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Morphology and systematics of *Acanthococcus antarcticus* (Cystocloniaceae, Rhodophyta)

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Acanthococcus (type species: *A. antarcticus* J.D. Hooker et Harvey), from southern South America and the Falkland Islands, is shown to be correctly placed in the Cystocloniaceae. Geographically remote from other members of the family, *Acanthococcus* is readily distinguished anatomically from the other genera. Successive axial cells each initiate a single cortical filament in an alternate-distichous arrangement. Periaxial and inner cortical cells first produce ascending rhizoids that form a bundle around the central axis. At a greater distance from the apex, the rhizoids may branch extensively between inflated medullary and inner cortical cells. Carpogonial branches are straight, 3-celled, with hypogynous cells initially broader than the basal cells. The supporting cell elongates after fertilization, cortical cells distal to the auxiliary cell are transformed into a nutritive tissue, and short files of nutritive filaments produced secondarily from vegetative cells surround the supporting cell. Terminal cells of these filaments fuse directly on to the supporting cell, depositing their nuclei and leaving behind secondary pit connections. The supporting cell, auxiliary cell and inner gonimoblast cells unite to form a central fusion cell bearing chains of carposporangia. Spermatangia develop on special filaments in shallow pits, and tetrasporangia with zonately arranged spores are embedded amongst cortical filaments. On the basis of type material from the Falkland Islands, the taxa known as *Cystoclonium obtusangulum* (J.D. Hooker et Harvey) Kützing or *Acanthococcus spinuligerus* (J. Agardh) J. Agardh are found to be conspecific with *A. antarcticus*.

INTRODUCTION

The family Cystocloniaceae Kützing 1843 (formerly known as the Rhodophyllidaceae Schmitz 1892; see Guiry 1978), currently contains 10 genera (Wynne & Kraft 1981), five of which are endemic to the southern hemisphere. Kylin (1932, 1956) recognized the following characters as being diagnostic of the Cystocloniaceae (as the Rhodophyllidaceae): thallus uniaxial; axial cells each typically bearing two periaxial cells; cortex compact, composed of large inner and small outer cells; carpogonial branches inwardly directed and typically 3-celled; female gametophytes procarpic, the auxiliary cell being an ordinary cortical cell borne directly on the supporting cell and cutting off a single, inwardly directed gonimoblast initial; carposporangia in chains; carposporophyte lacking both an enveloping sheath and an ostiole; and tetrasporangia zonately cleaved. Kylin (1956) identified two types of cystocarp in the Cystocloniaceae: one in which a large central fusion cell is surrounded by carposporangia-bearing filaments (as found in the genera *Cystoclonium, Rhodophyllis,* and *Fimbrifolium*), and the other in which gonimoblasts are secondarily connected to a small-celled nutritive tissue situated in the floor of the cystocarp (as found in the genera *Calliblepharis* and *Craspedocarpus*).

Acanthococcus J.D. Hooker et Harvey (1845, p. 261) is known from southern South America and the Falkland Islands (Pujals 1963, 1977; Papenfuss 1964). According to Hariot (1889, p. 79), *A. antarcticus* J.D. Hooker et Harvey is one of the most common subtidal red algae in Tierra del Fuego. The record of *A. antarcticus* from Îles Kerguelen (Reinbold 1908) on almost the opposite site of the globe requires confirmation.

Acanthococcus antarcticus was originally described by J.D. Hooker & Harvey (1845, p. 261) on the basis of cystocarpic specimens from Cape Horn and the Falkland Islands. *Acanthococcus,* named for its spiny cystocarps, was further characterized as having a cellular medulla surrounding a central bundle of rhizoids (as 'tubes'). The

habit, external view of a cystocarp, and cross-section of a vegetative axis were illustrated in Part II of *Flora Antarctica* (J.D. Hooker 1847, pl. 181).

Hooker & Harvey (1845) and Hooker (1847) were unsure about the taxonomic position of *Acanthococcus*, first placing it in the Delesserieae next to *Plocamium*, and subsequently in the Sphaerococceae next to *Hypnea*. J. Agardh (1852, p. 434) first placed *Acanthococcus* in his 'Ordo' Hypneaceae next to *Hypnea* and later (J. Agardh 1876, p. 349) in his 'Ordo' Rhodymeniaceae next to *Plocamium*. When Schmitz (1892, p. 19) erected the Rhodophyllidaceae (=Cystocloniaceae), he assigned *Acanthococcus*, together with *Rhodophyllis*, to his new 'subgroup' Rhodophyllideae. *Acanthococcus* was retained in the Rhodophyllidaceae by Kylin & Skottsberg (1919, p. 16) without the addition of further morphological information. Subsequently, Kylin (1932, p. 39, 1956) mentioned the presence of a large post-fertilization fusion cell in the cystocarp of *Acanthococcus*. Joly *et al.* (1964) described and illustrated aspects of the vegetative and reproductive morphology of a robust form of *A. antarcticus* from Puerto Deseado, Prov. Santa Cruz, Argentina. Additional morphological data that we have been able to provide as a result of recent collections contribute significantly to our understanding of *Acanthococcus* and its position in the Cystocloniaceae.

At present, we recognize only one species in *Acanthococcus*, *A. antarcticus*, in which we include plants reported as *Cystoclonium obtusangulum* (J.D. Hooker et Harvey) Kützing or *Acanthococcus spinuligerus* (J. Agardh) J. Agardh from southern South America and the Falkland Islands.

MATERIALS AND METHODS

The specimens examined in this study were collected by R.B. Searles, G.L. Leister and J.F. Brauner during the 1972 and 1973 NSF R/V *Hero* cruises to southern Argentina and Chile (Fig. 1).

Liquid-preserved material in 5% Formalin/seawater was hand-sectioned with a platinum-chrome double-edged razor blade. For longitudinal sections, branchlets were held with forceps and split into two halves. Material was stained with aceto-iron-haematoxylin-chloral hydrate (Wittmann 1965) and mounted in 1 : 1 Hoyer's medium : water (Hommersand & Fredericq 1988), or was stained with 1% aniline blue and mounted in glycerine. Herbarium abbreviations follow those of Holmgren *et al.* (1981).

OBSERVATIONS

Acanthococcus J.D. Hooker et Harvey (1845: 261)

DESCRIPTION: Plants uniaxial, with successive axial cells each cutting off a single periaxial cell on opposite sides, producing cortical filaments in an alternate-distichous arrangement; carpogonial branch ascending, 3-celled, with all cells uninucleate and with the second cell initially broader than the first; carpogonium with straight trichogyne; procarpic, auxiliary cell distal to supporting cell; supporting cell elongating after fertilization, and cortical cells distal to auxiliary cell enlarging and developing into a nutritive tissue; additional nutritive filaments produced secondarily around supporting cell, the terminal cells fusing with it and thereby establishing secondary pit connections; gonimoblast initial single, cut off more inwardly from auxiliary cell; fusion cell formed by fusion of supporting cell, auxiliary cell and inner gonimoblast cells; carposporangia in branched chains; sterile gonimoblasts lacking; pericarp weakly developed, ostiole lacking; cystocarps sessile, hemispherical to subglobose, with or without spiny outgrowths; spermatangia borne on special filaments in shallow pits; tetrasporangia formed terminally, zonately cleaved, embedded amongst cortical cells.

TYPE SPECIES: *Acanthococcus antarcticus* J.D. Hooker et Harvey (1845, p. 261)

Acanthococcus antarcticus J.D. Hooker et Harvey (1845: 261)

Figs 2–43

DESCRIPTION: Thalli up to 18 cm tall, erect, attached by a fibrous holdfast; main axes compressed to subcylindrical, 0.5 to 2(–3) mm wide; branching up to 5(–6) orders, dense to sparse or denuded, repeatedly alternate-distichous to irregularly subdichotomous, sometimes secund; branches of any but the final order may bear slender determinate branchlets up to 2 mm long; ultimate branchlets short and tapering abruptly, or long and tapering gradually; branch tips acute to acuminate; axial cells elongated, typically surrounded by a bundle of rhizoids that are often

