–35). The two sterile groups remain separate and distinct from the fusion cell (Figs. 26, 27, 30–32) and are later usually seen detached (Fig. 33). The haploid nuclei of the two sterile groups enlarge and stain heavily with hematoxylin (Figs. 26, 27, 31–33), whereas the multinucleate central cells in the floor of the cystocarp distend and their nuclei also enlarge (Figs. 32, 33). Gonimoblast filaments first grow unilaterally in a fan-shaped fashion, arching forward and backward around the central fusion cell (Figs. 27, 34, 35), ultimately surrounding it completely. An ostiole develops above the first sterile group (Figs. 30–33) and slightly off-center (Fig. 33).

Vegetative cells in the vicinity of the young gonimoblasts divide periclinally to produce a pericarp five to seven cell layers thick, in which the cells are rectangular in cross-section and organized roughly into horizontal tiers and longitudinal rows (Figs. 36, 38). Mucilaginous material is secreted into the cystocarp cavity beginning in the vicinity of the sterile groups (Fig. 30) and extending above the plane of the central cells (Fig. 33). Cells of the upper pericarp detach from the central cells, leaving no remnant of the original pit connections. Mucilage secretion and lateral extension of the cystocarp cavity proceed well in advance of radial growth and extension of the gonimoblast filaments (Fig. 33).

The gonimoblasts and carposporangia develop differently and have a different appearance in young and old cystocarps. At first, the gonimoblasts grow and branch monopodially, and carposporangia mature basipetally, forming branched chains. The central fusion cell is initially small, nuclei are variable in size, and most of the central cells in the floor of the cystocarp remain intact. Later, a few central cells are sometimes incorporated into the fusion cell, and the gonimoblast filaments become highly branched (Fig. 36) and bear carposporangia in branched chains (Figs. 37, 38).

As the first crop of carpospores mature and are released, intercalary gonimoblast cells elongate, their nuclei divide, and secondary gonimoblast filaments are generated that bear carposporangia in clusters at their tips (Figs. 39–43). Terminal gonimoblast cells distend and divided obliquely near their apices, cutting off two to three initials (Figs. 39, 40), each of which produces a branched chain of cells that mature into a club-shaped cluster of carposporangia (Figs. 41, 42). Repeated nuclear divisions and branching of intercalary gonimoblast cells produce additional carposporangia as long as the cystocarp remains productive. Inner gonimoblast cells are added progressively to the fusion cell, which becomes highly branched and filled with many small nuclei (Fig. 43). The basal portion of the fusion cell continues to fuse with the central cells in the floor of the cystocarp. The fusion cell of a fully mature cystocarp is massive, supported by basal extensions looking like the legs of a stool and gonimoblast filaments that resemble a candalabra bearing clusters of carposporangia terminally (Fig. 42).

It should be noted that, whereas the primary gonimoblasts grow and branch monopodially, secondary gonimoblasts develop sympodially. Cystocarps of intermediate age contain both monopodially and sympodially developed gonimoblasts and carposporangia borne both in branched chains and terminal, club-shaped branched clusters. Older cystocarps usually contain clusters of gonimoblasts of different ages and stages of development (Fig. 42). Functionally, these are like the gonimolobes found in genera of Ceramiaceae and Rhodymeniaceae. Mature cystocarps measure 1 mm in diameter and are about 500–600 μm thick.

*Male reproduction.* Spermatangia are produced in small sori (Fig. 44) on both sides of the blade (Fig. 50), except along the margin. Sori are initiated in monostromatic parts of the blade as a result of resumption of cell division in otherwise mature cells (Fig. 45). Development follows the general pattern described by Kylin (1923) for *Phycodrys rubens* (Linnaeus) Batters (as *P. sinuosa*) and by Papenfuss (1939) for *Acrosorium acrospermum* (J. Agardh) Kylin.

