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# New perspectives in the taxonomy of the Gigartinaceae (Gigartinales, Rhodophyta)

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## Abstract

A revised description of the Gigartinaceae is provided, together with a key and short diagnosis of each genus and a list of the species examined. New combinations have been proposed where appropriate. Distinguishing cystocarp and tetrasporangial characters useful for separating genera are illustrated, and the distribution of the genera is shown on a world map.

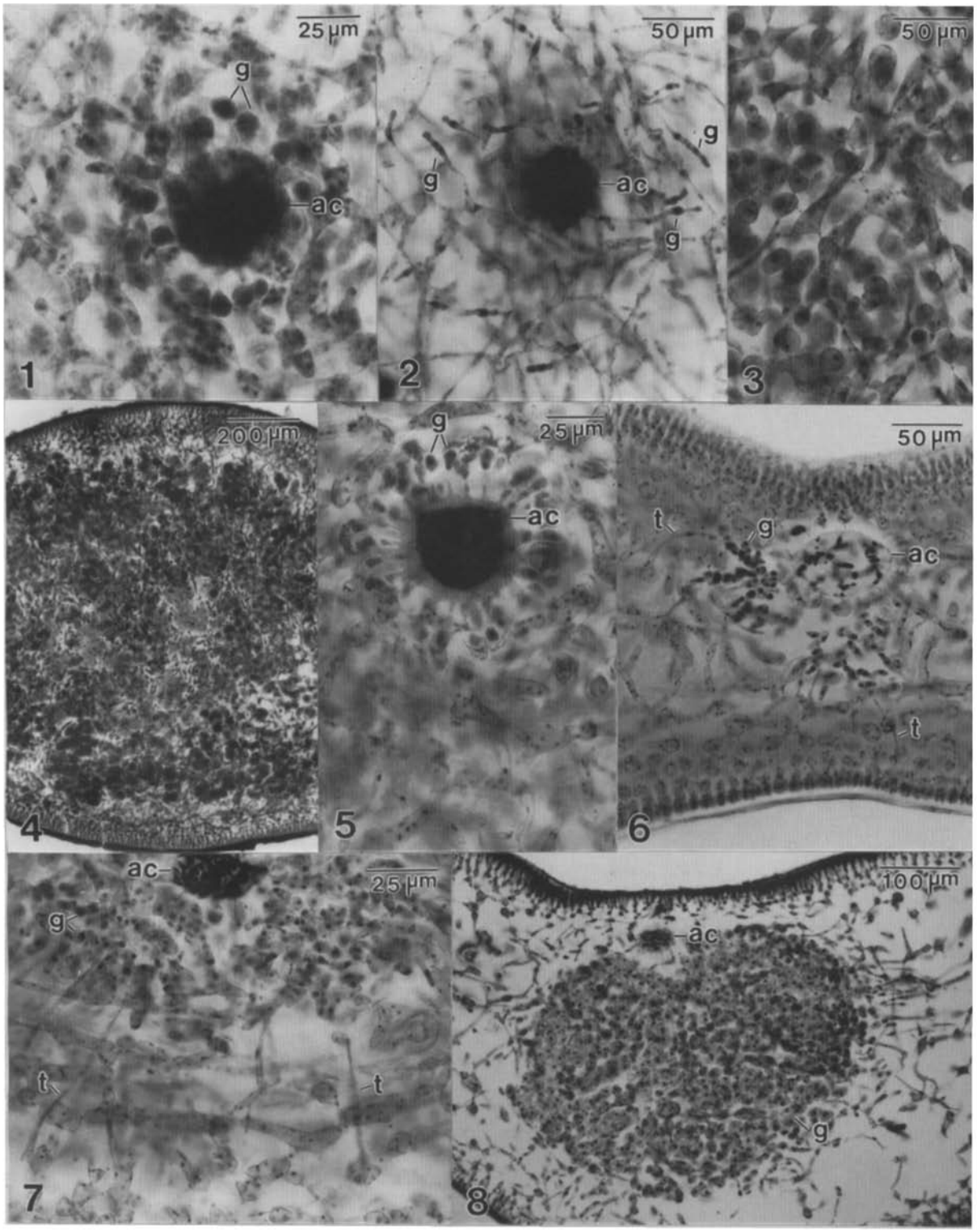
## Introduction

Four genera are generally accepted as belonging to the Gigartinaceae: *Chondrus* Stackhouse, *Gigartina* Stackhouse, *Iridaea* Bory *nom. cons.* and *Rhodoglossum* J. Agardh (Guiry & Garbary, 1990). *Chondracanthus* Kützing, *Mazzaella* G DeToni f., *Iridophycus* Setchell et gardner, *Sarcothalia* Kützing and *Chondrodictyon* Kützing are legitimate names currently placed in synonymy under other genera. We here present a revised description of the Gigartinaceae, a key and brief diagnosis of each of the seven genera we recognize, and a list of 69 species examined. Key diagnostic characters are illustrated for the type species of each genus (Figs 1–40), and the distribution of the genera is shown on a world map (Fig. 41). Synonymus species, doubtful species, and species not seen by us have been left out. Where known, the location of the Type or Lectotype specimens is given in brackets after the basionym, followed by an exclamation mark [!] if we have examined the type. Herbarium abbreviations follow Holmgren *et al.* (1990).

## Materials and methods

Material examined in this study was fixed and preserved in 5–10% Formalin/seawater. Transverse, longitudinal and periclinal sections were stained with aceto-iron-hematoxylin-chloral hydrate (Wittmann, 1965) and mounted in 1:1 Hoyer's mounting medium:water according to the procedure of Hommersand *et al.* (1992), or stained with 1% aniline blue and mounted in 50% Karo® corn syrup. Photographs were taken with a Zeiss photomicroscope III using Pan-X or T-Max film.