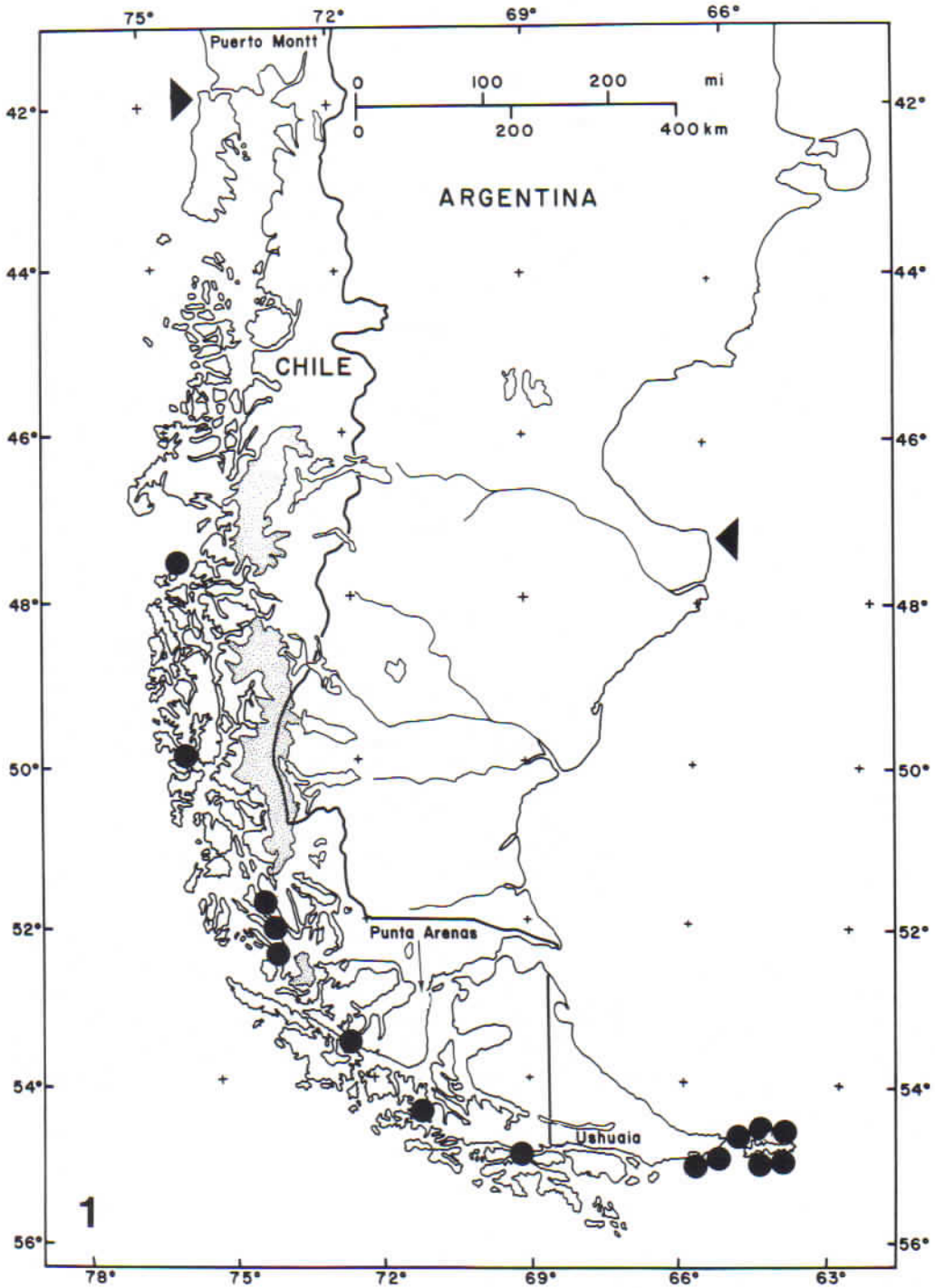
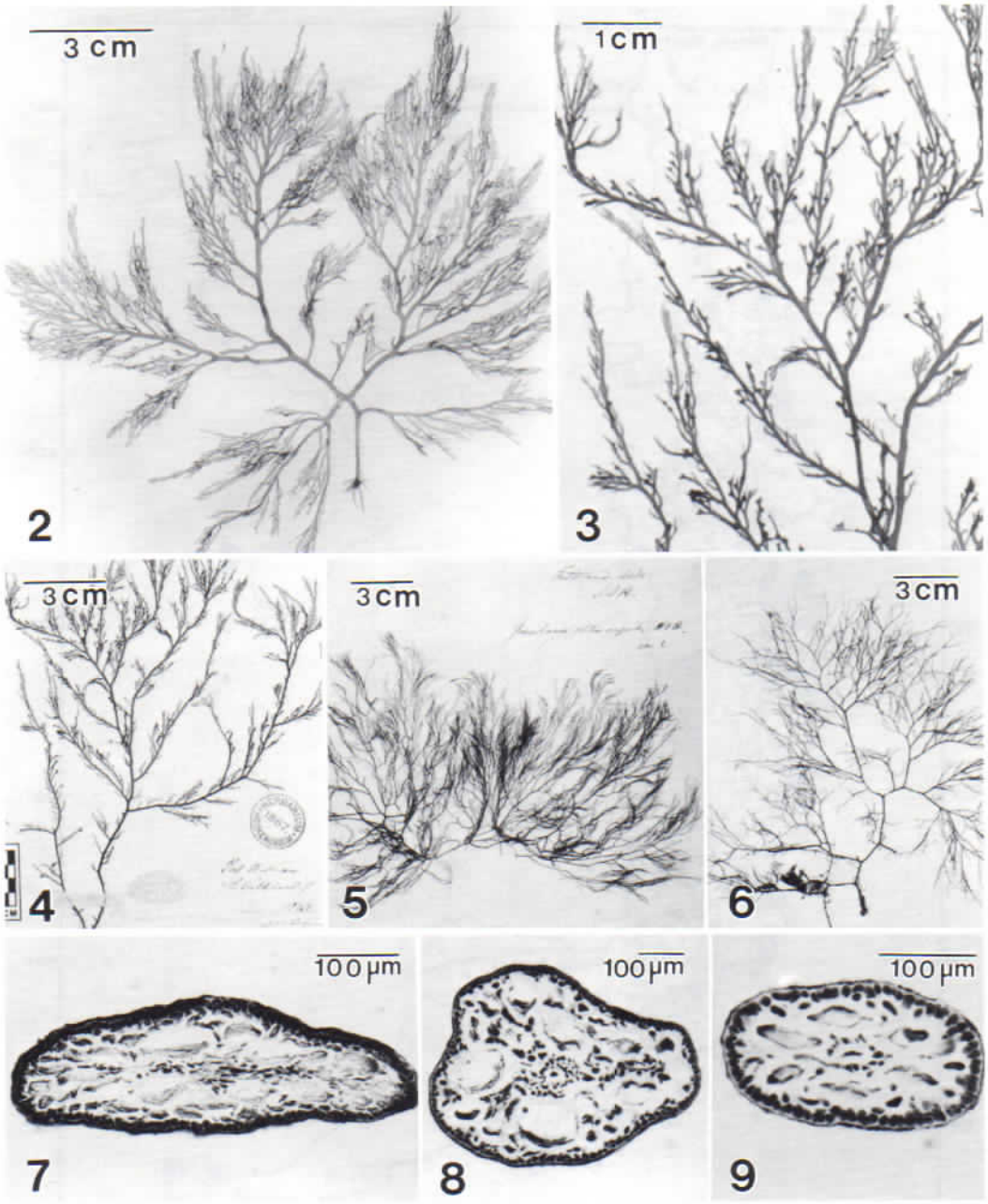


Fig. 1. Distribution map of *Acanthococcus antarcticus* showing R/V *Hero* cruise collections (circles) and presumed east and west coast distribution limits (triangles). Records from the Falkland Islands are not shown.



Figs 2–9. *Acanthococcus antarcticus.*

Fig. 2. Habit of robust cystocarpic specimen of *Acanthococcus antarcticus, Searles, Leister & Brauner 73-37-3*, Punta Valparaïso, Tierra del Fuego, Chile, NCU.

Fig. 3. Upper left portion of lectotype of *Acanthococcus antarcticus* showing sessile, protuberant cystocarps.

Fig. 4. Lectotype, *Acanthococcus antarcticus* J.D. Hooker et Harvey (*Capt. Crozier*, 1842, Port Williams, E. Falkland Island, BM).

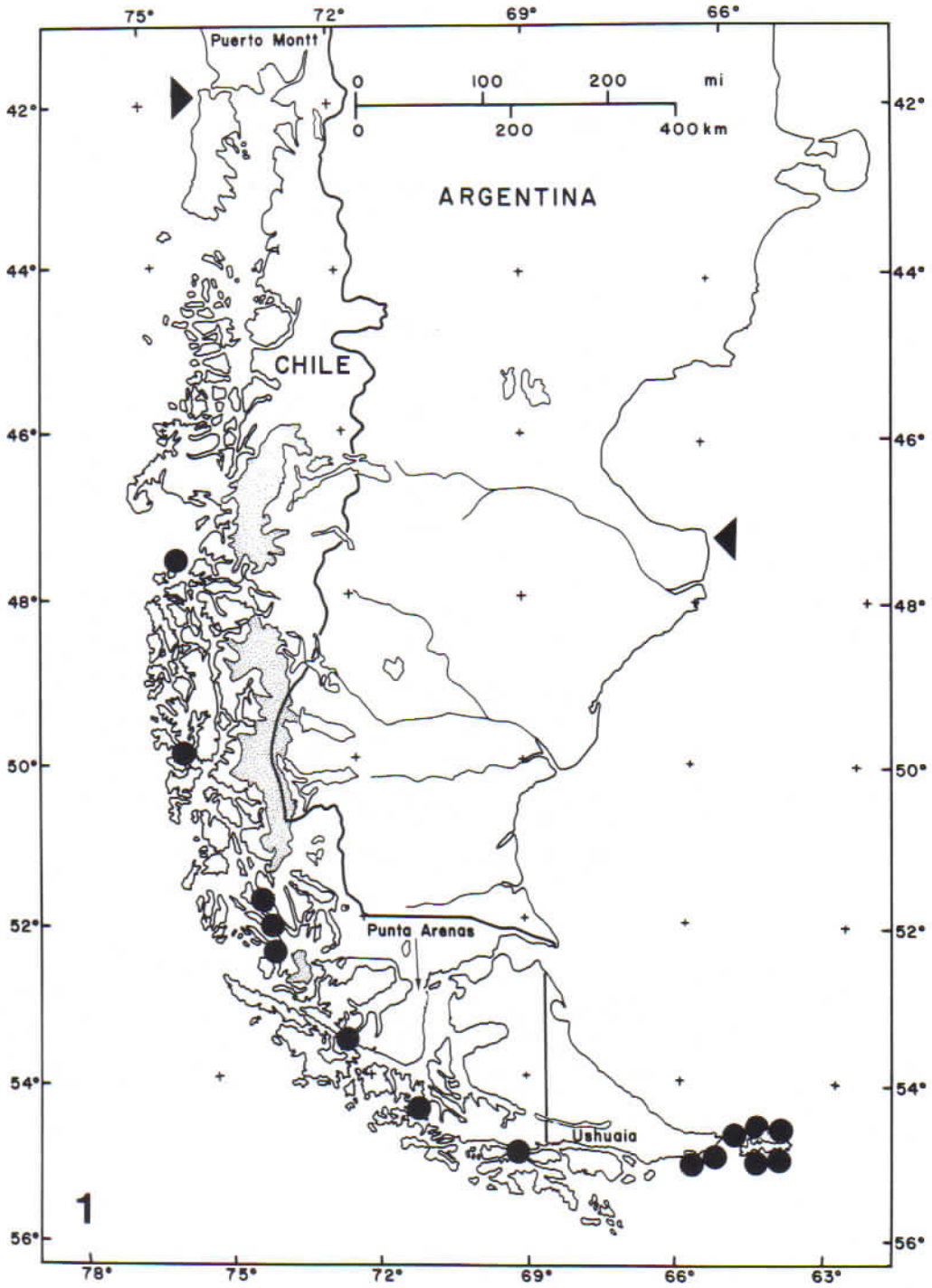
Fig. 5. Syntype, *Gracilaria? obtusangula* var. α (J.D. Hooker et Harvey, Falkland Islands, *J.D.S.*, BM).

Fig. 6. Holotype, *Sphaerococcus subulatus* var. *nigrescens* C. Agardh (*Freycinet, LD-28225*, Falkland Islands, LD).

Fig. 7. Cross-section close to apex of fourth-order branch through specimen in Figs 3–4.

Fig. 8. Cross-section close to apex of fourth-order branch through specimen in Fig. 5.

Fig. 9. Cross-section close to apex of fourth-order branch through specimen in Fig. 6.



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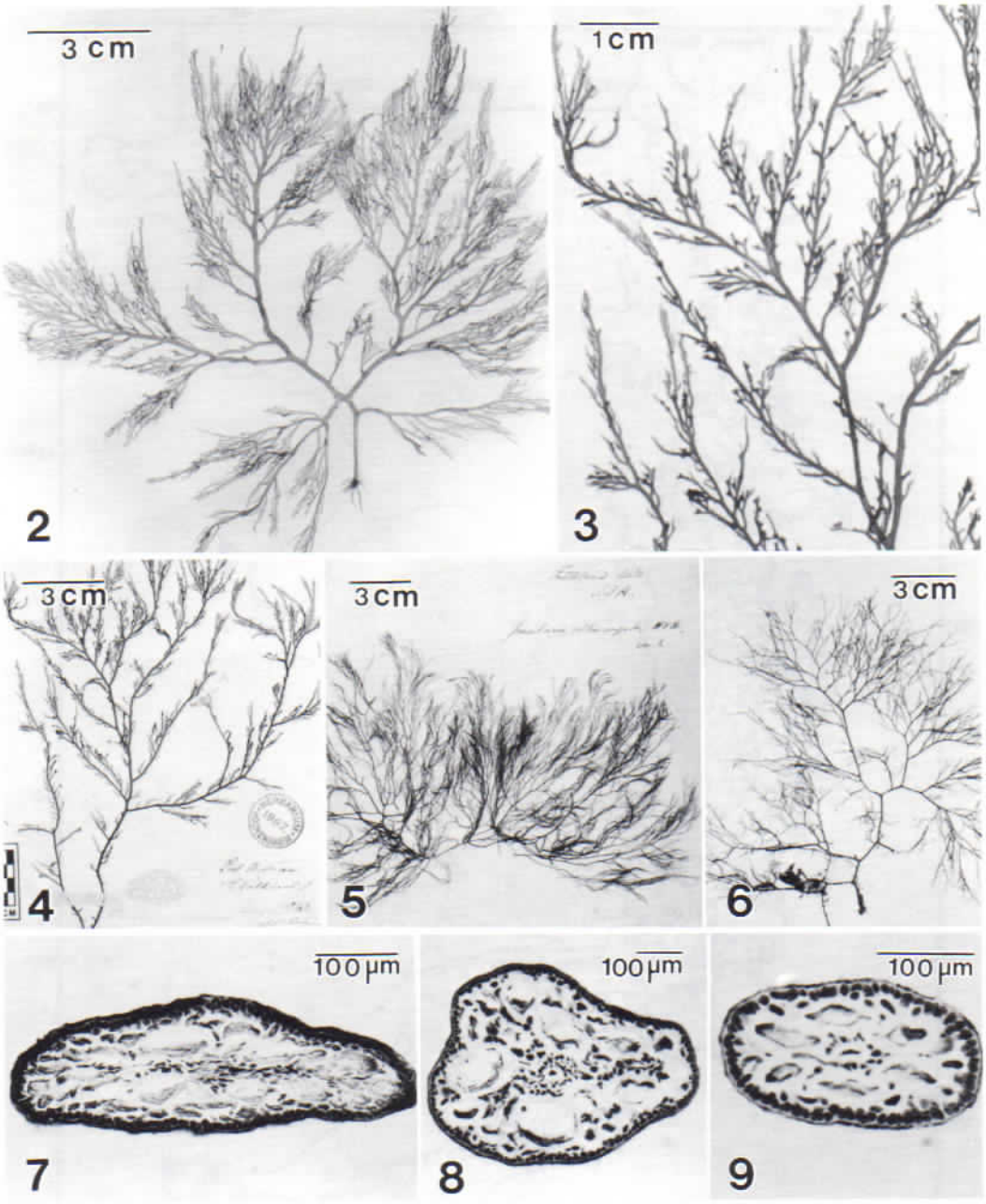