←

nucleus. FIG. 26. Residual auxiliary cell and primary gonimoblast cell bearing one distal and one lateral gonimoblast filament. FIG. 27. Residual auxiliary cell and primary gonimoblast cell bearing a distal and two lateral gonimoblast filaments. Hematoxylin.
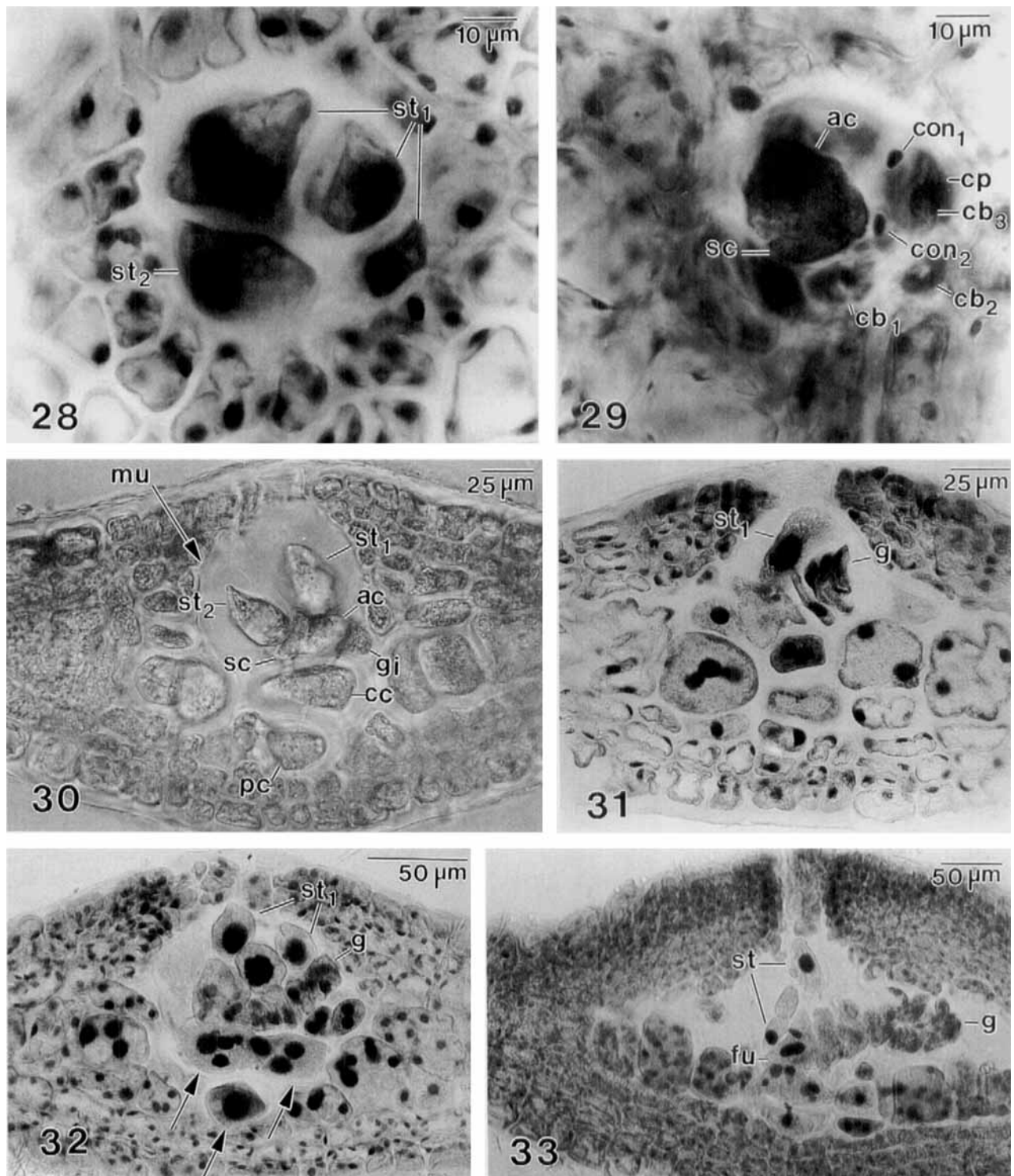
FIGS. 28–33. Cystocarp development in *Myriogramme livida*. FIGS. 28, 29. Surface and median focal planes of early postfertilization stage showing divided sterile group 1 ($st_1$), sterile group 2 ($st_2$), supporting cell (sc), auxiliary cell (ac), first, second, and third cells of the carpogonial branch ($cb_1$, $cb_2$, $cb_3$) and the carpogonium (cp) that has cut off two connecting cells ($con_1$ and $con_2$). FIG. 30. Cross-section of early postfertilization stage showing central cell (cc), supporting cell (sc), two sterile groups ($st_1$ and $st_2$) surrounded by a mucilaginous envelope (mu), gonimoblast initial (gi), residual auxiliary cell (ac), and a second pericentral cell (pc) below. FIG. 31. Cross-section of young cystocarp showing the first sterile group ($st_1$) beneath the ostiole and recently divided gonimoblasts (g). FIG. 32. Cross-section of young cystocarp with gonimoblasts (g). (Note enlarged nuclei in cells of sterile group [$st_1$] and in cells in floor of cystocarp.) FIG. 33. Cross-section of cystocarp with an ostiole, sterile groups (st), gonimoblasts (g), and fusion cell (fu). (Note that the cystocarp cavity has formed in advance of the ramifying gonimoblasts.) Figures 28, 29, 31–33, hematoxylin; Figure 30, unstained.
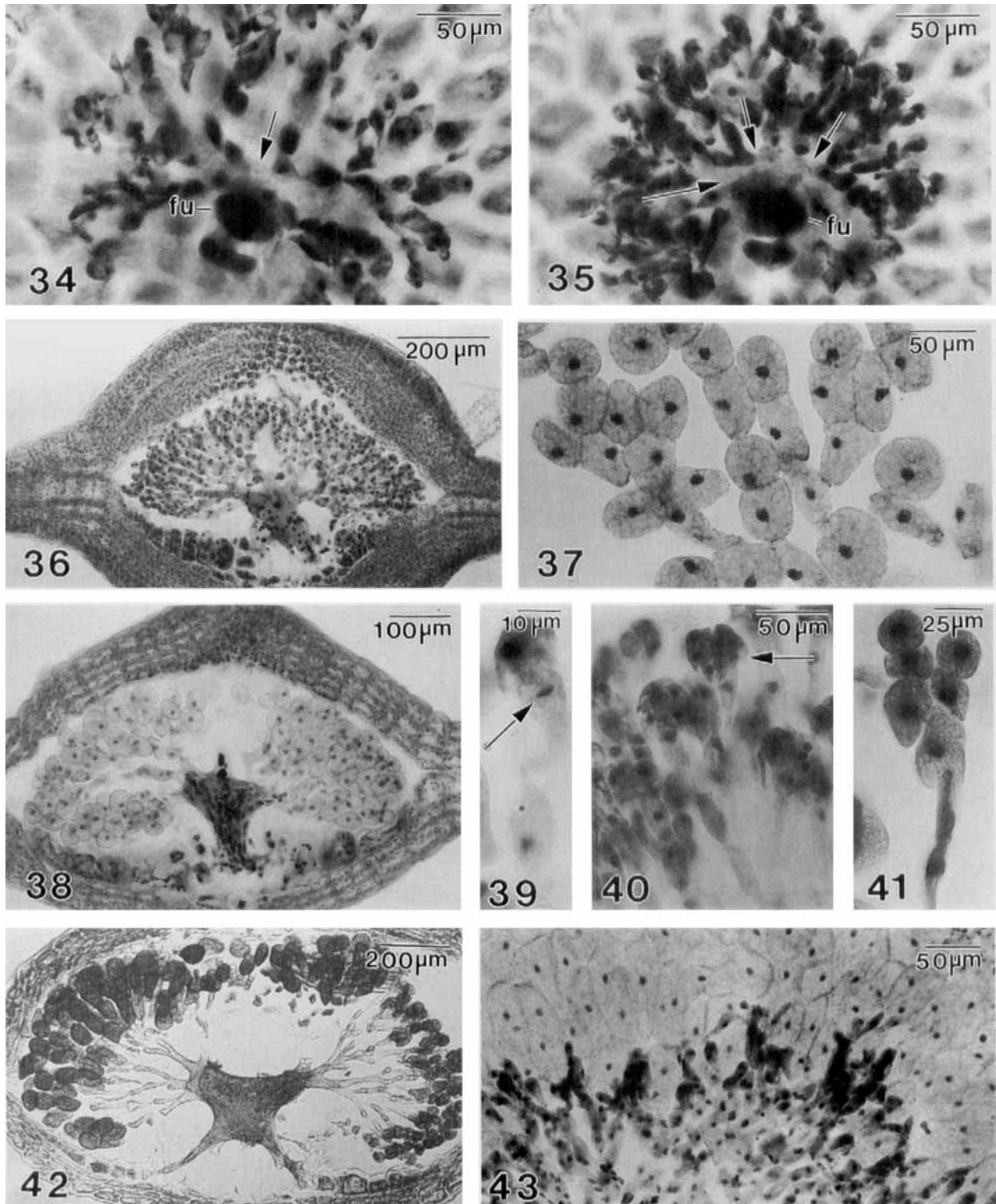
FIGS. 34–43.   Cystocarp development in *Myriogramme livida*. FIGS. 34, 35. Median optical section showing branching pattern of gonimoblasts around central fusion cell (fu) and incorporation of inner gonimoblast cells onto fusion cell (arrows). FIG. 36. Cross-section of cystocarp showing central fusion cell and monopodially branched immature primary gonimoblasts. FIG. 37. Primary carposporangia in branched chains. FIG. 