

**Transfer of the Hawaiian red alga *Cladhymenia*
pacifica to the genus *Acanthophora*
(Rhodomelaceae, Ceramiales)**

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KRAFT, G. T. 1979. Transfer of the Hawaiian red alga *Cladhymenia pacifica* SETCHELL to the genus *Acanthophora* (Rhodomelaceae, Ceramiales). Jap. J. Phycol. 27: 123-135.

The tropical red alga *Cladhymenia pacifica* SETCHELL (Chondrieae, Rhodomelaceae), from Hawaii and Tahiti, is geographically removed from the temperate New Zealand spp. on which *Cladhymenia* is based. This study shows that although *C. pacifica* resembles the type (*C. oblongifolia* H. & H.) in its flattened fronds and lack of correspondence in length between central axial cells and associated pericentrals, it differs from *C. oblongifolia* in its possession of acute spines and its radially-branched main axes, which are features within the Tribe Chondrieae of the tropical genus *Acanthophora*. The morphology of Hawaiian *C. pacifica* is compared with *Acanthophora spicifera*, *A. dendroides* and *Cladhymenia oblongifolia*, and the new combination *Acanthophora pacifica* (SETCHELL) KRAFT is made after consideration of generic criteria within the *Chondria*-group.

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Cladhymenia pacifica SETCHELL (1926, p. 102) is a shallow subtidal species locally abundant at scattered localities in the Hawaiian Islands. Apart from Hawaii the alga has been recorded only from its type locality, Tahiti, and is thus rather remote geographically from the bulk of *Cladhymenia* species, which are endemic to the cool temperate waters of New Zealand. *Cladhymenia oblongifolia*, the lectotype of the genus (KYLIN 1956, p. 550) and *C. lyallii* were originally described by HOOKER fil. & HARVEY (1845, p. 539) from the South and North Islands respectively, while a third New Zealand species was recently transferred to the genus as *C. coronata* (LINDAUER & SETCHELL) SAENGER in SAENGER, DUCKER & ROWAN (1971, p. 105). A fifth species, based on sterile deep-dredged specimens and referred to *Cladhymenia* with doubt, is *C. lanceifolia* TAYLOR (1942, p. 137, pls 3, 4) from the Caribbean.

SETCHELL described *Cladhymenia pacifica* from tetrasporangial collections and tenta-

tively allied it to *Cladhymenia* on the basis of the flattened fronds and distinct rhizomes. Major defining features of the tribe Chondrieae, to which *Cladhymenia* belongs, are the distinctive morphology of the spermatangial branchlets and the prominent central axial filaments within the generally pseudoparenchymatous cross sections of the fronds, both of which were lacking in SETCHELL's material. He thus left the possibility open that the species might ultimately prove to belong to a genus of the Laurencieae such as *Rodriguezella*.

The Chondrieae contains 7-8 genera of fairly uniform anatomy, although most are little-known and geographically limited (such as *Cladurus*, *Coeloclonium*, *Dolichocelis* and *Husseyella* from southern Australia, and *Cladhymenia* itself from New Zealand). The two main genera of the group, *Chondria* and *Acanthophora*, are widespread, however. *Chondria* is common from tropical to high latitudes and is the most broadly defined genus of the tribe. It contains both terete

and flattened members and includes species with growing tips that are either in apical depressions or prominently exserted (DETONI 1903; FELDMANN 1949). *Chondria* differs from the closely-related *Cladhymenia* in the far greater degree of thallus flattening of the latter, which also (FALKENBERG 1901, p. 219) produces hyphal filaments of varying diameters among the pseudoparenchymatous cells of the medulla, unlike *Chondria*. *Acanthophora* is pantropical, extending into warm, temperate seas in the Southern Hemisphere, and is distinguished by the presence of short acute spines that are produced in spiral order along the lateral branchlets. Unlike *Chondria*, all *Acanthophora* species described so far are terete.

Recent collections of Hawaiian *Cladhymenia pacifica*, as well as the type species of the genus (*C. oblongifolia*) from New Zealand and two species of *Acanthophora* (the type, *A. spicifera* (VAHL) BOERGESEN from Hawaii and the Philippines and *A. dendroides* HARVEY from Australia) have confirmed the position of *C. pacifica* in the Chondrieae but have led me to question its association with the genus *Cladhymenia*. On the basis of my observations this species seems most strongly allied to *Acanthophora*, to which it is herein transferred as the first flattened representative of that genus, *Acanthophora pacifica* (SETCHELL) comb. nov.

Materials studied: The following collections have been examined:

A. *Cladhymenia pacifica* i) Hanauma Bay, Oahu, Hawaii. 1.5 m deep on coral rubble at innermost reef margin (Kraft & Mitchell Hoyle, 28. i. 1978. MELU, K 6486). ii) Kukii Point, Nawiliwili Harbor, Kauai, Hawaii. 1.0–1.5 m deep on rock mounds (Kraft, 11. ii. 1977. MELU, K 6499).

B. *Acanthophora spicifera*: i) Nangalao I., northern Sulu Sea, Philippines. 1.5 m deep on coral debris (Kraft, 22. iv. 1968. MELU, K 556). ii) Kaneohe Bay, Oahu, Hawaii (Doty, vii. 1977. MELU, K 6587). Kahala, Oahu, Hawaii (Kraft, 19. ii. 1978. MELU, K 6588).

C. *Acanthophora dendroides*: i) Port Denison, W. Aust. 0.5–1.5 m deep on jetty pilings (Kraft, 14. xii. 1971. MELU, K 3926). ii) Gladstone, Queensland. Drift (Kraft, 2. viii. 1978. MELU, K 6589).