Collection data for the taxa illustrated in Figs 1–40 are: *Chondrus crispus* Stackhouse, lower intertidal, Sidmouth, Devon, U.K., 5.v.91, J. Brodie; *Mazzaella californica* (J. Agardh) G. DeToni f., 17 mile Drive, Pebble Beach,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Monterey Co, California, USA, 20.vi.74, M. H. Hommersand; *Iridaea cordata* (Turner) Bory, Bahia Buen Suceso, Tierra del Fuego, Argentina, 23.iv.73, Meñez & Shinn (SOSC#71-2-8, Ref. 592); *Sarcothalia stiriata* (Turner) Leister comb. nov., Platboombaai, Cape Peninsula, So. Africa, 9.xii.77, M. H. Hommersand; *Rhodoglossum lanceolatum* (Harvey) J. Agardh, drift, Elwood, Victoria, Port Phillip Bay, Australia, 3.i.82, P. W. Gabrielson & M. L. May; *Chondracanthus chamissoi* (C. Agardh) Kützing, Ancon, Peru, 22.xii.76, M. H. Hommersand; *Gigartina pistillata* (S. G. Gmelin) Stackhouse, Santec, Brittany, France, 12.vi.91, J. Cabioch.

## Revised description of the Gigartinaceae Bory (1828:149, 'Gigartineae')

Basal holdfast discoid or crustose, of limited extent bearing few to many erect thalli; erect juvenile thalli initially cylindrical with a dome-shaped apex; adult thalli cylindrical, compressed or flattened, dichotomously or pinnately branched to foliose, smooth or proliferating from the margin or surface, or the tetrasporophyte smooth and the gametophyte proliferously branched. Growth monopodial, multiaxial, fountain-type, composed initially of converging adaxial and radiating abaxial pseudodichotomously branched filaments; meristem apical, extending along the margin, or dispersed over the thallus surface. Conjunctor cells cut off laterally from intercalary cells close to surface and forming secondary pit connections; primary filaments spreading to form a network in which every cell is characteristically linked to each of its neighboring cells by a single primary or secondary pit connection. Cortex typically 6–8 layers thick; cortical filaments subdichotomously branched, composed of spherical to rod-shaped cells. Medulla thin or thick, increasing in thickness secondarily through transformation of inner cortical cells into medullary cells; secondary filaments few to many, usually descending, forming short chains 1–2(–3) cells long, linked terminally by secondary pit connections, sometimes rhizoidal.