38. Cross-section of cystocarp showing multinucleate central fusion cell bearing primary and immature secondary carposporangia. FIG. 39. Intercalary gonimoblast cell showing metaphase plate (arrow). FIG. 40. Fused gonimoblast filaments terminated by immature clusters of secondary carposporangia (arrow). FIG. 41. Branched chain of secondary carposporangia terminating fused gonimoblast filament. FIG. 42. Cross-section of old cystocarp with large central fusion cell that has incorporated most central cells in floor of cystocarp. (Note fused gonimoblast filaments bearing older [left side] and younger [right side] crops of secondary carposporangia.) FIG. 43. Chains of mature secondary carposporangia terminating fused gonimoblast filaments. Figures 34–41, 43, hematoxylin; Figure 42, aniline blue.
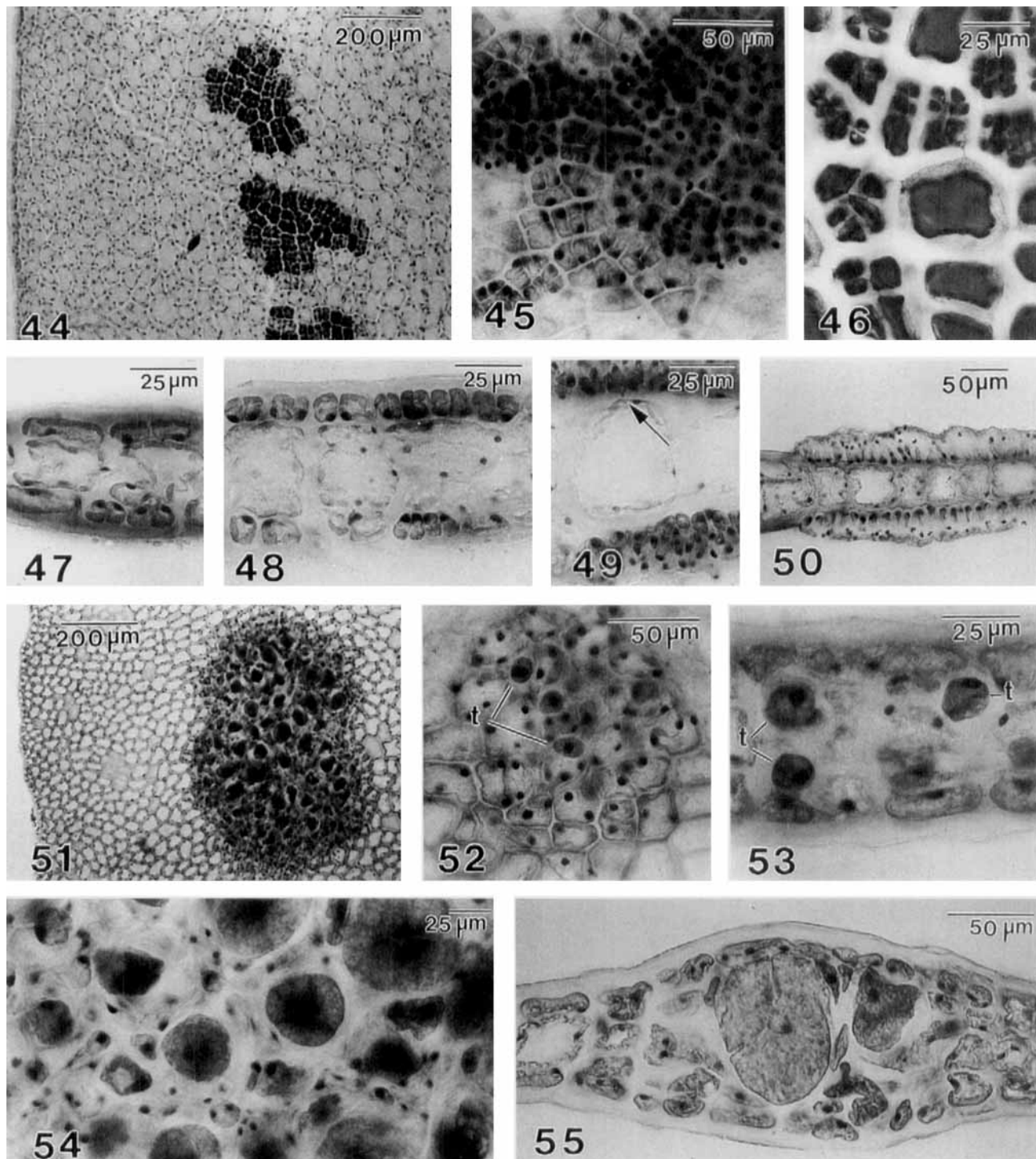
FIGS. 44–55.   Spermatangial and tetrasporangial development in *Myriogramme livida*. FIG. 44. Spermatangial sori near margin. FIG. 45. Surface view of young spermatangial sorus showing cortical cells, spermatangial parent cells and spermatangia. FIG. 46. Patterns of anticlinal division of cortical cells and spermatangia with primary pit connections as seen in surface view. FIG. 47. Cross-section of sorus showing young cortical cells. FIG. 48. Cortical cells undergoing anticlinal divisions. FIG. 49. Spermatangia and a few spermatia. (Note pit connection to central cell [arrow]). FIG. 50. Cross-section of mature sorus showing basal nuclei in spermatangia and nuclei in released spermatia. FIG. 51. Tetrasporangial sorus in monostromatic blade near margin. FIG. 52. Developing tetrasporangia (t) in median focal plane cut off from primary cells (= central cells). FIG. 53. Cross-section of sorus at three-layered stage showing tetrasporangia (t) connected to primary cells (= central cells). FIG. 54. Surface view showing dividing tetrasporangia surrounded by cortical filaments. FIG. 55. Cross-section of sorus with mature tetrasporangia. Figures 44–54, hematoxylin; Figure 55, aniline blue.