D. *Cladhymenia oblongifolia*: i) Evening cove, Ringa Ringa, Stewart I., N.Z. 2–3 m deep on rock (Kraft, 9. xi. 1972. MELU, K 4377). ii) Bethells Beach, North Auckland, N.Z. Mid-eulittoral on rock (Kraft & Karl Johnson, 22. v. 1974. MELU, K 4766). iii) Oaro, N.Z. Drift (Tatjana Parsons, 20. iii. 1973. CHR 230906). iv) Old Wharf, Kaikoura, N.Z. 3 m deep (V. Hoggard & G. Fenwick, 13. xi. 1973. CHR 319471).

Morphology

A. *Cladhymenia pacifica*: The plants reach lengths of 3–10 cm and form gregarious clumps (Fig. 8) on solid substrata such as coral blocks and basaltic rocks. The primary axes are anchored by fleshy, fluted holdfasts 3–4 mm in diam. above which both erect and semi-prostrate axes issue. The lower axes of erect fronds are initially subterete, 1–3 mm in diam. and 4–6 mm long before expanding into the distal flattened blades. Prostrate axes form holdfasts where they contact the substratum and can give rise to either erect or further rhizomatous axes. Sections through the rhizomes and lower erect fronds show a prominent central filament surrounded by roughly isodiametric cells (80–100 μ m diam.) without interspersed rhizoids or hyphae. The outer cortex is usually a single layer of radially elongated cells about twice as deep as wide (ca 50 \times 25 μ m), although occasionally all or part (Fig. 19) of the cortex may be covered by a second layer, giving a growth-ring like appearance.

The flattened blades range from 1–4 mm in width and 200–600 μ m in thickness. Except near the apices most branching is from the margins and consists of either short spinous enations, longer determinate branchlets, or more or less indeterminate laterals. Branching may be somewhat pinnate (Fig. 1) or subdichotomous (Fig. 2). Substance of

the fronds and rhizomes is cartilaginous, and colors range from reddish-yellow to a deep reddish-brown.

Growing apices of both main axes and lateral branchlets (Figs. 3, 5) are generally pyramidal and beset with a few short trichoblasts, although some apices are nearly flush with the surrounding branch tissue and lack trichoblasts altogether. The unbranched or sparingly dichotomous trichoblasts of female gametophytes and tetrasporophytes are confined to the apices and are seldom more than 5-6 cells long. Trichoblasts of spermatangial plants differ in being a few cells longer, bushier, and persistent on the faces of the axes for some distance from the tips as well as at the apices themselves.

Sections cut near the apices show 5 distinct pericentral cells surrounding the central axial filament, but these may all be obscured lower in the blades by growth of the peripheral inner cortical cells into a densely compact pseudoparenchyma (Fig. 20). The outer cortex consists of a single layer of pigmented cells (Fig. 6) 1.5-6 times longer than broad which are longitudinally aligned and laterally pit-connected. Two features distinguishing the isodiametric hyaline cells of the interior of the thallus are occasionally numerous lenticular thickenings (Fig. 6) and the secondary pit-connections which in lower parts of the blade can become very wide (7.5-10 μm in diam.) and blocked by a circular aniline-blue staining plate 10-12 μm in diam. (Fig. 21). Adjacent cells of the central axial filament form prominent bulges at their junctions and do not correspond in length with their associated pericentral cells beyond the first few articulations of the axis (Fig. 22).

Unequal growth of lateral pericentral cells and their derivatives results in the almost immediate flattening of the major branch orders. Nevertheless the characteristic spirally produced spines occur on the faces of the blades (Fig. 5) as well as the margins for some distance from the apices, particularly on gametophytic plants. The spines are initiated from the abaxial sides of the

basal segments of trichoblasts (Fig. 23) but do not themselves bear trichoblasts.

Determinate branchlets that become tetrasporangial stichidia (Fig. 3) remain terete but otherwise resemble the main axes in giving rise to spirally arranged spinous laterals. Tetrasporangial branchlets are formed either singly or in dendroid clusters along the margins of the fronds (Fig. 2). Several tetrasporangia form in a whorl at each tier of the central axial filament, the sporangia reaching 100 μm in diam.

Spermatangial thalli (Fig. 1) bear spermatangial platelets typical of the Chondrieae on modified trichoblasts mostly associated with the faces of the upper frond and lower portions of the upper spines (Fig. 4). The platelets are attached to the frond by a 1-2 celled uniseriate stalk and are surrounded by a 1-2 layered sterile margin.

Cystocarpic plants produce spinous laterals in a spiral arrangement, with most procarys and subsequent cystocarp development taking place on the marginal spines (Fig. 5). A single procary forms on the adaxial side of each fertile spine and is surrounded by a pericarp prior to fertilization. Conspicuous features of the carpogonial branch are its more-or-less horizontal alignment along the spine axis and the prominently staining basal and suprabaasal cells (Fig. 24). Although the complete procary has not been seen in this material, it appears to be strictly comparable to that of *Acanthophora spicifera* (Fig. 25, and see below).

B. The genus *Acanthophora*: *Acanthophora* contains two groups of species, both represented in the Indian and tropical Pacific Oceans. In the first group, comprised of the imperfectly delimited taxa *A. delilei* [= *A. najadiformis* (DELILE) PAPENFUSS 1968, p. 96], *A. dendroides* (Fig. 7), *A. muscoides* and *A. ramulosa*, acute spines are present on both the lateral branchlets and the main axes of the thallus. The taxonomy of several species of this section has been discussed recently by ISAAC & CHAMBERLAIN (1958) and STEENTOFT (1967). The second group contains members in

which spines are spirally ordered on determinate lateral branchlets but absent from the main axes. Although a number of species have been attributed to this section, recent taxonomic treatments (reviewed by DOTY, 1961) have tended to regard them as expressions of the one widely distributed species *A. spicifera*.