Gametophytes dioecious, sometimes monoecious. Spermatangial sori forming extensive patches, superficial or slightly nemathecial; spermatangial parent cell transformed from surface cell and cutting off 1–2 spermatangia. Procarp initiated from terminal cell of a leading cortical filament at thallus surface and consisting of a supporting cell, a terminal 3-celled carpogonial branch, and a lateral vegetative cortical filament; carpogonial branch initial cut off by concavo-convex septum from supporting cell, dividing twice anticlinally by concavo-convex divisions and producing a curved carpogonial branch with the carpogonium directly above or adjacent to supporting cell; supporting cell and cells of carpogonial branch, except the carpogonium, multinucleate at maturity. Carpogonium fusing with supporting cell ( = auxiliary cell) after fertilization; diploid nucleus transferred directly to auxiliary cell, which ultimately contains a mixture of large haploid nuclei containing amplified levels of DNA, and smaller diploid nuclei; auxiliary cell enlarging and forming enucleate protrusions, each of which may receive a diploid nucleus and cut off a gonimoblast initial. Secondary filaments absent or present, produced from inner cortical or medullary cells in vicinity of a functional auxiliary cell, if present forming a loose network or organized into a compact envelope around the auxiliary cell. Gonimoblast filaments ramifying freely through the medulla and secondary filaments, or displacing the envelope, or penetrating it and linking to envelope cells by direct fusions, secondary pit connections, or terminal tubular gonimoblast cells; envelope evanescent or persistent, present in mature cystocarps. Carposporangial chains produced directly from gonimoblasts, and some-

Female reproduction. *Figs 1–4. Chondrus crispus. Fig. 1.* Auxiliary cell (ac) bearing gonimoblast initials (g). *Fig. 2.* Auxiliary cell (ac) bearing gonimoblast filaments (g). *Fig. 3.* Portion of network bearing carposporangial chains. *Fig. 4.* Mature cystocarp. *Figs 5–8. Mazzaella californica. Fig. 5.* Auxiliary cell (ac) bearing gonimoblast initials (g). *Figs 6 & 7.* Auxiliary cell (ac) and gonimoblast filaments (g) with terminal tubular cells (t) fusing with cells of medulla and cortex. *Fig. 8.* Mature cystocarp.

times also from heterokaryotic medullary or envelope cells that have received diploid nuclei. Carposporangia uninucleate, borne in short unbranched or branched chains with the ends free, or linked by secondary pit connections to cells in other filaments; carpospores released at maturity through breaks in the wall or through a preformed ostiole, followed by the production of secondary filaments and wall repair.

Tetrasporangial sori circular to elliptical, sometimes confluent, either immersed within cortex, generated progressively at boundary between cortex and medulla, or produced entirely within the medulla. Tetrasporocytes uninucleate, borne in chains transformed from primary cortical filaments (which may be nemathecial), from lateral branches on primary cortical filaments, or in secondary filaments initiated from inner cortical or medullary cells and, then, usually linked to other cells in neighboring filaments by secondary pit connections; specific developmental features characteristic of the genus or species. Tetrasporangia cleaving successively; tetraspores cruciately arranged, released by gelatinous extrusion through breaks or pores in the wall, or by excision of entire sorus, followed by the production of secondary filaments in the damaged area and wall repair.

Life history of the *Polysiphonia*-type, the gametophyte and tetrasporophyte generations being of similar size and morphology; mixed-phase reproduction occasionally occurring.

References: Kylin (1956), Kim (1976), Guiry & Garbary (1990).

*Key to the genera of the Gigartinaceae (see Figs 1–40)*

1. Functional auxiliary cell forming numerous lateral and inwardly directed protrusions bearing gonimoblast initials, not surrounded by an envelope... 2
1. Functional auxiliary cell forming few, inwardly directed protrusions bearing gonimoblast initials, surrounded by an envelope composed of secondary filaments... 3

2. Gonimoblast filaments diffuse, filiform, penetrating between the medullary and secondary filaments, often linking to them by secondary pit connections; inner gonimoblast cells remaining narrow. Tetrasporangia borne in secondary filaments formed entirely within the medulla... ***Chondrus***
2. Gonimoblast filaments compact, short-celled, displacing the medulla and secondary filaments, often linking to them by terminal tubular cells; inner gonimoblast cells expanding, becoming broad. Tetrasporangia transformed from primary cortical cells, or borne in secondary filaments originating from inner cortical or medullary cells...***Mazzaella***

3. Gonimoblast filaments displacing the envelope which forms a distinct boundary penetrated only by tubular gonimoblast cells... 4
3. Gonimoblast filaments penetrating between cells of the envelope, linking to them with formation of heterokaryotic cells, and surrounded by an outer envelope... 6

4. Gonimoblast filaments irregularly branched, uniting to form a network linked by secondary pit connections; carposporangia borne in clusters inside network. Tetrasporangia in depressed nemathecial crypts, formed in rows by repeated transverse division of superficial cortical cells... ***Rhodoglossum***
4. Gonimoblast filaments radiating inwardly, subdichotomously branched, initially free and separate. Tetrasporangia not in depressed crypts...5