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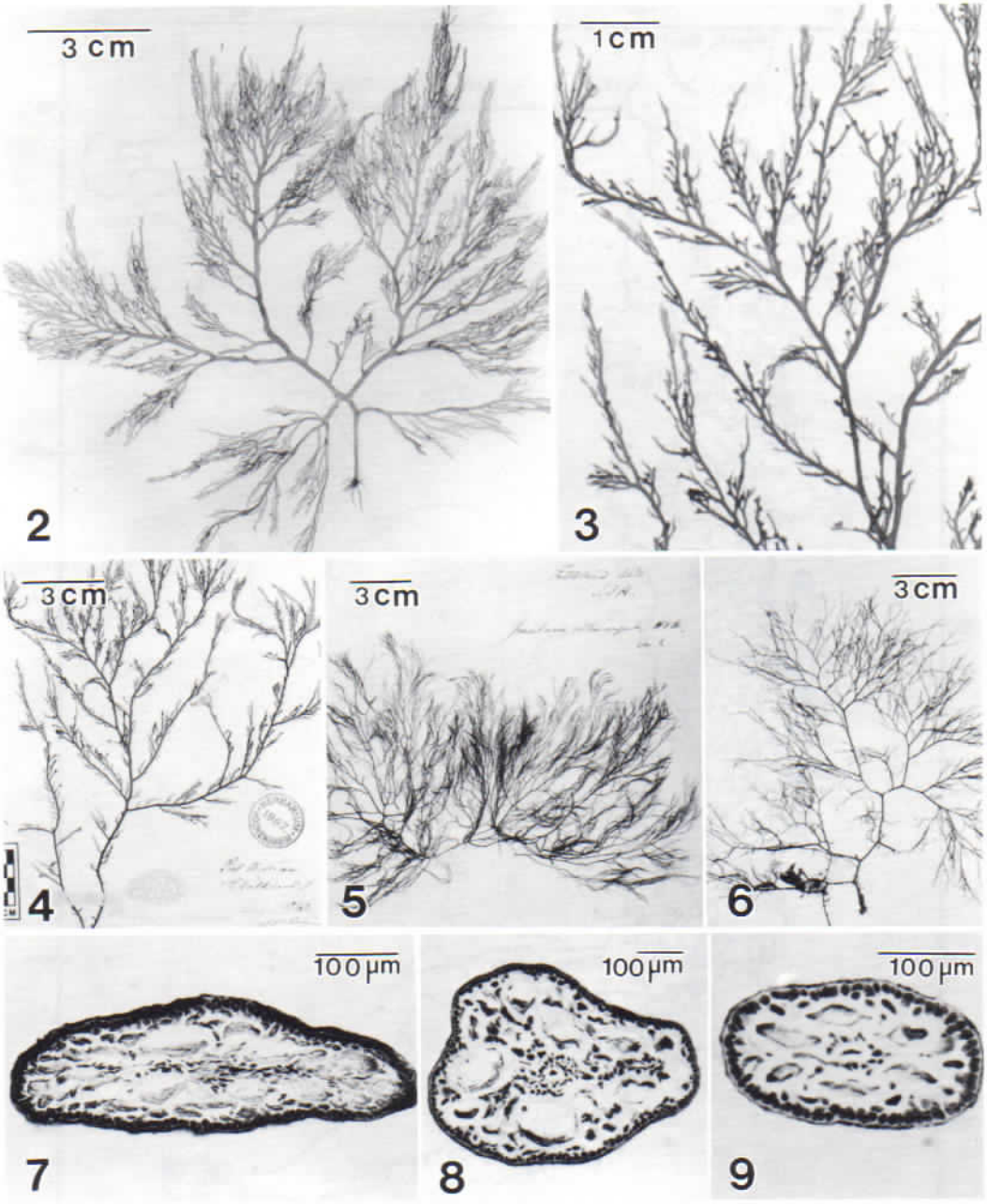

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indistinguishable from them in lower cross-sections; medulla composed of 1–3 layers of large, inflated cells reaching 300 × 400 μm; cortex of 1–3 layers of progressively smaller cells; surface layer uniformly distributed, composed of rectangular to irregularly polygonal cells averaging 6 × 10 μm. Rhizoids at first ascending, later also descending, confined to central core in distal branches, or sparsely distributed between medullary and cortical cells, later branching secondarily, becoming abundant between medullary and inner cortical cells in main axes or towards the base; cystocarps intercalary or subterminal on lateral branches, naked or bearing up to six spiny outgrowths; carposporangia up to 50 μm in diameter; branched carposporangial chains 200–250 μm long; spermatangial pits averaging 50 μm in diameter; tetrasporangia up to 20–50 × 50–100 μm, immersed in modified cortex.

LECTOTYPE: We have chosen as the lectotype a cystocarpic specimen that corresponds closely to the reverse image of the left-hand side of the habit drawing in J.D. Hooker 1847, pl. 181, Port Williams, E. Falkland I., *Capt. Crozier,* 1842, BM (Figs 3–4, 7). No material was found that corresponded to the base and sterile part of the habit drawing (right-hand side) in this plate.

NOMENCLATURAL SYNOMYM: *Callophyllis antartica* (J.D. Hooker et Harvey) Kützing (1849, p. 747).

TAXONOMIC SYNONYMS: *Gracilaria? obtusangula* J.D. Hooker et Harvey (1845, p. 261). *Cystoclonium* ? *obtusangulum* (J.D. Hooker et Harvey) Kützing (1849, p. 757). *Sphaerococcus subulatus* var. *nigrescens* C. Agardh (1822, p. 329). *Gracilaria* ? *nigrescens* J.D. Hooker et Harvey in J.D. Hooker (1847, p. 477). *Gracilaria*? *nigrescens* var. *tenuior* J.D. Hooker et Harvey in J.D. Hooker (1847, p. 477). *Cystoclonium spinguligerum* J. Agardh (1849, p. 87). *Sphaerococcus nigrescens* (J.D. Hooker et Harvey) Kützing (1849, p. 777). *Sphaerococcus nigrescens* (J.D. Hooker et Harvey) var. *tenuior* Kützing (1849, p. 777). *Acanthococcus spinuligerus* (J. Agardh) J. Agardh (1852, p. 437). *Acanthococcus spinuligerus* (J. Agardh) J. Agardh var. *tenuior* (J.D. Hooker et Harvey) Hariot (1889, p. 80). *Acanthococcus spinuliger* (J. Agardh) J. Agardh as cited in De Toni (1897, p. 351). *Gigartina spinifera* Kützing (1849, p. 750).

The literature contains numerous references to a narrow, filiform species usually cited as *Cystoclonium obtusangulum* based on *Gracilaria obtusangula* J.D. Hooker et Harvey or *Acanthococcus spinuliger* based on *Sphaerococcus subulatus* var. *nigrescens* C. Agardh (Pujals 1963, 1977; Papenfuss 1964). *Gigartina spinifera* Kützing was placed in synonymy under *Acanthococcus spinuligerus* by Hariot (1889, p. 80). Type material, presumably labeled 'Ad ins. Malouinas: Delise' was not found. It could be a syntype of *Sphaerococcus subulatus* var. *nigrescens.* We have concluded after examining numerous specimens from South America and the Falkland Islands that the narrow, subcylindrical forms fall within the range of variation of *Acanthococcus antarcticus* and are conspecific with it. All collections of these forms examined have proved to be sterile. Records of *Acanthococcus spinuliger* from the South Orkney Islands (Gepp & Gepp 1905) and *Cystoclonium obtusangulum* from the South Shetland Islands (Moe & DeLaca 1976), localities where *A. antarticus* has not been reported, require further investigation.

HISTORICAL SPECIMENS EXAMINED: Lectotype, Port Williams, E. Falkland Island (*Capt. Crozier,* 1842, BM, Figs 3–4, 7); syntype, Port Williams, E. Falkland Island (*Capt. Crozier,* vii. 1842, L, published as *Callophyllis antarctica* (J.D. Hooker et Harvey) Kützing 1849, 1867, pl. 93); NW Bay, Hermite Island, Cape Horn (spermatangial, undated, BM; tetrasporangial, undated, TCD; undated *LD-28224,* LD); St Martin's Cove, Hermite Island, Cape Horn (*Capt. Crozier,* September–October 1842, BM); outer coast Cape Pembroke, Falkland Islands (undated, TCD); Ancud, Chiloë, Chile (*Lechler,* undated, C); Falkland Islands (*det. Lenormand,* undated, S; C); Détroit de Magellan (undated, ex. Herb. Lenormand, UPS); Slogget Bay, Fuegia (*C. Skottsberg,* 16.iii.1909, GB); *Insula* Maclov (undated, Herb. Kjellman, UPS); Île de Tova, Patagonie (undated, Herb. Kützing, L). As *Cystoclonium obtusangulum* var. α: Falkland Islands (*JDH,* BM, Figs 5, 8); undated, no location (BM). As *Cystoclonium obtusangulum* var. β: NW Bay, Hermite Island, Cape Horn (*J.D.H.,* undated, BM); Cape Horn (undated, L-938 92 194, L, illustrated by Kützing 1868, pl. 17); Berkeley Sound, Falkland Islands (*D. Lyall,* as DL), v. 1842, TCD; PC); St Salvador Bay, E. Falkland Island (iv. 1842, BM); St Salvador Bay, Falkland Islands (*J.D.H.,* undated, BM); Falkland Islands (undated, BM); Fret. Magellan (*Hohenacker 486,* undated, L-938 92 128, L). As *Acanthococcus spinuligerus*: holotype, Falkland Islands (*Freycinet LD-28225, Sphaerococcus subulatus* var. *nigrescens* C. Agardh, Figs 6, 9); Syntype, Falkland Islands

(*Gaudichaud #130*, x. 1822, ex Herb. J. Gay, BM); Falkland Islands (#233 ex Herb. J. Ag., undated, BM).