As found in the Philippines and Hawaii, tetrasporophytes seem to be the most commonly encountered reproductive form of *A. spicifera* (Figs. 8, 9). The stichidia (Fig. 9) are short lateral shoots with spirally arranged spines lacking trichoblasts and whorls of sporangia in tiers at each central filament node. Apices of both the main axes and tetrasporangial branchlets (Fig. 10) are similar in *A. spicifera*, and consist of a pyramidal apex usually surrounded by a cluster of incurving, forked trichoblasts. In *A. dendroides* the apices of determinate branches can be either exserted or recessed in shallow pits, in which latter case they resemble closely any number of typical *Chondria* species.

Branch cross-sections of *Acanthophora* display 5 pericentral cells and a central axial filament that are usually distinctive even in mature axes. In the lower parts of Hawaiian *A. spicifera* and Queensland *A. dendroides* the cross-section is not uniformly "cellular" (as is usually indicated for the genus), but consists of large isodiametric cells interspersed with varying numbers of smaller or filamentous cells, particularly around the central axis. The outer cortex of *A. spicifera* consists of longitudinally aligned cells 4-5 times longer than wide.

Large plants of *A. spicifera* consist of conspicuously thicker lower axes that change rather abruptly to much thinner axes above, perhaps implying an association of persistent basal parts with seasonally shed branches. Holdfasts are usually thick and fluted or digitate, capable of emitting rhizoidal extensions near the base to form additional holdfasts where these contact the substratum, resulting in turfs or clumps of interconnected plants.

Male thalli have not been examined in

this study, but are shown by ASKENASY (1888) and BOERGESEN (1918) to be typical of the *Chondrieae*. Cystocarpic plants of *A. spicifera* are apparently not common in Hawaii. Procarys are characterized by a 4-celled carpogonial branch oriented parallel to the adaxial surface of the bearing spine, with the trichogyne emerging from the base of the pericarp (Figs. 11, 25). The basal cell of the carpogonial branch (Fig. 12) is particularly prominent in mature procarys. Cystocarps develop on the adaxial surface of the spine and are surrounded by a flask-shaped pericarp (Fig. 13).

C. Cladhymenia oblongifolia: This species is widespread in New Zealand from mid-intertidal to sublittoral habitats. Thalli arise in clusters (Fig. 14) from an aggregate holdfast of several discoid and rhizoidal basal parts and reach 10-30 cm lengths and widths of 1-4 cm. Apices of main axes (Fig. 15) and tetrasporangial branchlets (Fig. 16) are either very slightly protruding or recessed in shallow depressions, where they either lack trichoblasts entirely or bear them as a few short, unbranched filaments (Figs. 15, 16). All branch orders are strictly marginal, with few trichoblast scars even visible on the surfaces of the fronds.

Cross-sections of the lower blades usually display the central axial filament, but the 5 pericentral cells are only seen clearly in sections from the tip. The medulla consists of numbers of large isodiametric cells with smaller, sometimes distinctly filamentous cells interspersed between. In longitudinal sections of young axes, cells of the central axial filament are conspicuous (up to 450 μm long within 1 cm of the branch tip) and have flared, trumpet-like ends. Surrounding the central axis are some elongate cells 100-250 μm long by 25 μm wide which apparently derive from both pericentral and outer medullary cells along the axis, and by the growth of rhizoidal cells as adventitious filaments from some medullary cells. As reported by FALKENBERG (1901, p. 219), it can be difficult to tell which of the two sources any given filament of elongate cells is derived from. A major difference between

Cladhymenia and *Acanthophora* species concerns the relation between the lengths of pericentral cells and the central axial cell from which they originate. In *Acanthophora spicifera* and *A. dendroides*, both types of cell are the same length and together form the regularly tiered layers typical of most Rhodomelaceae. In *Cladhymenia oblongifolia*, there is no conformity of length between pericentrals and central axial cells at any point behind the immediate apex.

Of particular prominence in *Cladhymenia* are the lenticular thickenings (Fig. 26) which can fill up to 3/4 the volume of scattered cells in the center of the thallus. Cells with lenticular thickenings usually remain roughly isodiametric rather than becoming elongate and stand out as glandular-like dots on the surfaces of dried herbarium specimens. These may be the structures which FALKENBERG (1901) and others have referred to as the distinctive *Cladhymenia*-type glands.

The outer cortex consists of angular, often hexagonal or cuboidal cells in surface view which are seldom more than 2 times as long as broad and often not strongly longitudinally aligned. The cells are secondarily pit-connected and contain dissected ribbon-like chloroplasts oriented perpendicular to the cell long axis.

The tetrasporangia (Fig. 17) are borne in terete, simple to variously-ramified marginal branchlets that are completely free of spinous appendages. Spermatangial platelets typical of the Chondrieae are borne spirally at trichoblast sites near the apices of terete marginal laterals. Cortication is continuous from the bearing branchlet to the expanded disc of the spermatangial plate, obscuring the uniseriate base of the male structure.

The determinate marginal branchlets of female gametophytes are compounded of a long axis on which 3-10+ lateral short shoots are spirally arranged. These short shoots are presumably homologous to the fertile spines in *Acanthophora*, for each bears a single procarp on its adaxial side. Unlike the spines of *Acanthophora* and *C. pacifica*, however, the procarpic laterals of

C. oblongifolia (Fig. 27 b) have the blunt apices of the other branch orders and do not form directly on the flattened main axes or main branches (Fig. 27 a). From 1-3 urceolate cystocarps develop on the fertile laterals.

Discussion

Someone accustomed to working with untidier red algal orders than the Ceramiales (the Gigartinales, for example) might be excused for finding generic distinctions within some tribes of the Rhodomelaceae a bit finely drawn at times. Such is certainly the case with the Chondrieae, which FALKENBERG (1901) shows to be exceptionally uniform in regards to most critical vegetative and reproductive features. Thus the separation between the two major genera *Chondria* and *Acanthophora* appears to be based entirely on the presence of the latter's spines, with species like *A. dendroides* (Fig. 7) being particularly *Chondria*-like (cf. Weber-van BOSSE, 1910) in the shape of the apices, determinate laterals and stichidial branchlets.