5. Inner gonimoblast filaments composed of narrow, cytoplasm-rich cells linked by broadened primary pit connections at maturity. Tetrasporangia transformed from cells in primary cortical filaments...***Iridaea***
5. Inner gonimoblast filaments composed of expanded cells which may become linked by secondary pit connections at maturity; pit connections not broadening secondarily. Tetrasporangia borne in secondary filaments initiated from clusters of medullary cells, the

filaments radiating and linking progressively to neighboring medullary cells...***Sarcothalia***

6. Carposporangial chains derived entirely from gonimoblast filaments, often separated by large sterile cells that are not organized into a network. Tetrasporangia transformed from cells in primary filaments within the cortex, the tetraspores released through pores in wall...***Chondracanthus***

6. Carposporangial chains derived from gonimoblast filaments and sometimes also heterokaryotic envelope cells, forming grape-like clusters separated by a network of sterile filaments. Tetrasporangia formed progressively at boundary between cortex and medulla, mostly in secondary filaments; tetraspores released by excision of entire sorus...***Gigartina***.

*Generic diagnoses*

*Chondrus* Stackhouse 1791:xv. Figs 1–4, 28–29
Type: *Chondrus crispus* Stackhouse, 1797:xxiv; basionym: *Fucus crispus* Linnaeus, 1767:134 *nom. illeg.*, non *Fucus crispus* Hudson, 1762:472 [see Papenfuss, 1950:19].

Growth by apical and marginal meristems; thalli compressed to flattened, dichotomously branched or foliose, sometimes with marginal or superficial proliferations. Gametophytes dioecious, rarely monoecious; procarps initiated at apex or along margin, cystocarps distributed over surface; auxiliary cell subspherical, forming protrusions and gonimoblast initials in all directions; secondary medullary filaments absent, few, or abundant, not organized into an envelope around the auxiliary cell; gonimoblast filaments narrow, filiform, loosely branched, growing between the medullary or secondary filaments; intercalary gonimoblast cells linking to swollen medullary and secondary cells by conjunctor cells forming secondary pit connections; carposporangia formed in branched chains or clusters from gonimoblast cells and sometimes also from heterokaryotic medullary cells; cystocarps inflated on one or both surfaces, sometimes ocellate; carpospores released through breaks in outer wall. Tetrasporangial sori circular to elliptical, filling the medulla or localized along its outer edges; tetrasporangia in short chains borne in secondary filaments initiated from medullary cells and linked to other medullary cells by secondary pit connections; tetraspores released by gelatinous extrusion through multiple pores or breaks in wall.

Distribution: boreal.

*Chondrus crispus* Stackhouse, 1797:xxiv [LINN] (N. Atlantic)
*Chondrus nipponicus* Yendo, 1920:4 [TI!] (Japan, Korea)
*Chondrus giganteus* Yendo, 1920:4 [TI] (Japan)
*Chondrus pinnulatus* (Harvey) Okamura, 1930:19 [TCD] (Japan, Korea, E. Siberia)
*Chondrus ocellatus* Holmes, 1895:252, pl. 9, figs 2a–c [BM?] (Japan, Korea, China)
*Chondrus yendoi* Yamada et Mikami in Mikami, 1965:236 [SAP] (Japan)
*Chondrus verrucosus* Mikami, 1965:248, pl. 9, figs 1a,b [SAP] (Japan)
*Chondrus elatus* Holmes, 1895:252 [BM?] (Japan, Korea)
*Chondrus canaliculatus* (C. Agardh) Greville, 1830:LV [LD!] (Peru, Chile)

References: Mikami (1965), Brodie *et al.* (1991), Fredericq *et al.* (1992)

*Mazzaella* G. DeToni f., May 1936, substitute for *Collinsia* J. Agardh 1899:78, non Nuttall, 1817. Figs 5–8, 30–31
Type: *Collinsia californica* J. Agardh, 1899:79. [LD!]. [Taxonomic synonym: *Iridophycus* Setchell et Gardner, Aug. 1936:469; type: *I. capensis* (J. Agardh) Setchell et Gardner, 1936:470; basionym: *Iridaea capensis* J. Agardh, 1847:85]. [LD!]