NEW RECORDS: R/V *Hero* cruises to southern Argentina and Chile: exposed island at entrance to Puerto Alert, Chile, 49°53.6′ S, 75°12.5′W, sublittoral fringe to 6 m (*Searles, Leister & Brauner 72-19-70*, tetrasporangial, 31.x.1972, NCU); Isla San Pedro, Gulfo de Peñas, Chile, 47°43.2′ S, 74°53.3′ W, low water to 3 m (*Searles, Leister & Brauner 72-32-52*, 6.xi.1972, NCU); Kelp bed, Punta Conway, Isla de los Estados, Argentina, 54°43.8′ S, 64°13.9′ W, 9–12 m (*Searles, Leister & Brauner 73-1-29*, cystocarpic, 4.v.1973, NCU); outer fringe of kelp bed, Bahia Colnett, Isla de los Estados, Argentina, 54°42.6′ S, 64°20.3′ W, 14 m (*Searles, Leister & Brauner 73-6-5*, cystocarpic, 5.v.1973, NCU); very exposed, Puerto Vancouver, Isla de los Estados, Argentina, 54°47.4′ S, 64°04.35′ W, 5–25 m (*Searles, Leister & Brauner 73-18-24*, cystocarpic, 10.v.1973, NCU); small cove, behind Islet Alexander, Isla de los Estados, Argentina, 54°50.5′ S, 64°23.8′ W, 20 m (*Searles, Leister & Brauner 73-22-20*, cystocarpic, 10.v.1973, NCU); outer edge of kelp bed, Bahia Crossley, Isla de los Estados, Argentina, 54°47.5′ S, 64°42.1′ W, 14 m (*Searles, Leister & Brauner 73-33-11*, 14.v.1973, NCU); very sheltered, Cta Awaia Kirrh, Canal Beagle, Chile, 55°0.0′ S, 69°02.2′ W, 0–2 m (*Searles, Leister & Brauner 73-35-50* cystocarpic & male, 16.v.1973, NCU); Punta Valparaïso, Tierra del Fuego, Chile, 54°22.2′ S, 71°21.7′ W (*Searles, Leister & Brauner 73-37-3* cystocarpic, 17.v.1973, NCU); Puerto Alert, Canal Trinidad, Chile, 49°53.6′ S, 75°12.7′ W, 5–18 m (*Searles, Leister & Brauner 73-42-11*, cystocarpic, 20.v.1973, NCU).

DISTRIBUTION: Distributional records of *Acanthococcus* are given by Papenfuss (1964), Pujals (1963, 1977) and Moe & DeLaca (1976). Robust, compressed forms and narrow, spinuligerous forms of *Acanthococcus antarcticus* were found at many of the same localities in Tierra del Fuego and the Falkland Islands in the expeditions of the last century. The most northerly records of *A. antarcticus* are from Ancud, Chiloë, Chile, and Puerto Deseado, Argentina (Fig. 1). We confirm that the Lechler specimen at Copenhagen (C) from