Primary cells of the monostromatic thallus divide periclinally to form a layer of cortical cells on both surfaces (Fig. 47). Alternatively, primary cells occasionally divide anticlinally into two or more cells before cutting off cortical cells on either side, with the result that both central cells and patches of cortical cells are variable in size (Figs. 45, 46, 48). Division of cortical cells is initially anticlinal with successive divisions usually taking place at right angles to generate a rectangular, filamentous cluster of surface cells united by primary pit connections (Fig. 46). As anticlinal divisions continue, every cell is converted into a spermatangium, with a nucleus located at its base. Spermatangia are cut off by concavo-convex walls and are initially ovoid to ellipsoid in shape (Figs. 45, 49). Released spermatia round up and accumulate beneath the outer cuticular layer (Fig. 50). Evidently, the spermatia are released upon dissolution of the outer layer. Spermatangial sori expand in area, and they sometimes link up to form irregular patches in upper parts of the thallus.

*Tetrasporangial development.* Like the spermatangia, tetrasporangia are produced in small circular to elliptical sori formed simultaneously on both sides of the blade by resumption of cell divisions in otherwise mature cells. Sori are formed anywhere except in the basal region and along the margin of the thallus (Fig. 51). New sori are often interpolated between preexisting soral patches, and sori sometimes merge but are never confluent over an extended area. Central cells first divide periclinally on both sides to produce a cortical layer (Fig. 52). The first tetrasporangia are cut off laterally to obliquely, in the plane of the blade from primary cells in the center at the three-layered stage (Figs. 52, 53). The cortical cells divide again to produce a five-layered structure, and additional tetrasporangia are cut off from the central cells. As the tetrasporangia enlarge, cells in the outer cortical layer divide anticlinally, forming a filamentous structure encircling each tetrasporangium (Fig. 54). Each central cell typically produces two (to four) tetrasporangia, which divide simultaneously into four tetrahedrally shaped tetraspores. Tetrasporangia are spherical to ellipsoidal in shape and measure 40–90 μm in length by 40–60 μm in width (Fig. 55).

## DISCUSSION

When Kylin (1924) established the Myriogramme group, he included four free-living and two parasitic genera: *Myriogramme, Platyclinia, Schizoseris, Neuroglossum,* and *Gonimocolax* and *Polycoryne.* The group was characterized as having bladelike thalli with branching or proliferations from the margin, a midrib or macroscopic veins present or absent; microscopic veins absent; transversely dividing apical cells absent; and gonimoblasts with spores in chains. Procarps were described as being of the *Phycodrys*-type with two groups of sterile cells, but with the number of cells in each sterile group reduced to one or two

(Kylin 1924:figs. 43, 47c). The carpogonium was said always to develop inwardly from the third cell of the carpogonial branch. No mention was made of "cover cells," which appeared to be absent. Our survey showed that this type of procarp occurs in *Myriogramme minuta* Kylin (= *Drachiella minuta* [Kylin] Maggs et Hommersand 1993) and in *Schizoseris* and *Neuroglossum* but not in the type species of *Myriogramme, M. livida,* or in most species assigned to *Myriogramme.* Instead, *Myriogramme livida* possesses procarps in which the central cell cuts off two pairs of pericentral cells opposite one another on each side of the thallus, with the first of each pair developing into a sterile vegetative cell, the cover cell, and the second forming the procarp. Each procarp contains two one-/to two-celled sterile groups, but the carpogonium is usually not inwardly curved to the extent seen in *Drachiella minuta. Schizoseris, Neuroglossum,* and *Drachiella* all have similar procarps and are distinguished from *Myriogramme* by a suite of characters that call for the establishment of a new tribe. This will be the subject of a separate paper.