Growth by apical, marginal or diffuse meristems; thalli dichotomously branched to foliose, smooth or with marginal or superficial proliferations. Gametophytes dioecious; procarps and cystocarps mostly scattered, sometimes in papillae; auxiliary cell subspherical, forming protrusions and gonimoblast initials in all directions; envelope absent; secondary filaments few to

many, typically composed of short, rectangular cells linked to medullary cells by terminal secondary pit connections; gonimoblast filaments initially composed of repeatedly branched subrectangular cells; terminal tubular cells formed successively at the gonimoblast periphery, fusing with medullary cells and cells of secondary filaments; inner gonimoblast cells enlarging, becoming multinucleate and bearing chains or clusters of carposporangia laterally; carpospores released through breaks in the outer wall. Tetrasporangial sori circular to elliptical, situated in the inner cortex or outer medulla; tetrasporangia in branched chains transformed from cells in primary cortical filaments or secondary lateral filaments initiated from cortical or medullary cells and linked to other cells by secondary pit connections; tetraspores released through a central pore or breaks in the outer wall.

Distribution: Japan, Pacific N. Amer., Pacific S. Amer., Gough I., S. Africa.

*Mazzaella californica* (J. Agardh) G. DeToni f., Not. Nomencl. Alg. 7 [4]. May 1936 (N. British Columbia to N. Baja Calif.)

*Mazzaella japonica* (Mikami) Hommersand comb. nov. (western N. Pacific, Japan, Korea, E. Siberia)

Basionym: *Rhodoglossum japonicum* Mikami, Sci. Papers Inst. Algol. Res. Hokkaido Univ. 5:264, figs 46–50, pl. 10, fig. 1. 1965. [SAP]

*Mazzaella cornucopiae* (Postels et Ruprecht) Hommersand comb. nov. (N. Pacific from Japan to N. California)

Basionym: *Iridaea cornucopiae* Postels et Ruprecht, Illustr. Algarum, p. 18, pl. 38, fig. b. 1840. [LE]

*Mazzaella lilacina* (Postels et Ruprecht) Leister comb. nov. (Alaska to N. Baja Calif.)

Basionym: *Iridaea lilacina* Postels & Ruprecht, Illustr. Algarum.., p. 17. 1840. [LE, Abbott!]

*Mazzaella flaccida* (Setchell et Gardner) Fredericq, comb. nov. (Alaska to N. Baja Calif.)

Basionym: *Iridophycus flaccidus* Setchell et Gardner, Proc. Nat. Acad. Sci. USA, 23:171. 1937. [UC!]

*Mazzaella rosea* (Kylin) Fredericq comb. nov. (Alaska to Baja Calif.)

Basionym: *Iridaea rosea* Kylin, Lunds Univ. Årsskr., N.F., Avd. 2. 37:24, pl. 9, fig. 22. 1941. [LD!]

*Mazzaella affinis* (Harvey) Fredericq comb. nov. (Alaska to Baja Calif.)

Basionym: *Chondrus affinis* Harvey in Hooker and Arnott, The Botany of Captain Beechy's voyage... p. 408. 1841. [TCD]

*Mazzaella heterocarpa* (Postels et Ruprecht) Fredericq comb. nov. (S.E. Alaska to S. Calif.)

Basionym: *Iridaea heterocarpa* Postels et Ruprecht, Illustr. Algarum.., p. 18. 1840. [LE]

*Mazzaella linearis* (Setchell et Gardner) Fredericq comb. nov. (S.E. Alaska to S. Calif.)

Basionym: *Iridophycus lineare* Setchell & Gardner, Proc. Natl. Acad. Sci. (USA)., 23:171. 1937. [UC]

*Mazzaella leptorhynchos* (J. Agardh) Leister comb. nov. (Calif., Baja Calif.)

Basionym: *Gigartina leptorhynchos* J. Agardh, Lunds Univ. Årsskr., 21(8):28. 1885. [LD!]

*Mazzaella volans* (C. Agardh) Fredericq comb. nov. (N. Oregon to Baja Calif.)

Basionym: *Sphaerococcus volans* C. Agardh, Icon. Alg. Ined., Fasc. 2, pl. 18. 1821. [LD!]

*Mazzaella cobinae* (Dawson) Fredericq comb. nov. (Pacific Baja Calif.)

Basionym: *Rhodoglossum cobinae* Dawson, Pacific Naturalist. 2:256, pl. 47. 1961. [LAM!]