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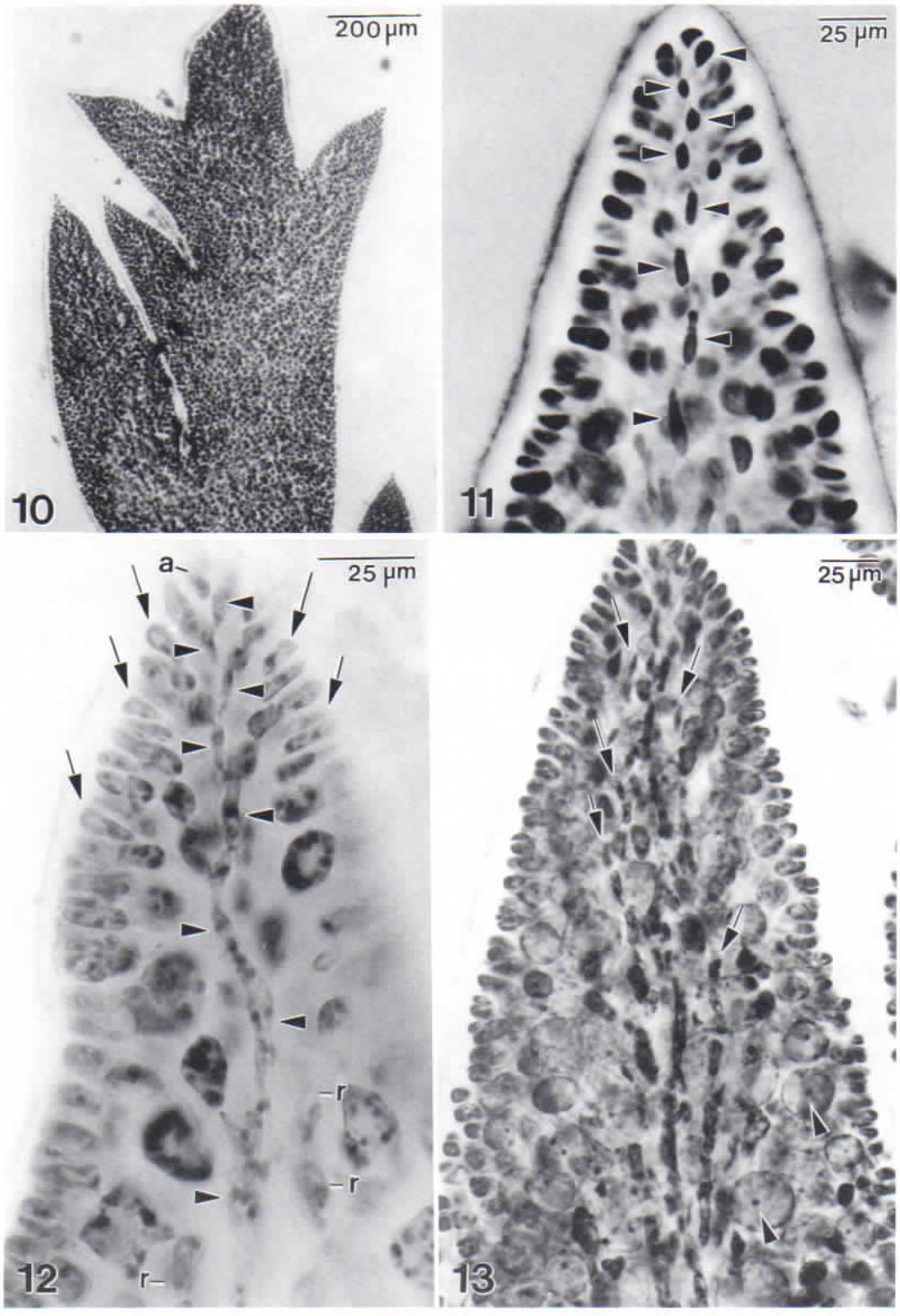
Figs 10–13. *Acanthococcus antarcticus. Searles, Leister & Brauner 73-35-50.* Vegetative morphology.
Fig. 10. Side branch showing uniaxial tips, surface cells, and rhizoids beneath.
Fig. 11. Optical section through spine on cystocarp showing apical cell, uniaxial construction and branching of cortical filaments (aniline-blue stained). Each axial cell (arrowhead) has cut off a periaxial cell bearing a cortical filament.
Fig. 12. Longitudinal section through tip showing apical cell (a), axial cells (arrowheads) and apical cells of corticating filaments (arrows). Periaxial cells and inner cortical cells below have produced rhizoids (r).
Fig. 13. Optical section of tip showing rhizoids (arrows) ascending from periaxial cells and inner cortical cells. Darkly staining spherical bodies are visible in some cortical cells (arrowheads).
Figs 14–19. *Acanthococcus antarcticus. Searles, Leister & Brauner 73-35-50.* Vegetative morphology.
Fig. 14. Axial cells (ax) and periaxial cells (p) linked by enlarged pit connections (arrows).
Fig. 15. Axial cells (ax) and periaxal cell (p) bearing cortical filament (co). Rhizoids (r) arising from periaxial and cortical cells form numerous secondary pit connections (arrows). A conjunctor cell from a rhizoid is shown on the left-hand side (arrowhead).
Fig. 16. Longitudinal section through upper part of third-order branch showing rhizoids primarily restricted to central core.
Fig. 17. Longitudinal section through stipe showing abundant rhizoids in thick, central bundle and between surrounding medullary and cortical cells.
Fig. 18. Cross-section through third-order branch showing few central and interspersed (arrowhead) rhizoids.
Fig. 19. Cross-section through stipe showing abundant central and interspersed rhizoids.
Figs 20–24. *Acanthococcus antarcticus. Searles, Leister & Brauner 73-37-3.* Female reproductive system.
Fig. 20. Longitudinal section of branchlet tip showing position of carpogonial branches (arrows) and auxiliary cells (ac).
Fig. 21. Supporting cell (sc) bearing 3-celled carpogonial branch terminated by carpogonium (arrow); auxiliary cell (ac) is pit-connected (arrowhead) to supporting cell.
Fig. 22. Post-fertilization stage. Nutritive filaments (nf), supporting cell (sc), first and second cells of carpogonial branch (cb_1, cb_2) and auxiliary cell (ac) containing a central haploid (hn) and proximal diploid (dn) nucleus. Cells are slightly displaced due to squashing.
Fig. 23. Elongated supporting cell (sc) and auxiliary cell (ac) with gonimoblast initial (gi) and surrounded by nutritive filaments (nf) and modified terminal cortical filaments (mcf).
Fig. 24. Detail of central region shown in Fig. 20. Supporting cell (sc) is uninucleate, except where a conjunctor cell derived from a nutritive filament has fused with it, depositing a nucleus and leaving a small process (arrow). Auxiliary cell (ac) distal to supporting cell has cut off a gonimoblast initial (gi).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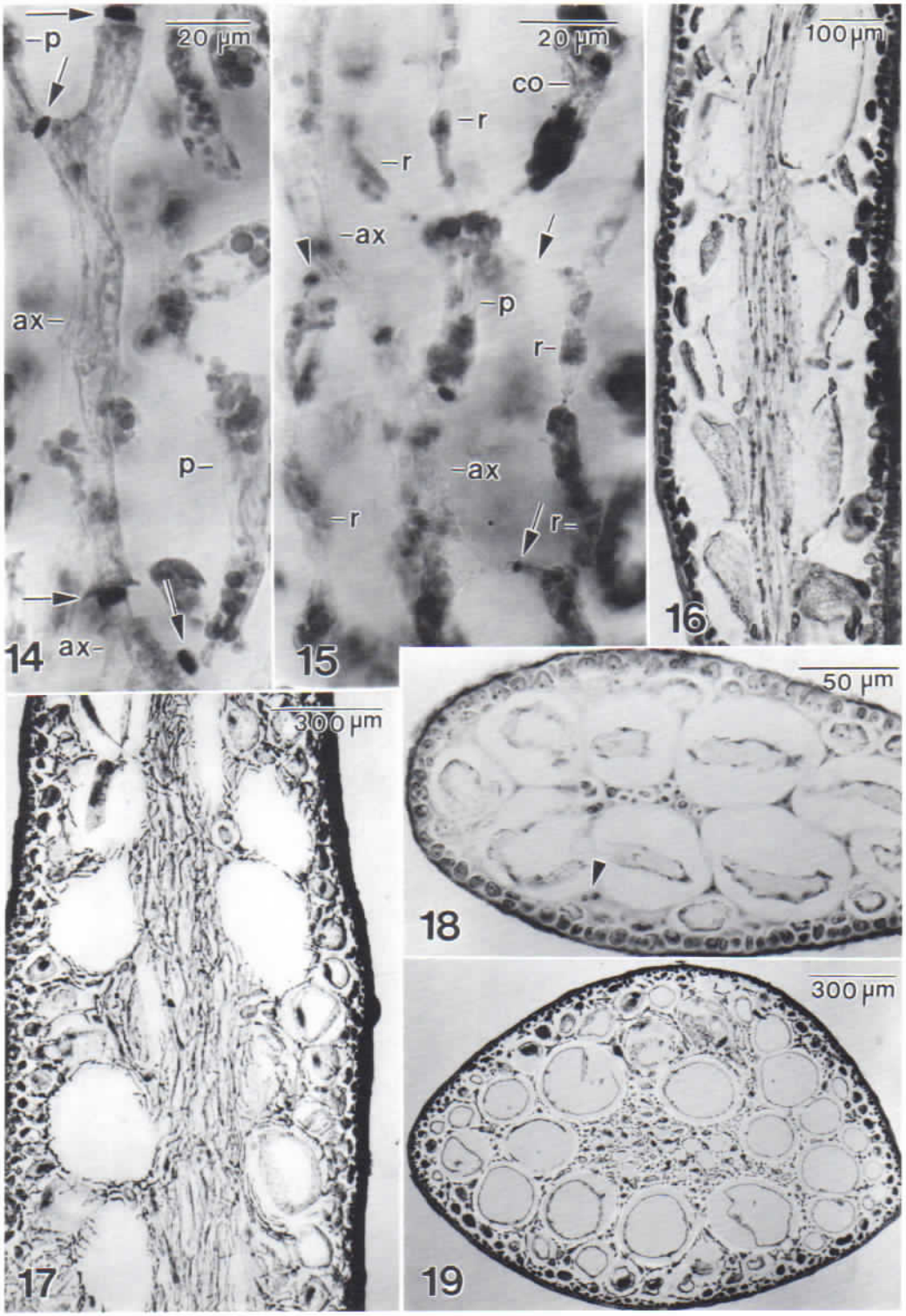
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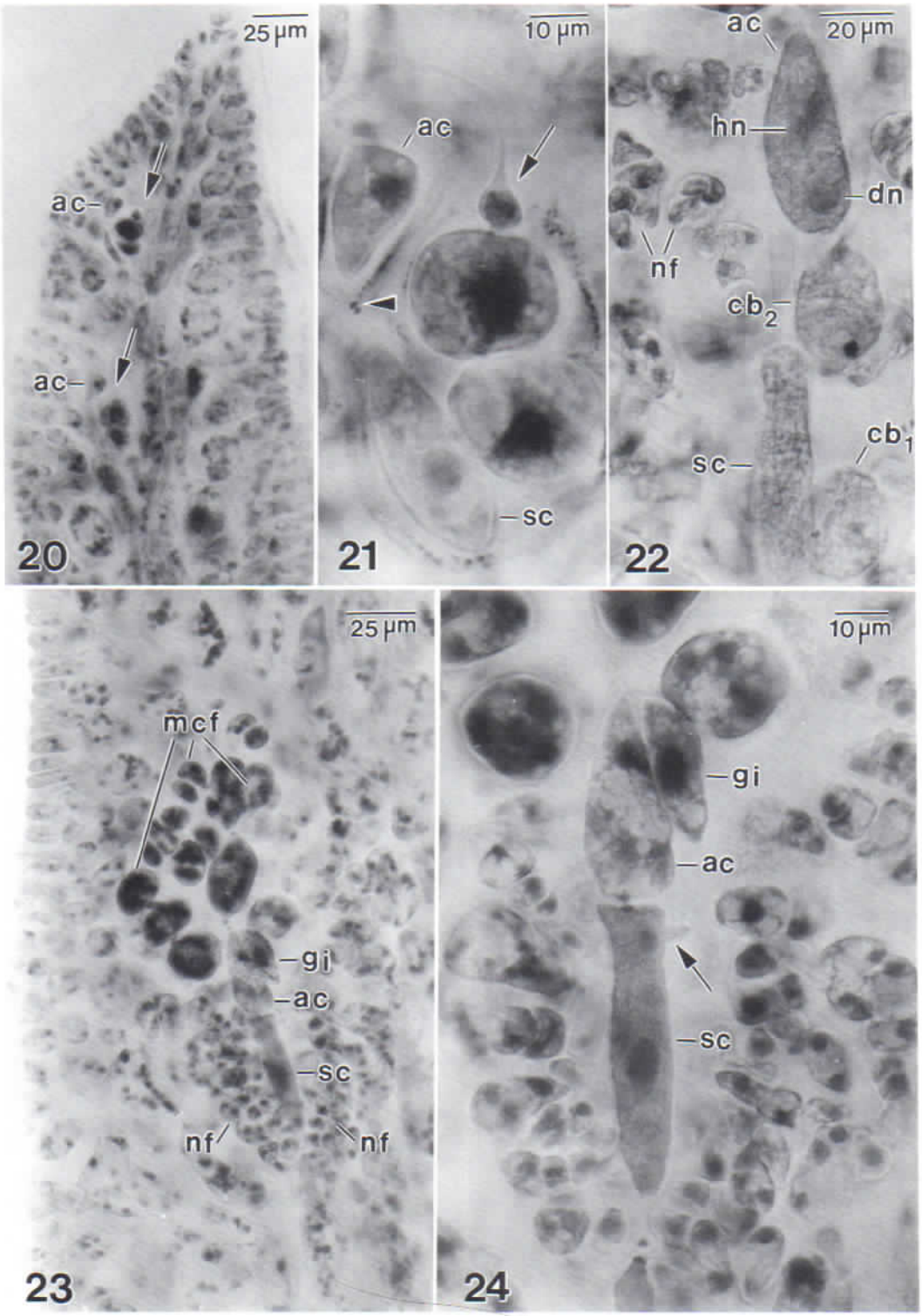
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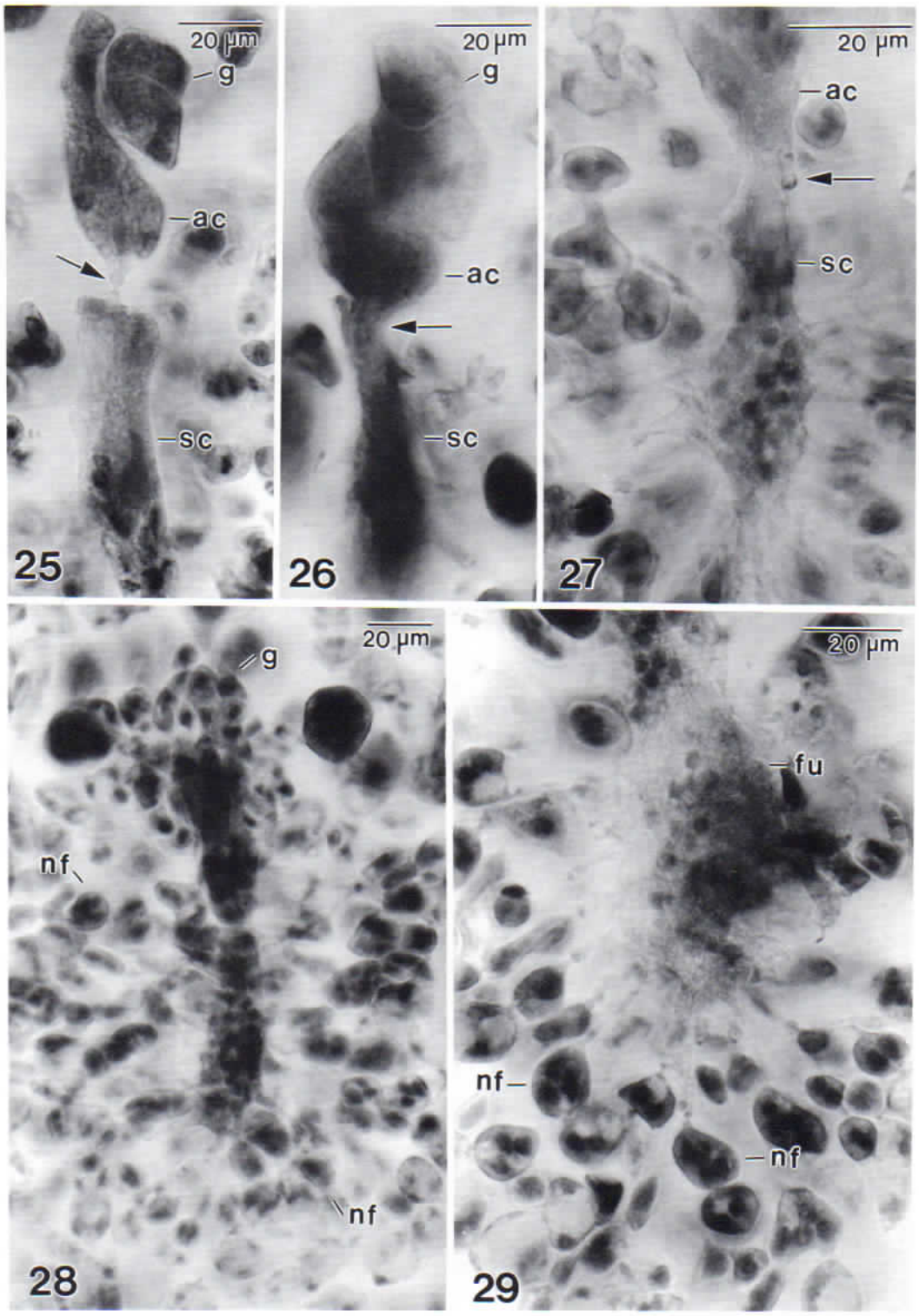
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Ancud, Chiloë, is *A. antarcticus*, but its geographical origin requires reinvestigation.

HABITAT: The larger, more robust specimens come from wave-exposed habitats in the vicinity of Cape Horn (Fig. 2), and from Puerto Deseado, Santa Cruz, Argentina (Joly *et al.* 1964). Plants from more northerly latitudes along the coast of Chile and from the Falkland Islands are usually narrower and less robust.

Vegetative morphology

Plants are uniaxial, with a single wedge-shaped apical cell that protrudes slightly at the apex (Figs 10–12). An apical cell has two oblique faces from which it alternately cuts off axial segments by concavo-convex septa at angles of 50–60°. Successive divisions (Figs 11, 12) alternate to one side and then the other, generating a file of axial cells in a zig-zag pattern. Each axial cell cuts off a single periaxial cell from its upper side in an alternate-distichous arrangement (Figs 11, 12, 14). A periaxial cell first produces the initial of the leading determinate filament (Fig. 12). When this filament is 2–3 cells long, laterals are initiated obliquely on opposite sides that also develop into ascending, branched cortical filaments.

Branching of the cortical filaments is initially irregularly trichotomous or subdichotomous. Approximately 6–7 cells behind the apex, inner cells expand into isodiametric shapes, except for the basal periaxial cell, which first expands but later becomes elongated (Figs 12, 14). Subcortical cells may generate as many as five or six lateral filaments as the thallus elongates and expands, forming an outer cortex two or three layers thick and composed of progressively smaller, predominantly uninucleate or binucleate, subovoid to subspherical cortical cells (Figs 16, 18). Surface cortical cells are of nearly uniform size (Fig. 10), and contain a single, parietal, lobed chloroplast. Both medullary and cortical cells typically include one to few spherical globules, separate from the chloroplasts, that stain darkly with aniline blue (Fig. 13).