The type of procarp that characterizes *Myriogramme livida* was first observed in *Nitophyllum bonnemaisonii* sensu Greville from Roscoff, France (Kylin 1934:fig. 1). Kylin showed that, in contrast to the type species of *Nitophyllum, N. punctatum* (Stackhouse) Greville, the cover cell occupies an anterior rather than a lateral position, procarps on each side of the thallus stand directly opposite one another rather than diagonally opposite, and the procarp contains both a lateral and a basal sterile group rather than just a lateral sterile group. Reinterpreting his figures of the procarps of *Nitophyllum mirabile* Kylin from Friday Harbor, Washington (Kylin 1925:fig. 41), Kylin (1934) concluded that the procarp of that species developed in the same manner as in *N. bonnemaisonii.* In 1934, Kylin suggested that *Nitophyllum bonnemaisonii* and *N. mirabile* should probably be placed in a new genus; however, he ultimately retained both species in *Nitophyllum* (Kylin 1956).

In 1981, Zinova investigated the systematic position of *Nitophyllum bonnemaisonii* and *Myriogramme yezoense* Yamada et Tokida, which Mikami (1972) had transferred to *Nitophyllum* based on the presence of cover cells and two sterile groups similar to those found in *Nitophyllum bonnemaisonii.* Zinova redefined *Nitophyllum* to include species in which the fertile central cell gives rise to a vegetative and a fertile pericentral cell at right angles to adjoining vegetative cells, the fertile pericentral cell (= supporting cell) forms a single sterile group, and carposporangia are solitary and terminal. At the same time, she erected two new genera, *Haraldiophyllum* A. Zinova, based on *Delesseria bonnemaisonii* sensu Greville, and *Hideophyllum* A. Zinova, based on *Myriogramme yezoense,* to contain species in which the fertile central cell produces two pericentral cells situated vertically with respect to the thallus axis with the top cell forming one to three cover cells and the bottom cell

becoming the supporting cell bearing two one-/to two-celled sterile groups and a four-celled carpogonial branch. *Haraldiophyllum* was characterized as having terminal carposporangia and *Hideophyllum* as having carposporangia in chains. In addition to *H. bonnemaisonii* (Greville) A. Zinova, it was proposed that *Haraldiophyllum* contained *H. mirabile* (Kylin) A. Zinova and *H. versicolor* (Harvey) A. Zinova.

Wynne (1983) reviewed and updated the classification of the Delesseriaceae. He accepted all the groups in Nitophylloideae recognized by Kylin (1924, 1956), except the Yendonia group. Most groups and genera were defined in accordance with characters recognized by Kylin. Wynne placed *Hideophyllum*, with carposporangia in chains, in the Myriogramme group and *Haraldiophyllum*, with terminal carposporangia, in the Nitophyllum group. *Haraldiophyllum versicolor* (Harvey) A. Zinova became *H. heterocarpum* (Chauvin *ex* Duby) Wynne, and *Nitophyllum nottii* R. Norris et Wynne (1969) was transferred to *Haraldiophyllum*. Wynne (1996) kept the same taxonomic arrangement with *Hideophyllum* in the Myriogramme group and *Haraldiophyllum* in the Nitophyllum group.

Recently, Maggs and Hommersand (1993) transferred *Haraldiophyllum heterocarpum* and *Myriogramme minutum* to *Drachiella* as *Drachiella heterocarpa* (Chauvin *ex* Duby) Maggs et Hommersand and *Drachiella minuta* (Kylin) Maggs et Hommersand and placed them in the Schizoseris group, a new group that they did not characterize. They retained *Haraldiophyllum bonnemaisonii* (Kylin) A. Zinova, established on a new basionym, *Myriogramme bonnemaisonii* Kylin, and placed *Haraldiophyllum* in the Myriogramme group.

All of the taxa listed in this paper under "specimens of other taxa examined" possess procarps of the *Myriogramme livida* type and on that basis alone are referable to the Myriogramme group. As important as procarp development has been historically for classification at the generic and suprageneric levels, it is not the only feature that unites a cluster of taxa with *Myriogramme livida*. Other vegetative and reproductive characters are equally important. Taxa related to *Myriogramme* lack transversely dividing apical cells, except occasionally in juvenile thalli. An apical cell, if present, divides obliquely along two cutting faces or, more often, growth is maintained by a marginal meristem, and intercalary cell divisions are abundant along the margin and in the interior of the thallus. The same is true of taxa that cluster with *Cryptopleura*, *Nitophyllum*, and *Schizoseris* or *Drachiella*. The differences lie in the behavior of nuclei and plastids during cell division and the appearance of the mature vegetative cells. In *Myriogramme*, mature vegetative cells are large, polygonal, highly vacuolate, and transparent when viewed from the surface, with the nuclei situated along the transverse walls and the chloroplasts superficial and breaking up into small subunits (Figs. 7–15). Micro-

scopic veins are absent. In *Cryptopleura*, the nuclei are scattered across the surface of the cell beneath a layer of discoid chloroplasts, and microscopic veins are usually present; in *Nitophyllum* the nuclei are initially parietal along the lateral walls but are later distributed uniformly across the cell surface just below the discoid chloroplasts, whereas in *Drachiella* the nuclei are situated beneath a single parietal platelike chloroplast or several convoluted, ribbonlike chloroplasts formed through the fusion of many discoid plastids (Maggs and Hommersand 1993). The cell type and nuclear and chloroplast behavior characteristic of *Myriogramme livida* were seen in all the species listed in this paper under "specimens of other taxa examined."