*Mazzaella hancockii* (Dawson) Fredericq comb. nov. (Gulf of Calif., Peru)

Basionym: *Rhodoglossum hancockii* Dawson, Allan Hancock Pac. Exped. 3:304, pl. 71, fig. 1. 1944. [LAM!]

*Mazzaella denticulata* (Dawson, Acleto et Foldvik) Fredericq comb. nov. (Peru, Chile)

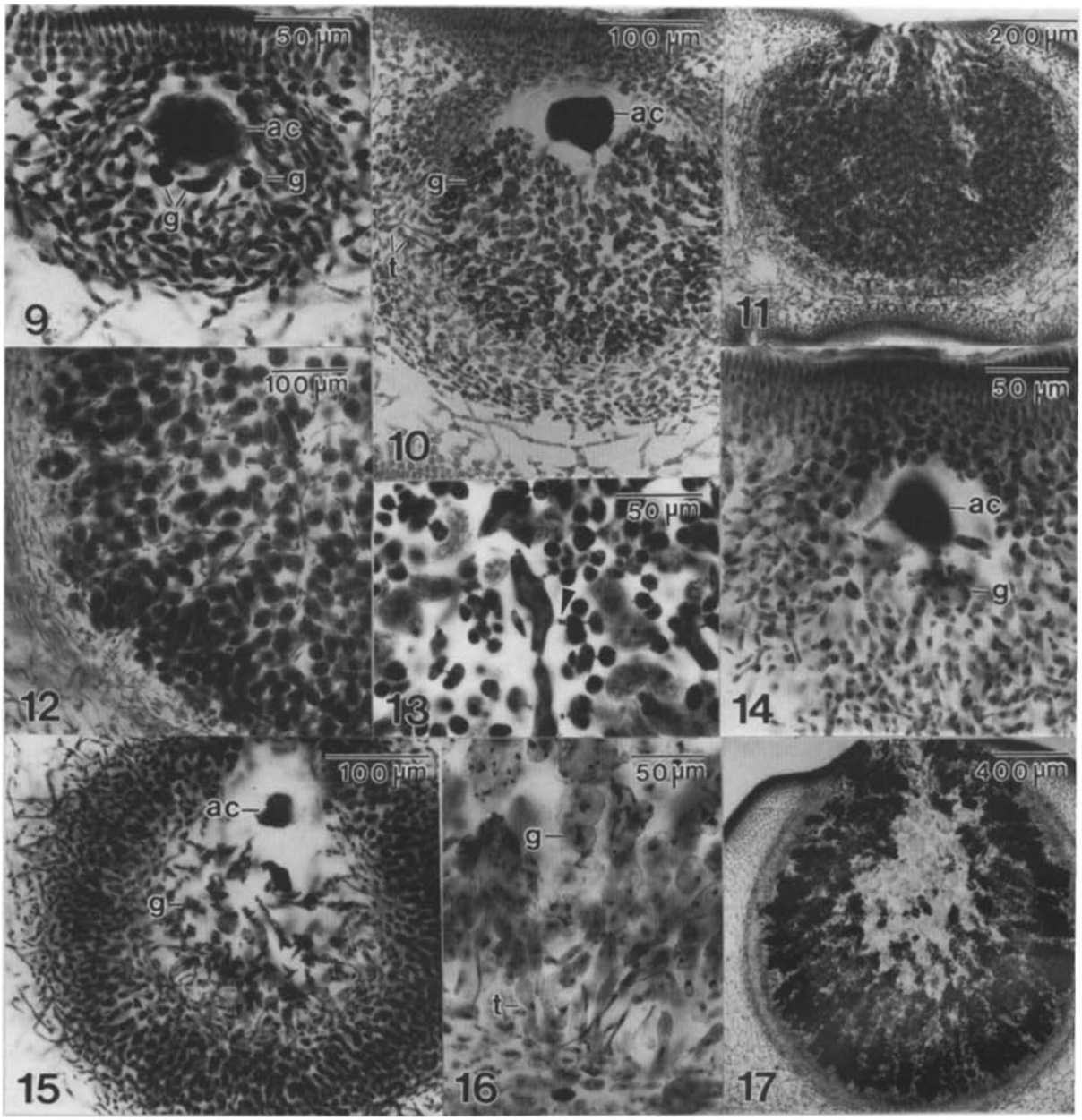
Basionym: *Rhodoglossum denticulatum* Dawson, Acleto et Foldvik, Beih., Nova Hedwigia 13:69, pl. 54, fig. c. 1964. [LAM!]