Rhizoidal initials issue from periaxial cells approximately 10 segments below the apex (Figs 12, 13). Close to the apex they arise singly, primarily from the upper sides of periaxial cells, and produce ascending, septate rhizoids (Figs 13, 15), although they may also originate in lesser numbers from lower sides and form descending rhizoidal filaments. Lower down the axis, additional rhizoidal filaments are produced on periaxial cells and inner cortical cells, which are either added to the central core surrounding the axial filament, or grow between the medullary and inner cortical cells (Figs 16–19). Rhizoids form numerous secondary pit connections with axial cells, inner cortical cells and each other (Fig. 15). As a result, most cells in the interior of the thallus become multinucleate. Rhizoids may be localized primarily in a central bundle with only a few filaments distributed between medullary and cortical cells (Figs 7–9, 16, 18; Kützing 1868, pl. 17, *'Cystoclonium obtusangulum'*), or may branch secondarily, becoming abundant between medullary and inner cortical cells in the main axes or towards the base (Figs 17, 19; Hooker 1847, pl. 181, fig. 3; Joly *et al.* 1964, figs 4–7, 10, 11).

Axial cells start to elongate within a few cells of the apices in vegetative tips (Fig. 12), becoming up to 120 μm long (Fig. 14). Pit connections linking axial cells progressively enlarge up to 10 μm in diameter (Fig. 14). Cortical filaments ascend at a steep angle (> 60°) alongside two or more successive axial segments (Figs 11, 12). As a result, the inflated cells surrounding any given axial cell, together with the core of rhizoidal cells seen in cross-section (Figs 18, 19), are derived

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Figs 25–29. *Acanthococcus antarcticus. Searles, Leister & Brauner 73-1-29.* Female reproductive system.
Fig. 25. Detail of multinucleate supporting cell (sc) showing pit connection (arrow) to distal auxiliary cell (ac) and 2-celled gonimoblast (g).
Fig. 26. Auxiliary cell (ac) fused (arrow) to supporting cell (sc) and bearing a 2-celled gonimoblast (g).
Fig. 27. Remnant of pit plug (arrow) between fused auxiliary cell (ac) and supporting cell (sc). Nutritive filaments have become linked to supporting cell, which now contains many nuclei.
Fig. 28. Gonimoblasts (g) arising from fusion cell and surrounded by nutritive filaments (nf). Gonimoblast cells are uninucleate; cells of nutritive filaments are mostly multinucleate.
Fig. 29. Close-up of nutritive filaments (nf) linked by secondary pit connections to multinucleate fusion cell (fu).

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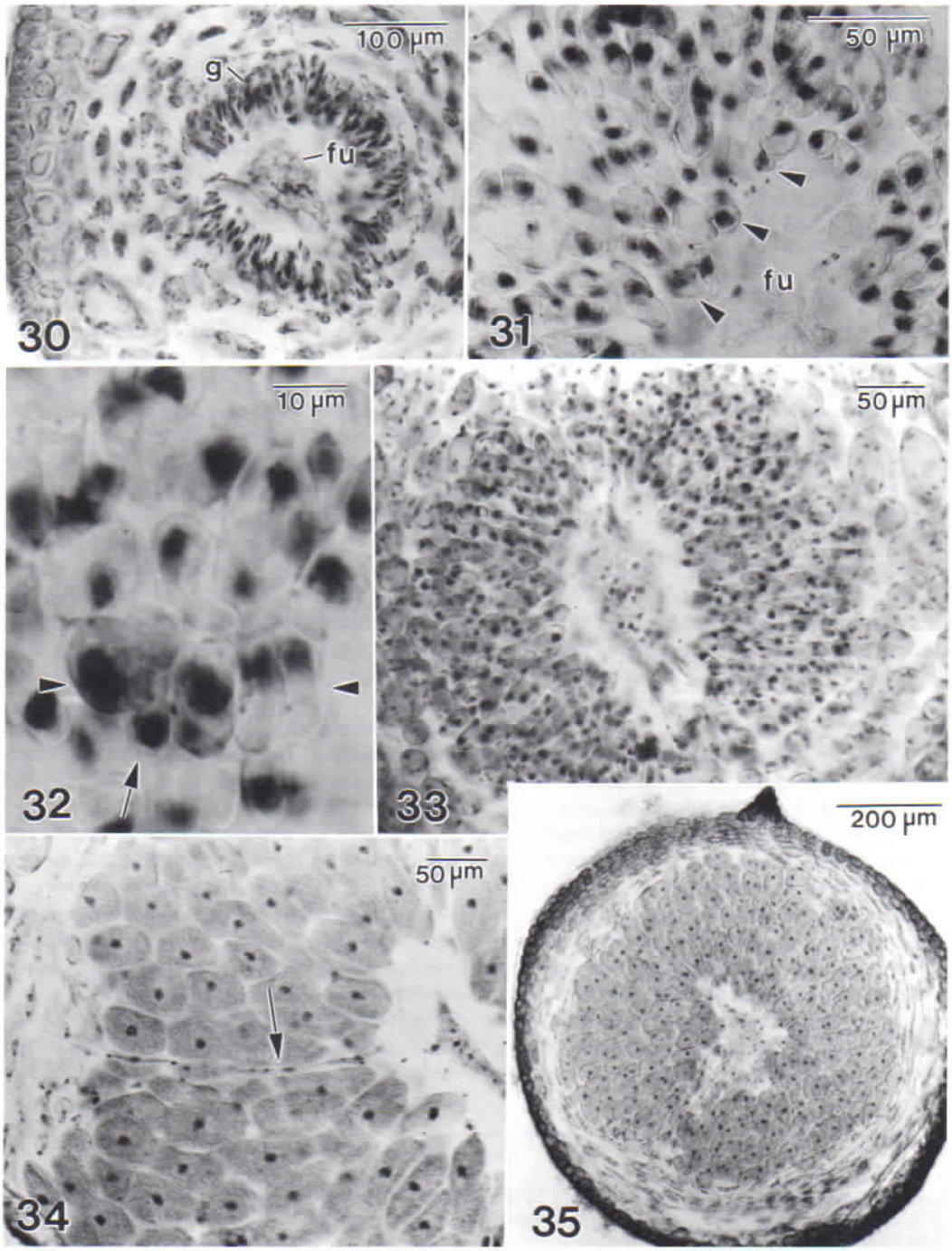

Figs 30–35. *Acanthococcus antarcticus. Searles, Leister & Brauner 73-33-11.* Female reproductive system.
Fig. 30. Cross-section showing early gonimoblasts (g) surrounding fusion cell (fu).
Fig. 31. Gonimoblast filaments cutting off conjunctor cells (arrows) that are fusing on to the fusion cell (fu).
Fig. 32. Innermost gonimoblast cells that have divided anticlinally (between arrowheads). One conjunctor cell is visible (arrow).
Fig. 33. Branched gonimoblast filaments directed outwardly, and linked by secondary pit connections to fusion cell.

from two or more files of overlapping cortical filaments on each side.

Female reproduction

Carpogonial branches are formed near the apices of ultimate branchlets. The supporting cell is an intercalary cortical cell borne on a periaxial cell. It can either be the suprabasal cell of the leading cortical filament or the corresponding cell of a lateral filament. Occasionally, more than one carpogonial branch is produced in adjacent branches of the same filament system. The carpogonial branch initial is cut off adaxially from the supporting cell and develops into a 3-celled carpogonial branch directed towards the thallus apex (Fig. 20). The supporting cell elongates, becoming crescent-shaped at maturity (Figs 20, 21). Prior to fertilization, all cells of the carpogonial branch, the supporting cell, and the auxiliary cell are uninucleate (Fig. 21). The hypogynous cell is the largest cell of the young carpogonial branch (Fig. 20), although at maturity the basal cell reaches the same size as the hypogynous cell (Fig. 21). The carpogonium is more or less conical, remains small, and bears a straight to slightly curved trichogyne directed towards the thallus surface (Fig. 20). There are no sterile cells on any of the carpogonial branch cells.

The auxiliary cell lies just distal to the supporting cell and is linked to it by a primary pit connection (Fig. 21). Prior to fertilization, it is barely distinguishable in shape from the surrounding cortical cells (Figs 20, 21). The fertilization nucleus is transferred to the auxiliary cell, probably as a result of direct fusion of the carpogonium with the auxiliary cell. The diploidized auxiliary cell is binucleate, containing a central haploid nucleus and a proximal diploid nucleus (Fig. 22). The basal and hypogynous cells of the carpogonial branch are still visible at this stage, but they soon disintegrate.

Carposporophyte development

Following presumed fertilization, cortical cells distal to the auxiliary cell become densely staining and their nuclei replicate and enlarge. Concurrently, the supporting cell extends in length parallel to the central axis and short, densely staining, branched nutritive filaments develop from the surrounding rhizoidal and medullary cells and grow towards the supporting cell (Figs 22–24). In contrast to the darker staining distal filaments, which are transformed from pre-existing cortical cells, the nutritive filaments below are produced secondarily.

The auxiliary cell cuts off a single gonimoblast initial towards the thallus interior by an oblique, concavo-convex division (Figs 23, 24). Pit connections between the auxiliary cell and the modified distal cortical cells enlarge (Fig. 23), and the secondary nutritive filaments become linked to the supporting cell. Terminal cells of nutritive filaments fuse directly on to the supporting cell, depositing their nuclei (Fig. 24) and leaving behind secondary pit connections. By the time the gonimoblast is 2-celled, the supporting cell already contains several nuclei derived from nutritive cells (Fig. 25). Ultimately, all of the nutritive filaments become linked to the supporting cell, with the deposition of many nuclei (Figs 27–29). The auxiliary cell fuses with the supporting cell (Fig. 26) around the primary pit connection (Fig. 27), and inner gonimoblast cells also fuse with it (Figs 26, 29). Young gonimoblast cells at the anterior end of the fusion cell are readily distinguished because they are uninucleate (Fig. 28). The nutritive cells linked to the supporting cell are mostly multinucleate, stain darkly at this stage, and their pit connections broaden (Figs 28, 29). Ultimately, the outline of the supporting cell, auxiliary cell and fused inner gonimoblast cells becomes indistinct, and the fusion cell rounds up.