The work of FALKENBERG (1901, p. 218) still constitutes the bulk of our knowledge concerning the genus *Cladhymenia*. After examining the two species *C. lyallii* and *C. oblongifolia*, he concluded that their affinities with *Chondria* were so great as to nearly warrant the abandoning of *Cladhymenia*. FALKENBERG found the habit and structure of *C. lyallii* to be particularly *Chondria*-like, reasons which may have prompted him and SCHMITZ (SCHMITZ & FALKENBERG 1897, p. 433) to switch the lectotypification of the genus from the earlier *C. lyallii* of SCHMITZ (1889, p. 447) to the rather more distinctive *C. oblongifolia*. FALKENBERG based a justification for *Cladhymenia* mainly on two features which he thought peculiar to the two New Zealand species. The medullary hyphae, which intrude themselves between pericentral cells and expand to become virtually indistinguishable from them are apparently absent in *Chondria*, although adventitious medullary cells (DAWSON &

TözÜN 1964) and rhizoids (FELDMANN 1949) have been reported. FALKENBERG also noted without particular emphasis the non-stratified arrangement of central axial and surrounding pericentral cells that is so prominent a feature of *C. oblongifolia*. Most unusual of all to FALKENBERG were the "mucilage" cells within the thalli of both species. It appears from the present study, however, that these structures may simply be extreme cases of the lenticular thickenings which are found in several species of *Chondria*, as well as *Cladhymenia pacifica*.

It would seem that a fair continuum runs through the genera of the Chondrieae, with *Acanthophora*, *Chondria* and *Cladhymenia* grading into one another in several respects. There are species of *Chondria* in which internal rhizoidal filaments intrude themselves between the cells of the medulla, central axis and pericentrals (FELDMANN 1949), apparently as they do in *Acanthophora*. *Acanthophora dendroides* can particularly resemble species of the subgenus *Coelochondria*, in which the growing points are also located in apical pits. *Cladhymenia* is similar to many of the *Chondrias* in lateral branchlet structure, location of procarps and possession of lenticular medullary cell-wall thickenings. It seems to differ from most *Chondria* species primarily in the non-tiered arrangement of its pericentral cells.

The morphological characters of *Cladhymenia pacifica* pose somewhat of a classification problem. Their most striking resemblances to *C. oblongifolia* consist externally in the broadly flattened habit and internally in the non-tiered arrangement of the central axial and pericentral cells. Opposed to this are attributes more characteristic of *Acanthophora* than *Cladhymenia*, the most conspicuous being the spirally produced spines and exerted apices with radially organized, forked trichoblasts. As in *Acanthophora spicifera*, the spines of *C. pacifica* subtend the procarps (Fig. 27 a), invest the tetrasporangial short shoots, and arise in a spiral fashion around the apices of all branch orders.

At present the genera of the Chondrieae seem insufficiently well known to judge the absolute importance of either spines or non-tiered pericentrals in separating taxa. The latter feature seems rather fundamental, but is not stressed in taxonomic treatments of the tribe (KYLIN 1956), possibly because it can also occur in *Chondria* (DAWSON & TözÜN 1964). The development of *Acanthophora* procarps adaxially on spines which themselves arise abaxially on trichoblast basal segments may prove the one major distinction between it and *Chondria* (and *Cladhymenia*?), in which procarps are said to be produced on the suprabasal segments of dwarf trichoblast filaments (KYLIN 1928, p. 86) at branch tips. The weight of evidence inclines me to include *Cladhymenia pacifica* in *Acanthophora*, and it is proposed as a result of these studies to transfer it to that genus as *Acanthophora pacifica* (SETCHELL, Tahitian Algae..., U. Calif. Pubs. Bot. 12: 102. pl. 22, 1926) **comb. nov.**

Although attribution of a flattened species to *Acanthophora* is made here for the first time, similar ranges of terete to flattened forms occur in *Chondria* itself and in genera of closely neighboring tribes such as *Laurencia* (SAITO & WOMERSLEY 1974). Owing to the presence of spines on both the main axes and the lateral branchlets, the alliances of *A. pacifica* would be with the *A. najadiformis* group of species rather than the *A. spicifera* section of the genus.

With morphological links between *Acanthophora* and *Chondria* already well-established by the apical and determinate lateral branch morphology of species such as *A. dendroides* (cf. Weber-van BOSSE 1910, p. 29, as *Acanthochondria falkenbergii*) and by some *Chondrias* in which apparently spine-like laterals subtend the cystocarps (DANGEARD 1951, p. 15); and with similar strong links between *Chondria* and *Cladhymenia* arguable in particular from *Cladhymenia lyallii*, the ties between *Acanthophora* and *Cladhymenia* through *A. pacifica* appear to close the circle and point even more strongly to the overall unity of the distinctive Chondrieae Tribe.

Acknowledgements

My sincere thanks to Prof. Maxwell S. DOTY, University of Hawaii, in whose lab most of this work was done during a sabbatical. I appreciate the guidance of my swimming partner, Dr. Mitchell HOYLE, and particularly the help of Dennis RUSSELL, who gave such precise directions to *Cladhymenia pacifica* habitats on Kauai. I thank Dr. Murray J. PARSONS, D.S.I.R., Christchurch, for loan of preserved *C. oblongifolia*, and him and Dr. Sophie C. DUCKER for review of the manuscript. Financial support was provided by the University of Melbourne.