*Mazzaella membranacea* (J. Agardh) Fredericq comb. nov. (Chile)

Basionym: *Iridaea membranacea* J. Agardh, Lunds Univ. Årsskr. 8(6):8. 1872. [LD!]

*Mazzaella laminarioides* (Bory) Fredericq comb. nov. (Chile, Argentina, Falkland Is, Gough I.)

Basionym: *Iridaea laminarioides* Bory in Duperrey, Voyage autour du Monde sur...'La




Female reproduction. *Figs 9–13; Iridaea cordata.* Fig. 9. Auxiliary cell (ac) bearing gonimoblast initials (g) surrounded by envelope. *Fig. 10.* Auxiliary cell (ac) and homogenous mass of gonimoblast cells (g) with tubular terminal gonimoblast cells (t) penetrating envelope. *Figs 11–12.* Mature cystocarp with radiating gonimoblast filaments, carposporangial chains, and tubular gonimoblast cells penetrating envelope. *Fig. 13.* Portion of mature cystocarp showing enlarged pit connections between gonimoblast cells (arrowhead). *Figs 14–17. Sarcothalia stiriata. Fig. 14.* Auxiliary cell (ac) with young gonimoblast filaments (g), and envelope. *Figs 15–16.* Older cystocarp with gonimoblast filaments, envelope, and terminal tubular gonimoblast cells (t) fusing with cells of envelope. *Fig. 17.* Mature cystocarp.

Coquille'...Botanique, p. 105, pl. 11, fig. 1. 1828. [PC!]

*Mazzaella capensis* (J. Agardh) Fredericq comb. nov. (western Cape, South Africa)

Basionym: *Iridaea capensis* J. Agardh, K. svenska Vet.-Akad. Förh., 4:85, pl. 1, 1847. [as *Iridaea capense*]. [LD!]

*Iridaea* Bory, 1826:15, *nom. cons.* Figs 9–13, 32–33

Type: *Iridaea cordata* (Turner) Bory, 1826:16; basionym: *Fucus cordatus* Turner Fuci 2:118, pl. 116. 1809. [E!]

Growth by apical, marginal, or diffuse meristems; vegetative thalli dichotomously branched or foliose. Gametophytes dioecious; cystocarps immersed to strongly protruding; auxiliary cell forming few protrusions and gonimoblast initials from inner side, surrounded by a compact envelope; gonimoblast filaments radiating inwardly, displacing envelope, filiform, pseudodichotomously branched, and bearing small lateral clusters of carposporangia between the radial filaments; pit connections between inner gonimoblast cells enlarging at a late stage of cystocarp development; tubular gonimoblast cells penetrating the envelope, fusing with envelope cells; carpospores released by breakdown of wall overlying auxiliary cell. Tetrasporangial sori circular, separate or confluent, localized in subcortex; tetrasporangia in branched chains derived by transformation of primary cortical cells; tetraspores released by gelatinous extrusion through a central pore in wall.

Distribution: antiboreal.

*Iridaea cordata* (Turner) Bory, 1826:16 (Cape Horn, Antarctica, Falkland Is., Scotia Sea, Is. West Wind Drift) [See Leister, 1977].

*Iridaea tuberculosa* (J. D. Hooker et Harvey) Leister comb. nov. (Chile, Cape Horn, Antarctica, Falkland Is., Tristan da Cunha, Gough I., Is. Campbell Plateau).

Basionym: *Chondrus tuberculosa* J. D. Hooker et Harvey, in W. H. Harvey and J. D. Hooker, Algae. In J. D. Hooker. The Botany of the Antarctic Voyage... Vol 1, pt. 1, p. 188. 1845. [BM!, TCD!]

*Sarcothalia* Kützing, 1849:739. Figs 14–17, 34–35

Type: *Sarcothalia burmannii* (C. Agardh) Kützing, 1849:739; basionym: *Sphaerococcus burmannii* C. Agardh, 1822:272 [LD!] [ = *Sarcothalia stiriata* (Turner) Leister comb. nov.].