Gonimoblast filaments that were initially localized at the anterior end of the supporting cell (Fig. 28) continue to divide until the carposporophyte completely surrounds the fusion cell (Figs 30, 33). Apical gonimoblast cells adjacent to the fusion cell divide anticlinally as the gonimoblasts spread, followed by periclinal divisions (Fig. 32) forming branched chains up to six cells in length that radiate outwardly (Figs 30, 33). The innermost gonimoblast cells cut off conjunctor cells (Figs 31, 32) basally that unite with the fusion cell, leaving behind secondary pit connections

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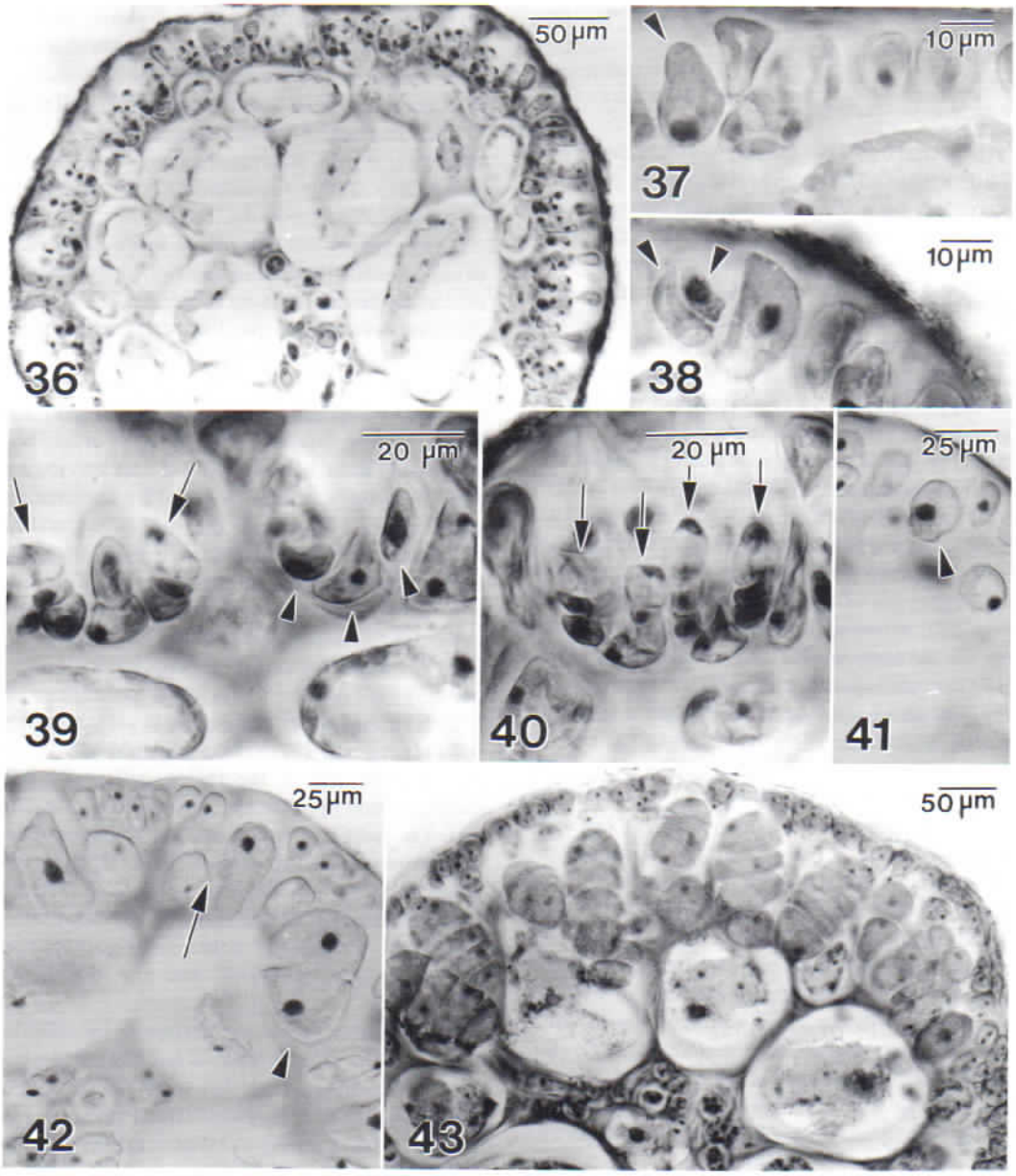
Fig. 34. Fusion cell bearing chains of carposporangia and stretched, remnant cortical filament (arrow).
Fig. 35. Cross-section of mature cystocarp with central fusion cell and chains of carposporangia filling the cystocarp cavity.



Figs 36–43. *Acanthococcus antarcticus.* Male (*Searles, Leister & Brauner 73-35-50*) and tetrasporangial (*Searles, Leister & Brauner 72-19-70*) reproductive systems.

Fig. 36. Cross-section of mature male reproductive structures organized in shallow, superficial sori.

Fig. 37. Spermatangial parent-cell initial (arrowhead).

Fig. 38. Two-celled spermatangial filament (arrowheads).

Fig. 39. Right, 3-celled spermatangial filament (arrowheads); left, sorus of branched spermatangial filaments bearing terminal spermatangia (arrows).

Fig. 40. Sorus of spermatangial filaments bearing terminal spermatangia (arrows).

Fig. 41. Terminal tetrasporocyte (arrowhead).

Fig. 42. Centre, tetrasporocyte laterally pit-connected (arrow) to its bearing cell; right, tetrasporocyte (arrowhead) after first division.

Fig. 43. Cross-section of mature tetrasporangia surrounded by elongated cortical cells and outer covering of cortical filaments.

(Fig. 33). Both cortical and secondary nutritive filaments lose their stainable contents and become indistinct in old cystocarps. All gonimoblast cells that are not incorporated into the fusion cell become carposporangia (Figs 34, 35), there being no sterile gonimoblast cells in the mature cystocarp. Except for an occasional stretched inner cortical filament (Fig. 34), the entire space between the fusion cell and the surrounding cortex becomes filled with branched chains of carposporangia up to six cells long (Figs 34, 35). A strongly developed multilayered pericarp and ostiole are lacking (Fig. 35). Cystocarps are sessile, hemispherical, subglobose, wider than the subtending branch (Figs 2, 3), and may bear up to six spiny outgrowths (Hooker 1847, pl. 181).

Male reproduction

Male reproductive structures occur on separate plants in shallow sori (Fig. 36) covering the thallus surface on the higher-order branches. Sorus development begins with the transformation of a terminal cortical cell into the primordium of a spermatangial filament. This cell loses its plastid, stains uniformly with haematoxylin, and its nucleus enlarges and stains darkly (Fig. 37). The cell divides obliquely, first to one side (Fig. 38) and then to the other (Fig. 39). Each of the resulting three cells may function directly as a spermatangial parent cell, or may undergo transverse and oblique divisions that extend the spermatangial filaments (Figs 39, 40). Terminal cells cut off a single, hyaline, uninucleate spermatangium in which the nucleus is displaced towards the apex (Figs 39, 40). Cortical cells adjacent to spermatangial filaments elongate to form the borders of the soral cavity (Figs 36, 39, 40).

Tetrasporangial reproduction

Mature tetrasporangia are scattered over the surface of higher order branches. They are zonately cleaved (Fig. 43) and embedded amongst the cortical filaments. Tetrasporocytes (Figs 41, 42) are terminal cortical cells that may be distinguished from neighbouring vegetative cells by the presence of an enlarged nucleus. At first a tetrasporocyte initial is connected to its bearing cell by a basal pit connection, but as the initial enlarges, increasing in length from its inner side, the pit connection comes to lie laterally at mid-level. Although pit connections are often difficult to see and persist for only a short time, the shape of the distended initial provides a reliable indication of the previous position of this pit connection (Fig. 42).

Cortical cells adjacent to a tetrasporocyte elongate, becoming stretched and thin as the initial expands. Surface cells continue to divide, covering the mature tetrasporangia (Fig. 43). Tetrasporangia cleave successively twice in the same plane, resulting in the formation of regularly zonately arranged tetraspores. Tetrasporangia are 50–100 μm long and 20–50 μm wide at maturity (Fig. 43).

DISCUSSION

Acanthococcus possesses all the familial characters that Kylin (1932, 1956) considered to be diagnostic of the Cystocloniaceae. The distinguishing generic characters of *Acanthococcus* within the family are: (1) axial cells each bearing one periaxial cell; (2) 3-celled carpogonial branch, with the hypogynous cell initially broader than the basal cell; (3) nutritive filaments produced after diploidization of the auxiliary cell, becoming linked by secondary pit connections to the elongated supporting cell largely before fusion cell formation; (4) spermatangia in sori borne on spermatangial filaments that develop from surface primordial cells.

Thallus growth is initiated by a wedge-shaped apical cell with two oblique cutting faces throughout the Cystocloniaceae. In other genera, each axial cell cuts off two periaxial cells at an angle of 90° in an alternating sequence (Kylin 1932, 1956; Min-Thein & Womersley 1976). *Acanthococcus* appears to be unique among the genera of the Cystocloniaceae in that each axial cell cuts off only one periaxial cell. Comparable single periaxials per axial cell are encountered in the uniaxial genera *Rhabdonia, Areschougia* and *Melanema* of the Solieriaceae (Min-Thein & Womersley 1976, as the Rhabdoniaceae). We interpret the single periaxial cell of *Acanthococcus* as an advanced character that evolved in combination with other changes in filament ontogeny at the thallus apex and independently from similar arrangements in solieriaceous genera. The potential loss of structural components in the axes that might result from halving the number of cortical filaments per axial cell is achieved in two ways in *Acanthococcus*: (1) each leading cortical filament extends alongside two axial cells above the bearing cell on one side of the thallus,

thus filling in the gaps; and (2) inner cortical cells produce up to four secondary filaments (5–6 filaments in total), which fill in the cortex as the thallus elongates and expands.

Acanthococcus antarcticus is characterized by ascending and descending rhizoidal filaments that form a central bundle around the axial filament surrounded by one or two layers of swollen medullary cells, later extending between the medullary and cortical cells to just beneath the thallus surface. Descending rhizoids are abundant in *Cystoclonium* (Kylin 1923, 1956), and are usually present to some degree in other members of the Cystocloniaceae and in the Solieriaceae, where they are often generated in species-specific patterns. The initially ascending rhizoids that characterize *Acanthococcus antarcticus* appear to be unique among the genera of the Cystocloniaceae, although ascending rhizoids have been reported in species of *Agardhiella* (Solieriaceae; Gabrielson & Hommersand 1982b). Enlarged inner cells that are separated from the central axis and each other by a network of bridging filaments are characteristic of *Mychodea* of the Mychodeaceae (Kraft 1978), several species of which had previously been placed in *Acanthococcus*. The early production of rhizoidal filaments from periaxial and inner cortical cells and their tendency to form numerous secondary pit connections with adjacent cells of all types rapidly obscures the basic uniaxial organization of the thallus.

The male reproductive system of *Acanthococcus* differs from that typically encountered in the Cystocloniaceae, where spermatangial parent cells are cut off outwardly, either from untransformed terminal surface cells or from surface cells in a rosette configuration (Kylin 1956; Min-Thein & Womersley 1976; Hansen 1980). In *Acanthococcus*, terminal cortical cells are first modified into spermatangial filament primordia, which then divide to form chains of spermatangial parent cells that cut off single spermatangia to the outside. The resulting spermatangial sori of *Acanthococcus* bear a resemblance to the 'pits' or 'conceptacles' that are found in species of *Gracilaria* in which spermatangial parent cells are also generated in filaments (Fredericq & Hommersand 1989). Further observations may reveal that this type of spermatangial sorus is more widespread in the Cystocloniaceae than existing studies have indicated.

In *Acanthococcus* no lateral filaments are borne on the carpogonial branch cells, such as occur in *Cystoclonium* (Kylin 1923). The basal and hypogynous cells are laterally expanded and contain an enlarged nucleus. Although the carpogonial branch resembles that of other members of the Cystocloniaceae or *Hypnea* (Hypneaceae; Kylin 1956), in none of these genera are the proximal cells of the carpogonial branch as enlarged as in *Acanthococcus*.