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G. T. クラフト: ハワイ産紅藻 *Cladhymenia pacifica*
 SETCHELL のトゲノリ属への移動

ハワイ及びタヒチからの熱帯性紅藻 *Cladhymenia pacifica* SETCHELL (フジマツモ科) は *Cladhymenia* 属のもととなったニュージーランド産の温帯種と地理的に離れている。*C. pacifica* はタイプ種の *C. oblongifolia* と扁平な葉体をもつこと、中心細胞と周縁細胞が対応しないことで似ているけれども、刺をもつこと及び主軸から放射状に分枝することで異なり、これらの特徴は熱帯性のトゲノリ属と共通である。ハワイ産の *C. pacifica* の形態を *Acanthophora spicifera*, *A. dendroides*, *C. oblongifolia* と比較し、Chondria-group 内での属の基準を考慮して *Acanthophora pacifica* (SETCHELL) KRAFT の新組合せを行った (Botany School, University of Melbourne, Parkville, Victoria 3052, Australia)

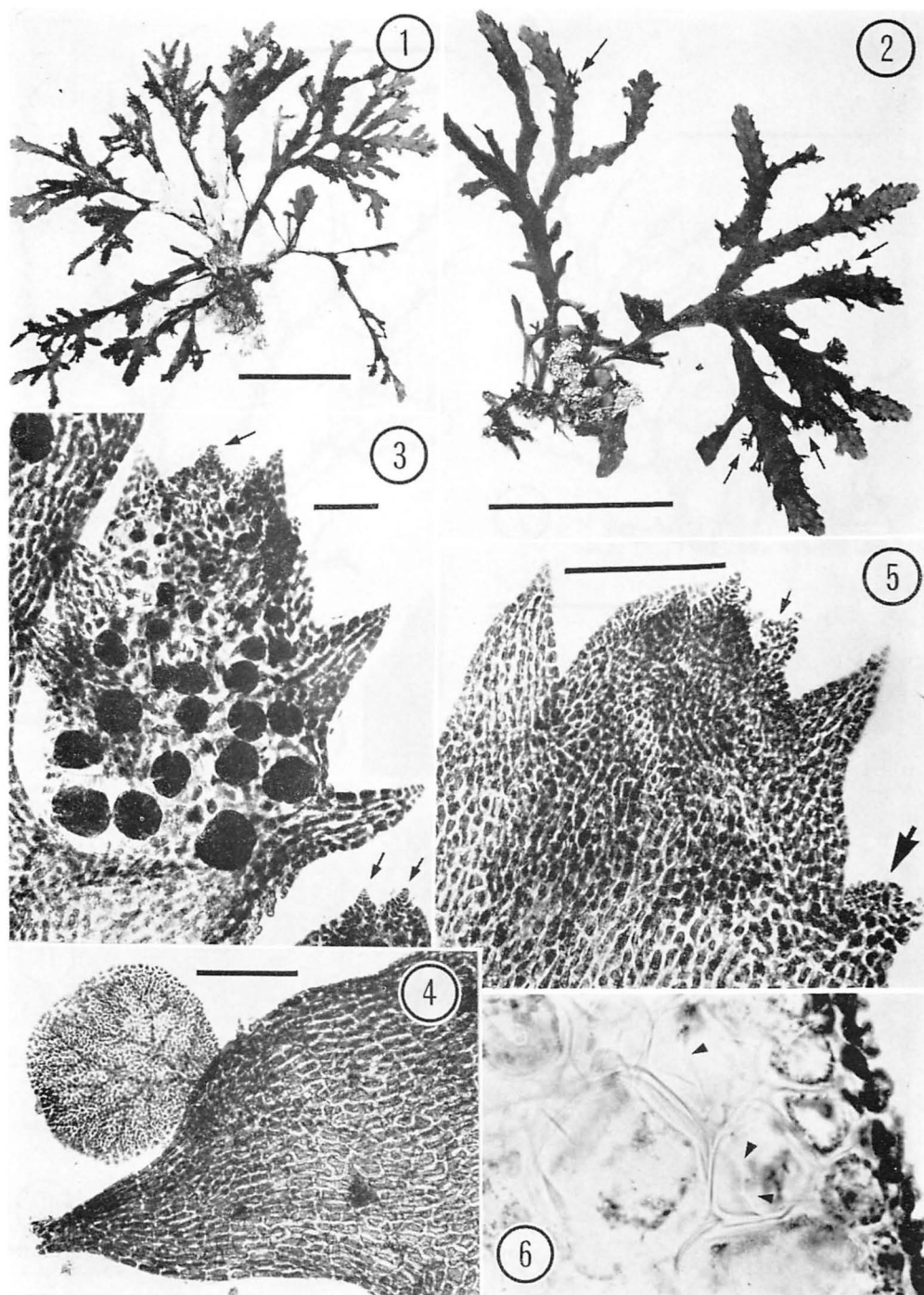
Figs. 1-6. *Acanthophora pacifica* (SETCHELL) comb. nov. 1. Habit of a spermatangial thallus. 2. Tetrasporophyte with marginal clusters of tetrasporangial short-shoots (arrows). 3. Tetrasporangial branchlets growing from exerted apices (arrows) and bearing spirally-arranged acute spines. 4. Spermatangial plate. 5. Gametophyte with procarps on the adaxial spine surfaces (arrows). The younger (small arrow) illustrated in Fig. 24. 6. Lenticular thickenings (arrow heads) within outer medullary cells. All material MELU, K 6499. Scales, 1, 2=2 cm; 3=100 μ m; 4, 5=200 μ m.

Fig. 7. *Acanthophora dendroides* HARVEY. Habit with spines on both main and lateral axes. MELU, K 3926. Figs. 8-12. *Acanthophora spicifera* (VAHL) BOERGESEN. 8. Habit showing spines confined to the determinate lateral branchlets. 9. The acute spines investing a tetrasporangial shoot. 10. Exserted, trichoblast-bearing apex of a stichidial branchlet. 11. Emergence of the trichogyne (arrow) from the base of the pericarp in a young procarp. Details in Fig. 25. 12. Prominent basal cell of a carpogonial branch in an older pericarp. 8=MELU, K 556; 9, 10=MELU, K 6588; 11, 12=MELU, K 6587. Scales, 7, 8=2 cm; 9=500 μ m; 10=100 μ m; 11, 12=50 μ m.