Blades form midribs and macroscopic veins or become polystromatic in two ways in the Nitophylloideae: either by periclinal division with the cells lying in horizontal tiers and vertical rows or by both periclinal and anticlinal divisions producing branched corticating filaments. Members of the Myriogramme group become polystromatic primarily by periclinal divisions. Periclinal divisions predominate in the Cryptopleura group and the Nitophyllum group intermixed with occasional anticlinal divisions (Kylin 1924, Wagner 1954), whereas periclinal and anticlinal divisions are both frequent in *Schizoseris* and *Drachiella* and give rise to regularly branched cortical filaments (Ricker 1987, Maggs and Hommersand 1993).

Among the Nitophylloideae, vegetative pericentral cells (cover cells) are present only in taxa allied with *Nitophyllum* or with those allied with *Myriogramme*. Both groups have large prismatic vegetative cells with conspicuous central vacuoles. While the central cells are not fully mature at the time they produce the procarps, they have usually ceased dividing and are larger than in other members of the Nitophylloideae. Cytoplasm is first concentrated to one side in *Nitophyllum* and to the anterior end in *Myriogramme*, where it is cut off with the cover cells, which quickly become vacuolate. Most of the cytoplasm remaining in the central cell is cut off with the fertile pericentral cell (= supporting cell). This behavior appears to be related to the larger cell size and state of vacuolation of a potential fertile central cell in *Nitophyllum* and *Myriogramme* compared to that in other Nitophylloideae. If so, the striking differences in the arrangement of the cover cells and sterile groups in the two procarp types testifies to the independent origin of cover cells in each case and the separate evolutionary histories of their procarp types.

Connecting cells have rarely been seen in members of the Delesseriaceae. Papenfuss (1961) reported that the carpogonium cuts off a connecting cell on the side facing the auxiliary cell in *Caloglossa* that fuses with it and presumably delivers a diploid nucleus; however, he notes "that this feature has not heretofore been observed in the many genera of De-

lesseriaceae that have been studied." He further comments that the presence of a connecting cell in *Caloglossa*, similar to those found in the Ceramiaceae, lends support to the view that *Caloglossa* is one of the most primitive members of the Delesseriaceae. The reason, in our opinion, why connecting cells may have been missed is because they are small hyaline structures that consist of a nucleus and a bounding membrane without apparent associated cytoplasm. Thus, while they are easily seen with hematoxylin staining, they are not readily differentiated with aniline blue. We have conducted a broad survey of most of the groups placed in the Delesseriaceae and find that in each the carpogonium cuts off two connecting cells, one anterior and the other lateral, with the lateral connecting cell usually being the one that fuses with the auxiliary cell, as illustrated here for *Myriogramme livida* (Figs. 24, 29).

After diploidization, the auxiliary cell divides transversely in *Myriogramme livida*, cutting off a small gonimoblast initial containing a diploid nucleus and a remnant auxiliary cell containing a diploid and a haploid nucleus. The remnant cell corresponds to the foot cell seen in many Ceramiaceae; however, its size and the fact that it is filled with cytoplasm rather than being vacuolate mitigates against equating it with the ceramiacean foot cell. Initials are cut off from the anterior and lateral surfaces of the primary gonimoblast cell that produce the gonimoblasts (Figs. 26, 27). Of these, the anterior filament is more strongly developed and has the appearance of a basal row of cells when seen in transverse section. This arrangement, first reported by Kylin (1923) for *Phycodrys*, has been seen in many Delesseriaceae. None of the features of early cystocarp development—the formation of the ostiole above sterile group 1, the schizogenous development of the cystocarp cavity, the horizontal spread and vertical growth of the gonimoblast filaments or the fusions of the supporting cell, the remnant auxiliary cell, and inner gonimoblast cells to form a fusion cell—are unique to *Myriogramme*. Fusion cells are small in *Nitophyllum*, larger in *Cryptopleura*, and larger still in *Myriogramme* and *Schizoseris*, where the fusions extend to incorporate the inner gonimoblast cells (Kylin 1924), but the differences are differences of degree and, while diagnostic at the group or tribal level, are less easily defined than some other characters.

The interpretation of late stages in cystocarp development is fraught with difficulties, not the least of which is that mature young cystocarps may have a different appearance from mature older cystocarps. Such is the case in *Myriogramme livida*, in which the carposporangia are borne in openbranched chains in young cystocaps, only to be replaced by carposporangia borne in tight clusters at the ends of candalabra-like fusion cells in older cystocarps that have produced a second generation of carposporangia. We have found that the carpospo-

rangia are truly terminal in some species belonging to the Myriogramme group, whereas in others they are formed in succession and only appear to be terminal. In still others, they are first produced terminally and released in succession and only later remain attached, forming chains. Reports in the literature concerning the arrangement of the carposporangia may not be reliable unless all developmental stages have been taken into account.

### TAXONOMIC CONCLUSIONS

The morphological evidence presented here is for a single species, *Myriogramme livida*, the type species of *Myriogramme*. We have shown that the concept of the Myriogramme group of Kylin 1924, based as it was on nontype material, has led to an incorrect characterization of that group. We now propose a new tribe to replace the Myriogramme group of Kylin with a revised diagnosis and new circumscription that includes part of the taxa recognized by Kylin and excludes the rest. The diagnosis given below is based on the type species and on species listed in this paper under "specimens of other taxa examined."