Cortical filaments distal to the auxiliary cell enlarge and become densely staining after fertilization, and either before or immediately following diploidization of the auxiliary cell in *Acanthococcus*. The resulting structure resembles the auxiliary cell complex formed prior to diploidization of the auxiliary cell in *Solieria* and *Agardhiella* of the Solieriaceae (Gabrielson & Hommersand 1982a, 1982b). Cortical filaments distal to the auxiliary cell are transformed into a nutritive tissue in other genera belonging to the Cystocloniaceae and Hypneaceae, but it is unclear, at present, whether cells proximal to the auxiliary cell are similarly modified. However, in no instance has the supporting cell been shown to elongate after fertilization in the manner observed in *Acanthococcus*.

The suite of characters listed by Gabrielson & Kraft (1984) as being diagnostic of the Solieriaceae includes files of cells cut off around the auxiliary cell following diploidization, but prior to gonimoblast initiation. These files may or may not consolidate to form a distinct pericarp. This feature is also found in most members of the Cystocloniaceae and Hypneaceae. Such files of cells probably function as nutritive filaments that become linked in some characteristic way, either directly with the gonimoblasts or with a fusion cell. Details vary in different genera, and are unknown in many instances. *Acanthococcus* appears to be unique in that the nutritive filaments formed after fertilization become directly linked to the elongated supporting cell through fusion of terminal cells prior to the formation of a central fusion cell.

Examples of cases where gonimoblast cells link with vegetative nutritive cells, either through direct fusion or by means of secondary pit connections, are widespread among the Rhodophyta (Hommersand & Fredericq 1990). However, the opposite behaviour, in which secondary nutritive filaments initiate the fusion process, is less common and, to our knowledge, only occurs in some members of the Cystocloniaceae and Hypneaceae. In *Cystoclonium*, for example, cells at the ends of nutritive filaments elongate and fuse directly on to the highly ramified gonimoblast

fusion cell in the vicinity of the carposporangial chains (Thrainsson 1986). At present, direct linkage of nutritive filaments to the supporting cell or fusion cell is known only in *Cystoclonium purpureum* (Hudson) Batters and *Acanthococcus antarcticus*, but it may well occur in other cystocloniaceous genera.

In *Acanthococcus*, as in other members of the Cystocloniaceae, outer gonimoblast filaments are converted into chains of carposporangia that abut against the stretched inner cells of the pericarp. Some thickening of the pericarp takes place in *Acanthococcus* due to resumption of outward growth of the surface cortical filaments, but a massive pericarp is not produced, nor do sterile gonimoblast filaments form extensions or processes that link up with cells in the outer pericarp, as in some species of *Rhodophyllis*, *Craspedocarpus*, and *Calliblepharis* from Australia (Min-Thein & Womersley 1976), and *Hypnea musciformis* from North Carolina (Hommersand & Fredericq 1990). Ostiole-like structures are sometimes formed in these genera, but not in *Acanthococcus*.

Tetrasporangia are generally described as being scattered or localized in sori, either on the thallus surface or on proliferations in the Cystocloniaceae. The somewhat nemathecial character of the tetrasporangial sori in *Acanthococcus*, in which the neighbouring sterile cells are markedly elongated and the surface cells divide and branch to form a cover above the tetrasporangia, may be a specialized feature of this genus within the Cystocloniaceae.

The procarpial family Cystocloniaceae is proving to be as diverse an assemblage and as rich in genera and species as the non-procarpial family Solieriaceae. It is represented by some very distinct genera in boreal and antiboreal waters, as well as in the warm-temperate regions of the Atlantic and Indian oceans (Hommersand 1990). New morphological studies of the other genera of the Cystocloniaceae are required to elucidate the phylogeny and biogeography of the entities referred to this family.

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REFERENCES

AGARDH C.A. 1822. *Species Algarum . . . Vol. 1.* Mauritius, Greifswald, 189 pp.

AGARDH J.G. 1849. Algologiska bidrag. *Öfversight af Förhandlingar: Kongelige Svenska Vetenskaps-Akademien* **6:** 79–89.

AGARDH J.G. 1852. *Species Genera et Ordines Algarum . . . Vol. 2(2)*, pp. 337–786. C. W. K. Gleerup, Lund.

AGARDH J.G. 1876. *Species genera et ordines algarum . . . Vol. 3(1)*, Weigel, Leipzig, vii + 724 pp.

DE TONI, G.B. 1897. *Sylloge algarum . . . Vol. 4 (Florideae)*. Privately published, Padua, xx + lxi + 386 pp.

FREDERICQ S. & HOMMERSAND M.H. 1989. Proposal of the Gracilariales ord. nov. (Rhodophyta) based on an analysis of the reproductive development of *Gracilaria verrucosa*. *Journal of Phycology 25:* 213–227.

GABRIELSON P.W. & HOMMERSAND M.H. 1982a. The Atlantic species of *Solieria* (Gigartinales, Rhodophyta). Their morphology, distribution and affinities. *Journal of Phycology* **18:** 31–45.

GABRIELSON P.W. & HOMMERSAND M.H. 1982b. The morphology of *Agardhiella subulata* representing the Agardhielleae, a new tribe in the Solieriaceae (Gigartinales, Rhodophyta). *Journal of Phycology* **18:** 46–58.

GABRIELSON P.W. & KRAFT G.T. 1984. The marine algae of Lord Howe Island (N.S.W.): the family Solieriaceae (Gigartinales, Rhodophyta). *Brunonia* **7:** 217–251.

GEPP A. & GEPP E.S. 1905. Antarctic algae. *Journal of Botany* **43:** 105–109, pl. 470.

GUIRY M.D. 1978. Notes on some family names of Florideophyceae (Rhodophyta). *Taxon* **27:** 191–195.

HANSEN G.I. 1980. A morphological study of *Fimbrifolium*, a new genus in the Cystocloniaceae (Gigartinales, Rhodophyta). *Journal of Phycology* **16:** 207–217.

HARIOT P.A. 1889. Algues. In: *Mission Scientifique du Cap Horn, 1882-1883. Vol. 5*, pp. 3–119, pl. 10. *Botanique*. Gauthier-Villars et fils, Paris.

HOLMGREN P.K., KEUKEN W. & SCHOFIELD E.K. 1981. *Index Herbariorum, I. The Herbaria of the World*, 7th edn. Bohn, Scheltema & Holkema, Utrecht, 452 pp. [*Regnum Vegetabile* vol. 106].

HOMMERSAND M.H. 1990. Biogeography of the marine red algae of the North Atlantic Ocean. In: *Evolutionary Biogeography of the Marine Algae of the North Atlantic* (Ed. by D.J. Garbary & G.R. South), pp. 349–410. NATO Advanced Science Institutes

Series G: Ecological Sciences, Vol. 22. Springer-Verlag, Berlin.

HOMMERSAND M.H. & FREDERICQ S. 1988. An investigation of cystocarp development in *Gelidium pteridifolium* with a revised description of the Gelidiales (Rhodophyta). *Phycologia* **27:** 254–272.

HOMMERSAND M.H. & FREDERICQ S. 1990. Sexual reproduction and cystocarp development. In: *Biology of the Red Algae* (Ed. by K.M. Cole & R.G. Sheath), pp. 305–345. Cambridge University Press, New York.

HOOKER J.D. 1847. Algae. In: *The Botany of the Antarctic Voyage of H.M. Discovery ships 'Erebus' and 'Terror' in the Years 1839–1843 . . . Vol. I. Flora antarctica. . . Part II. Botany of Fuegia, the Falklands, Kerguelen's Land, etc. (1845–1847)*, pp. 209–574. Reeve, London.

HOOKER J.D. & HARVEY W.H. 1845. Algae antarcticae . . . *London Journal of Botany* **4:** 249–276.

JOLY A.B., CORDEIRO M. & YAMAGUISHI N. 1964. La estructura y reproducción de *Acanthococcus antarcticus* Hooker et Harvey. *Boletin del Instituto de Biologia Marina (Mar del Plata)* **5:** 1–9.

KRAFT G.T. 1978. Studies of marine algae in the lesser-known families of the Gigartinales (Rhodophyta). III. Mychodeaceae and Mychodeophyllaceae. *Australian Journal of Botany* **26:** 515–610.

KÜTZING F. 1843. *Phycologia generalis* . . . Brockhaus, Leipzig, xxxii + 458 pp.

KÜTZING F. 1849. *Species Algarum* . . . Brockhaus, Leipzig, vi + 922 pp.

KÜTZING F. 1867. *Tabulae phycologicae* . . . Vol. 17. Privately published, Nordhausen, 30 pp. + 100 pls.

KÜTZING F. 1868. *Tabulae phycologicae* . . . Vol. 18, Privately published, Nordhausen, 35 pp. + 100 pls.

KYLIN H. 1923. Studien über die Entwicklungsgeschichte der Florideen. *Kongelige Svenska Vetenskapsakademiens Handlingar* **63** (11): 1–139.

KYLIN H. 1932. Die Florideenordnung Gigartinales. *Lunds Universitets Årsskrift, N.F., Avd. 2* **28**(8): 1–88 pp., 28 pls.

KYLIN H. 1956. *Die Gattungen der Rhodophyceen.* C.W.K. Gleerup, Lund, xv + 673 pp.

KYLIN H. & SKOTTSBERG C. 1919. Zur Kenntnis der subantarktischen und antarktischen Meeresalgen. II. Rhodophyceen. In: *Wissenschaftliche Ergebnisse der schwedischen süd-polar Expedition 1901–1903, Vol. 4* (Ed. by O. Nordenskjöld). Lithographisches Institut des General stabs, Stockholm. 88 pp, 1 pl.

MIN-THEIN U. & WOMERSLEY H.B.S. 1976. Studies on Australian taxa of Solieriaceae, Rhabdoniaceae, and Rhodophyllidaceae (Rhodophyta). *Australian Journal of Botany* **24:** 1–166.

MOE R.L. & DELACA T.E. 1976. Occurrence of macroscopic algae along the Antarctic Peninsula. *Antarctic Journal of the United States* **11:** 20–24.

PAPENFUSS G.F. 1964. Catalogue and bibliography of Antarctic and subantarctic benthic marine algae. *Antarctic Research Series, Washington* **1:** 1–76.

PUJALS C. 1963. Catálogo de Rhodophyta citadas para la Argentina. *Revista del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (Botánica)* **3:** 1–139.

PUJALS C. 1977. Adiciones y correcciones al 'Catálogo de Rhodophyta citadas para la Argentina.' *Revista del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (Botánica)* **5:** 123–163.

REINBOLD T. 1908. Die Meeresalgen der deutchen Südpolar-Expedition 1901–1903. In: *Deutsche Südpolar Expedition 1901–1903, Vol. 8* (Ed. by E. Von Drygalski), pp. 177–202. Botanik, Berlin.

SCHMITZ [C.J.] F. 1892. [6. Klasse Rhodophyceae] 2. Unterklasse Florideae. In: *Syllabus der Vorlesungen über specielle und medicinische-pharmaceutische Botanik. Grosse Ausgabe* (Ed. by A. Engler), pp. 16–23. Gebrüder Borntraeger, Berlin.

THRAINSSON S.A. 1986. Morphological studies on some members of the family Cystocloniaceae (Gigartinales, Rhodophyta). Unpublished MA thesis, University of North Carolina at Chapel Hill, 101 pp.

WITTMANN W. 1965. Aceto-iron-haematoxylin-chloral hydrate for chromosome staining. *Stain Technology* **40:** 161–164.

WYNNE M.J. & KRAFT G.T. 1981. [Appendix]. Classification summary. In: *The Biology of Seaweeds, Botanical Monographs Vol. 17* (Ed. by C.S. Lobban & M.J. Wynne), pp. 743–750. Blackwell Scientific Publications, Oxford.

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