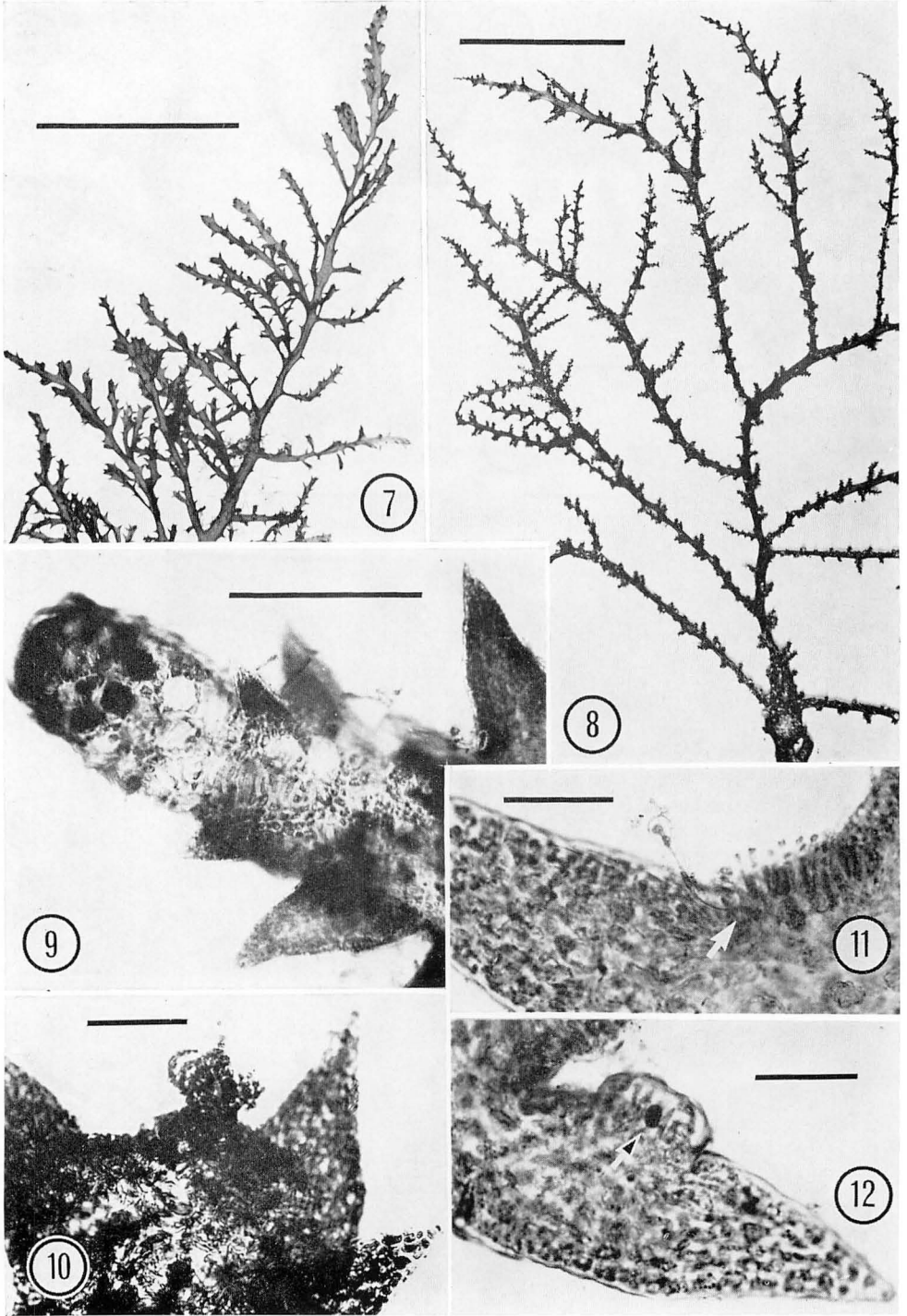
Fig. 13. *Acanthophora spicifera* (VAHL) BOERGESEN. Position of a maturing cystocarp on the adaxial spine surface. MELU, K 6588. Figs. 14-17. *Cladhymenia oblongifolia* HOOKER & HARVEY. 14. Habit of a subtidal specimen. 15. Apex of a main axis in which one apical row lacks (small arrow) while the other bears (large arrow) trichoblasts. 16. Apex of a tetrasporangial branchlet with unbranched trichoblasts. 17. The spine-free tetrasporangial branchlet typical of *Cladhymenia*. 14=MELU, K 4377; 15-17=CHR 319471. 13, 15, 16=100 μ m; 14=2 cm; 17=500 μ m.

Figs. 18-22. *Acanthophora pacifica* (SETCHELL) comb. nov. 18. Habit of a thallus dissected off an irregular limestone block. 19. Cross-section of a stoloniferous basal axis. 20. Cross-section of a mature blade. 21. Cells of the outer medulla and cortex showing the prominent pit-connections between inner cells. 22. Longitudinal-section from 1 cm behind the apex of a major axis. 18= $\times 4.2$; 19= $\times 100$; 20= $\times 68$; 21= $\times 240$; 22= $\times 262$.