### Myriogrammeae Hommersand et Fredericq trib. nov.

*Thallus foliosus monostromaticus aut tristromaticus margine, polystromaticus basaliter unico nervo basali aut nervi subdichotomi inferne. Veni microscopici absentes. Cellulae polygonales aspectu superficiali dispositae ordines horizontales et series verticales partibus polystromaticis. Incrementum diffuse meristematibus marginalibus intercalaribusque; nuclei lateriparietes in cellulas maturas, chloroplasti parietales, initio simplices, postea dissecti in parvas monades. Spermatangia in soros circulares ad ellipticos formatos fortuito in partibus supernis per renovationem divisionem cellularum maturarum. Procarpia opposita utrinque thalli, cellula centrali initio abscissa cellulam anteriorem pericentralem vegetativam (cellulam obtectam) post cellulam pericentralem fertilem posticam (cellulam sustinentem) constantia ex laterali turma sterili 1–2 cellularum, filo carpogonali quadricellulari et turma sterili basali unicellulari. Carpogonium abscissum 2 cellulas conjunctivas, 1 conjunctam cellula auxiliaris. Cellula auxiliaris dividens transversale in anticum cellulam gonimoblasti continentem nucleum diploideum, et in posticam cellulam residualem (cellulam pedalem) continentem diploideum nucleum 1–2 haploideosque nucleos. Filamenta gonimoblasti genita in arcu cellula primarii gonimoblasti cingenti cellulam sustinentam postea extrinseca radiantia praebentia carposporangia vel terminalia vel catenata. Cellula fusionalis formatur ad modum progressionis incorporans cellulam sustinentem, cellulam centralem, cellulam auxiliaris, primam cellulam gonimoblasti, internas cellulas gonimoblasti et nonnulas cellulas in pavimentum cystocarpii. Cryptia cystocarpii schizogenea formatur obtecta per pericarpium ostiolo singulari tegenti sterilem sturmam-1. Tetrasporangia in soros parvos circulares vel ellipticos usque ad quinquestromaticos fortuito in partibus supernis lami-*

*nae per renovationem divisionem cellularum maturarum. Tetrasporangia primaria genita 2(–4) per cellulam e cellulis centralibus. Tetrasporangia secunda genita uterque cellulis centralibus cellulis corticalibus interioribus, tetraedrica divisa.*

*Genus typicum:* Myriogramme *Kylin 1924.*

Plant body foliose monostromatic or tristromatic at margin, polystromatic toward base with a single basal nerve, or the nerves subdichotomously branched below. Microscopic veins absent. Cells polygonal in surface view, arranged in horizontal tiers and vertical rows in polystromatic parts. Growth diffuse by marginal and intercalary meristems; nuclei bordering the side walls in mature cells, chloroplasts parietal, at first simple, later dissected into small platelets. Spermatangia in circular to elliptical sori, formed randomly in upper parts of blade by renewed division of mature cells. Procarps directly opposite on both sides of thallus, the central cell first cutting off an anterior vegetative pericentral cell (cover cell) from anterior end followed by a posterior fertile pericentral cell (supporting cell) that bears a one-/to two-celled lateral sterile group, a four-celled carpogonial branch, and a one-celled basal sterile group. Carpogonium cutting off two connecting cells, one of which fuses with auxiliary cell. Auxiliary cell dividing transversely into an anterior gonimoblast cell and a posterior residual auxiliary cell containing a diploid nucleus and one to two haploid nuclei. Gonimoblast filaments developing from primary gonimoblast cell in an arc around the supporting cell, later radiating outwardly and bearing carposporangia either terminally or in chains. Fusion cell formed progressively, incorporating the supporting cell, central cell, auxiliary cell, primary gonimoblast cell, inner gonimoblast cells, and some cells in floor of cystocarp. Cystocarp cavity formed schizogenously with a single ostiole overlying sterile group 1. Tetrasporangia in small circular or elliptical sori up to five layers thick, formed randomly in upper parts of blade by renewed division of mature cells. Primary tetrasporangia arising two to four per cell from central cells. Secondary tetrasporangia formed from both central cells and inner cortical cells, tetrahedrally divided.

Type genus: *Myriogramme* Kylin 1924.

Besides *Myriogramme*, the tribe Myriogrammeae contains *Gonimocolax*, *Haraldiophyllum*, and *Hideophyllum*. *Myriogramme* possesses cystocarps in which the gonimoblasts fuse progressively with the central cells in the floor of the cystocarp through the supporting cell; the gonimoblasts initially develop monopodially and produce carposporangia terminally, sequentially, or in chains. *Gonimocolax* is very similar to *Myriogramme* and may be an adelphoparasite of *M. livida*. *Haraldiophyllum* was recognized by Maggs and Hommersand (1993) on the basis that the carposporangia are produced terminally, with the gonimoblasts branching sympodially from subterminal cells below the maturing carposporangia. *Hideophyl-*

*lum* is distinct in that an obliquely dividing apical cell has been shown to produce a recognizable central axis (Mikami 1972). Species belonging to the tribe Myriogrammeae that occur along the Pacific Coast of North and South America as far south as Concepción, Chile, have an unusual fusion cell, first described by Kylin (1925) for *Nitophyllum mirabile* [= *Haraldiophyllum mirabile*], in which inner gonimoblast cells fuse secondarily by lateral fusion onto the central cells in the floor of the cystocarp. *Schizoseris* and *Neuroglossum* are excluded from the Myriogrammeae, and *Polycoryne*, which is parasitic on both *Schizoseris* and *Myriogramme*, appears to be more closely related to *Schizoseris*. *Platyclinia* includes species that belong in the Myriogrammeae, notably the ones in South America, but the lectotype species, *P. stipitata* J. Agardh from Australia (Wynne 1983), requires reinvestigation.

Abbott, I. A. 1969. Some new species, new combinations, and new records of red algae from the Pacific coast. *Madroño* 20: 42–53.

Agardh, J. G. 1876. *Species Genera et Ordines Algarum*, Vol. 3(1). *Epicrisis Systematis Floridearum.* T. O. Weigel, Leipzig, vii + 724 pp.

———— 1898. *Species Genera et Ordines Algarum*, Vol. 3(3). *Die Dispositione Delesseriarum curae posterioires.* Lund, vi + 239 pp.