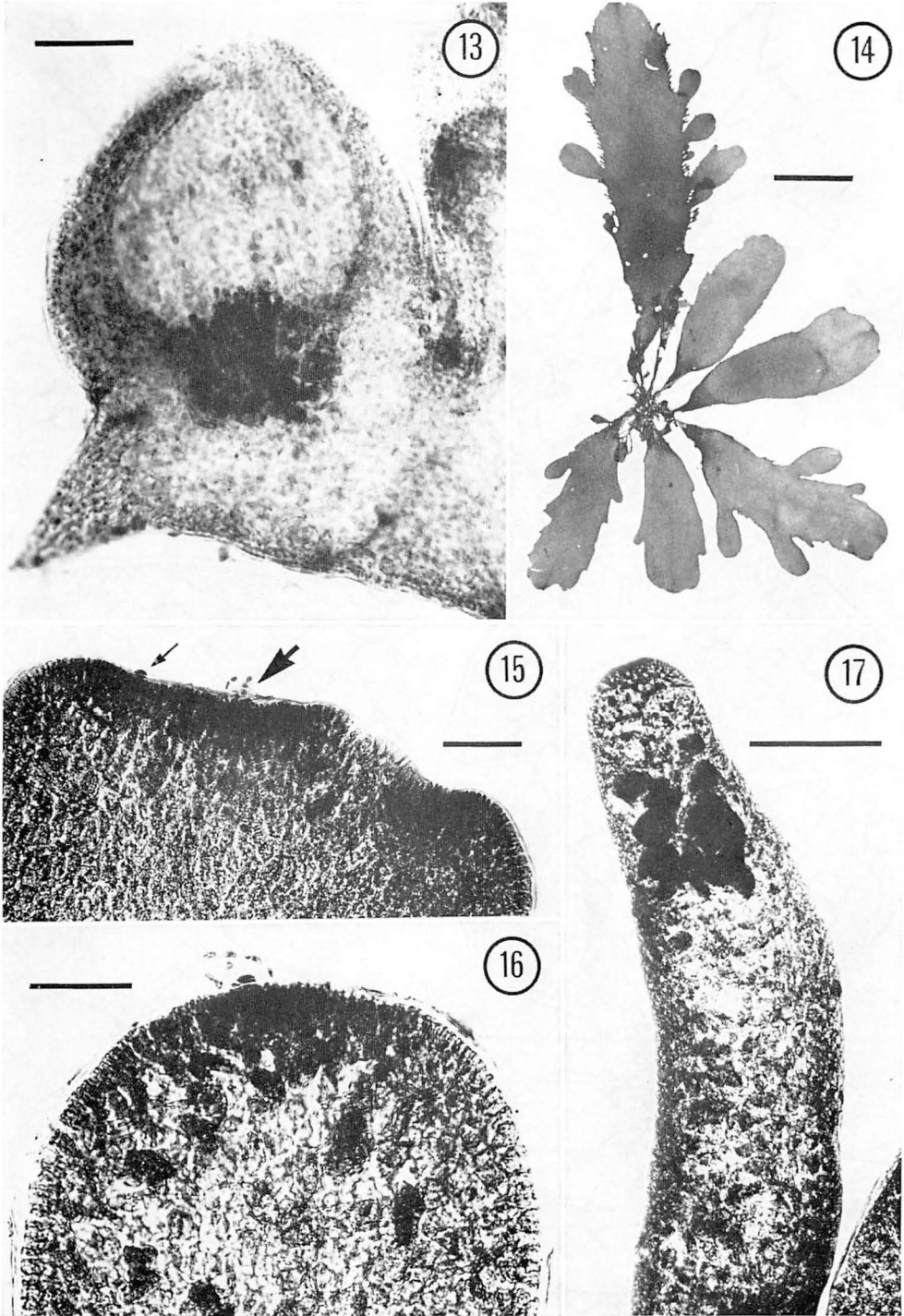
Figs. 23, 24. *Acanthophora pacifica* (SETCHELL) comb. nov. Initiation of a spinous lateral from the abaxial side of the basal cell of a trichoblast (arrow). 24. Early procarp on the adaxial side of a marginal spine (detail from Fig. 5). 25. *Acanthophora spicifera* (VAHL) BOERGESEN. Detail of the procarp in Fig. 11, showing the horizontally-aligned carpogonial branch and one of the two groups of sterile cells on the supporting cell. 26. *Cladhymenia oblongifolia* HOOKER & HARVEY. Section of a lower axis with three cells (arrows) displaying prominent lenticular thickenings. 27. Schematic diagrams of the difference in procarp placement between *Acanthophora* species, including *A. pacifica* (Fig. 27 a) and *Cladhymenia oblongifolia* (Fig. 27 b, c). 23-25= $\times 633$; 26= $\times 227$.



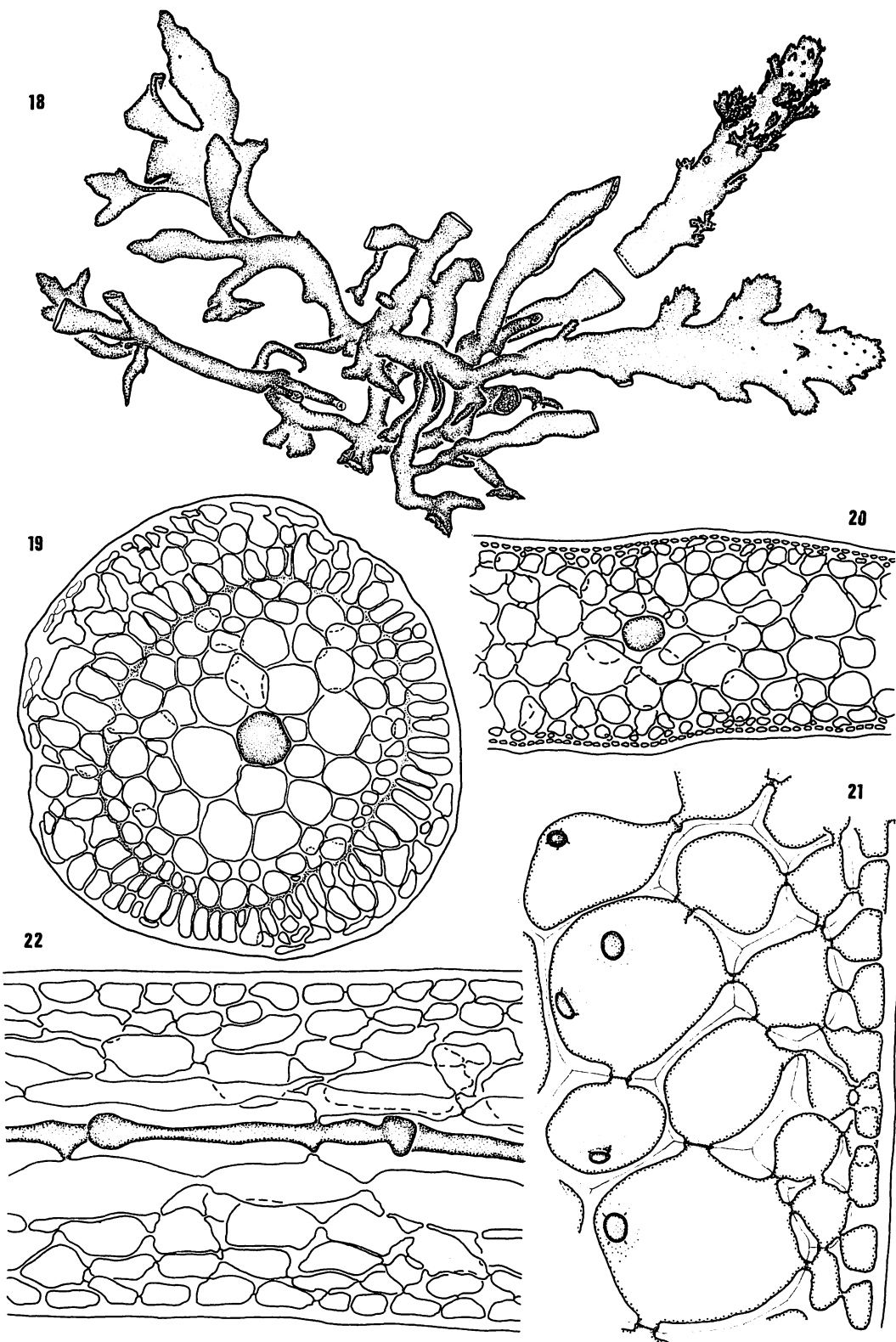
Figs. 1-6.



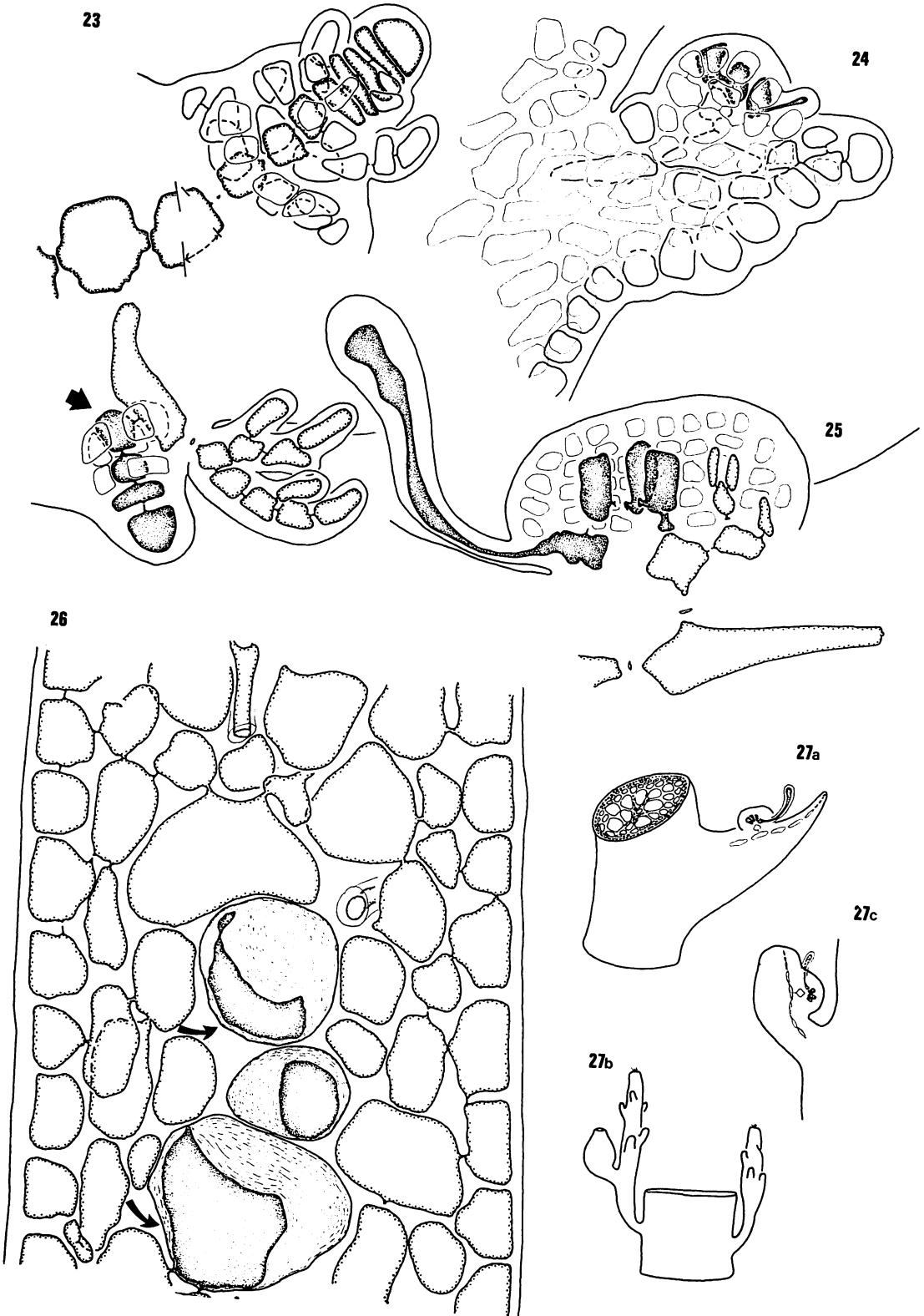
Figs. 7-12.



Figs. 13-17.



Figs. 18-22.



Figs. 23-27.