Cotton, A. D. 1915. Cryptogams from the Falkland Islands collected by Mrs. Valentin. *Linn. Soc. J. Bot.* 43:137–231, plates 4–10.

Greville, R. K. 1830. *Algae britannicae . . .* Edinburgh. lxxxviii + 218 pp., 19 plates.

Hollenberg, G. J. & Abbott, I. A. 1965. New species and new combinations of marine algae from the region of Monterey, California. *Can. J. Bot.* 43:1177–88.

Holmgren, P. K., Holmgren, N. H. & Barnett, L. C. 1990. *Index Herbariorum*, Pt. I. *The Herbaria of the World*, 8th ed. International Association for Plant Taxonomy, New York, and Botanical Garden, Bronx, 693 pp.

Hommersand, M. H., Fredericq, S. & Cabioch, J. 1992. Developmental morphology of *Gigartina pistillata* (Gigatinaceae, Rhodophyta). *Phycologia* 31:300–25.

Hooker, J. D. 1846–1847. *The Botany of the Antarctic Voyage of H. M. Discovery Ships 'Erebus' and 'Terror' in the years 1839–1843 . . .*, Vol. 1. *Flora antarctica . . .*, Pt. II. *Botany of Fuegia, the Falklands, Kerguelen's Land, etc (1845–1847).* Algae. London, pp. 454–502, plates 165–193.

Hooker, J. D. & Harvey, W. H. 1845. Algae antarcticae . . . . *London J. Bot.* 4:249–76.

Kützing, F. T. 1866. *Tabulae phycologicae oder Abbildungen der Tange*, Bd. 16. Nordhausen, pp. 1–35, plates 1–100.

Kylin, H. 1923. Studien über die Entwicklungsgeschichte der Florideen. *K. Sv. Vet.-Akad. Handl.* 63(11):1–139.

———— 1924. Studien über die Delesseriaceen. *Lunds Univ. Årsskr., N.F., Avd.* 2 20(6):1–111.

———— 1925. The marine red algae in the vicinity of the Biological Station at Friday Harbor, Wash. *Lunds Univ. Årsskr., N.F., Avd.* 2 21(9):1–87.

———— 1929. Die Delesseriaceen Neu-seelands. *Lunds Univ. Årsskr., N.F., Avd.* 2 25(2):1–15, 12 plates.

—— 1934. Bemerkungen über einige Nitophyllaceen. *K. Fysiogr. Sällsk. Lund Förhandl.* 4(1):1–8.

—— 1956. *Die Gattungen der Rhodophyceen.* C. W. K. Gleerups, Lund, xv + 673 pp.

Levring, T. 1960. Contributions to the marine algal flora of Chile. *Lunds Univ. Årsskr., N.F. Avd. 2* 56(10):1–83 + [2].

Maggs, C. A. & Hommersand, M. H. 1993. *Seaweeds of the British Isles,* Vol. 1. *Rhodophyta,* Pt. 3A *Ceramiales.* The Natural History Museum, HMSO, London; xv + 444 pp., 1 map.

Mendoza, M. L. 1969. Las Delesseriaceae (Rhodophyta) de Puerto Deseado, Provincia de Santa Cruz, Argentina. II. Estudio sistematico del genero *Myriogramme* Kylin. *Physis (Buenos Aires), Sec. A* 29:245–60.

Mikami, H. 1972. On the systematic position of *Myriogramme yezoensis* Yamada et Tokida. *Bull. Jap. Soc. Phycol.* 20:14–9.

Millar, A. J. K. 1990. Marine red algae of the Coffs Harbour region, northern New South Wales. *Aust. Syst. Bot.* 3:293–593.

—— 1994. *Haraldiophyllum infossum* sp. nov. (Delesseriaceae, Rhodophyta), a diminutive turf-forming alga from the southwest Pacific. *Bot. Mar.* 37:125–32.

Millar, A. J. & Huisman, J. M. 1996. *Haraldiophyllum erosum* comb. nov. (Delesseriaceae, Rhodophyta) from southern and Western Australia. *Aust. Syst. Bot.* 9:61–9.

Norris, R. E. & Wynne, M. J. 1969 ("1968"). Notes on marine algae of Washington and southern British Columbia, III. *Syesis* 1:134–46.

Papenfuss, G. F. 1939. The development of the reproductive organs in *Acrosorium acrospermum. Bot. Not.* (1939):11–20.

—— 1961. The structure and reproduction of *Caloglossa leprieurii. Phycologia* 1:8–31.

—— 1964. Catalogue and bibliography of Antarctic and Sub-Antarctic benthic marine algae. *Antarc. Res., Ser. 1, Am. Geophysical Union,* 76 pp.

Ricker, R. W. 1987. *Taxonomy and Biogeography of Macquarie Island Seaweeds.* British Museum (Natural History), London, viii + 344 pp.

Wagner, F. S. 1954. Contributions to the morphology of the Delesseriaceae. *Univ. Calif. Publ. Bot.* 27:279–346.

Wittmann, W. 1965. Aceto-iron–haematoxylin–chloral hydrate for chromosome staining. *Stain Technol.* 40:161–4.

Wynne, M. J. 1983. The current status of genera in the Delesseriaceae (Rhodophyta). *Bot. Mar.* 26:437–50.

—— 1986. Report on a collection of benthic marine algae from the Namibian coast (southwestern Africa). *Nova Hedwigia* 43:311–55.

—— 1996. A revised key to genera of the red algal family Delesseriaceae. *Nova Hedwigia, Beiheft* 112:171–90.

Zinova, A. D. 1981. De positione systematica nitophylli (myriogrammes) yezoensis (Yamada et Tokida) Mikami (Delesseriaceae). *Novit. Syst. Plant. non Vascul.* 18:10–5.