Growth by apical, marginal or diffuse meristems; thalli dichotomously branched or foliose, mostly dimorphic, with proliferously branched gametophytes and smooth tetrasporophytes; procarps and cystocarps in branchlets, pinnae or papillae, rarely superficial; auxiliary cell forming few protrusions and gonimoblast initials from inner side, surrounded by a compact envelope; gonimoblast filaments radiating inwardly, displacing the envelope, irregularly subdichotomously branched; inner gonimoblast cells expanding, becoming multinucleate, later often interconnecting by means of secondary pit connections, the rest bearing lateral clusters of carposporangia between the radiating filaments; pit connections between gonimoblast cells not enlarging secondarily; terminal tubular gonimoblast cells broad to narrow, fusing with envelope cells; carpospores released by rupture of wall overlying auxiliary cell. Tetrasporangia in small, circular sori in the inner cortex and outer medulla; tetrasporangia borne in chains in secondary filaments that typically originate from a small cluster of medullary cells, branch radially, and link at intervals to other cortical and medullary cells by secondary pit connections; tetraspores released by gelatinous extrusion through a central pore in the wall.

Distribution: antiboreal.

*Sarcothalia stiriata* (Turner) Leister comb. nov. (South Africa, Tristan da Cunha).

Basionym: *Fucus stiriatus* Turner, Fuci, 1:32, pl. 16. 1808. [BM!]

*Sarcothalia convoluta* (Areschoug ex J. Agardh) Hommersand comb. nov. (Cape Province, S. Africa)

Basionym: *Gigartina convoluta* Areschoug ex J. Agardh, Lunds Univ. Årsskr. Afd. 2, 35(4):32. 1899. [Isotype LD!]

*Sarcothalia lapathifolia* (Kützing) Leister comb. nov. (Cape Province, South Africa)

Basionym: *Iridaea lapathifolia* Kützing, Sp. Alg., p. 729. 1849. [L!].

*Sarcothalia scutellata* (Hering) Leister comb. nov. (W. Cape, South Africa)

Basionym: *Gigartina scutellata* Hering, Ann. Mag. Nat. Hist. 8:91. 1841. [HBG, see Simons, 1983]

*Sarcothalia marginifera* (J. Agardh) Hommersand comb. nov. (N. New Zealand)

Basionym: *Gigartina marginifera* J. Agardh, Sp. Gen. et Ord. Alg. 3(1):196, 683. 1876. [LD!]

*Sarcothalia livida* (Turner) Hommersand comb. nov. (New Zealand)

Basionym: *Fucus lividus* Turner, Fuci 4:140, pl. 254. 1819. [BM!]

*Sarcothalia decipiens* (J. D. Hooker et Harvey) Hommersand comb. nov. (New Zealand)

Basionym: *Iridaea decipiens* J. D. Hooker et Harvey, J. Bot., London 4:547. 1845. [BM!]

*Sarcothalia atropurpurea* (J. Agardh) Hommersand comb. nov. (New Zealand, Australia?)

Basionym: *Iridaea atropurpurea* J. Agardh, Sp. Gen. et Ord. Alg. 3(1):181. 1876. [LD!]

*Sarcothalia circumcincta* (J. Agardh) Hommersand comb. nov. (New Zealand, Is. Campbell Plateau)

Basionym: *Gigartina circumcincta* J. Agardh, Sp. Gen. et Ord. Alg. 3(1):202. 1876. [LD!]

*Sarcothalia lanceata* (J. Agardh) Hommersand comb. nov. (S. New Zealand, Is. Campbell Plateau)

Basionym: *Gigartina lanceata* J. Agardh, Lunds Univ. Årsskr., Afd. 2, 35(4):28–29. 1899. [LD!]

*Sarcothalia crispata* (Bory) Leister comb. nov. (Chile, Argentina, Falkland Is., Tristan da Cunha, Gough I.)

Basionym: *Iridaea crispata* Bory, Dict. Class. Hist. Nat. 9:16. 1826. [PC!]

*Sarcothalia dichotoma* (J. D.Hooker et Harvey) Leister comb. nov. (Argentina, Falkland Is.).

Basionym: *Iridaea dichotoma* J. D. Hooker et Harvey, J. Bot., London 4:262. 1845. [BM!]

*Sarcothalia papillosa* (Bory) Leister comb. nov. (Cape Horn, Scotia Sea, Grahamsland, Falkland Is.)

Basionym: *Iridaea papillosa* Bory, Dict. Class. Hist. Nat. 9:16. 1826. [PC!]

*Rhodoglossum* J. Agardh, 1876:183. Figs 18–21, 36–37

Lectotype: *Rhodoglossum lanceolatum* (Harvey) J. Agardh, 1876:186; basionym: *Gigartina lanceolata* Harvey, 1860:326. [TCD, Isolectotype BM!]

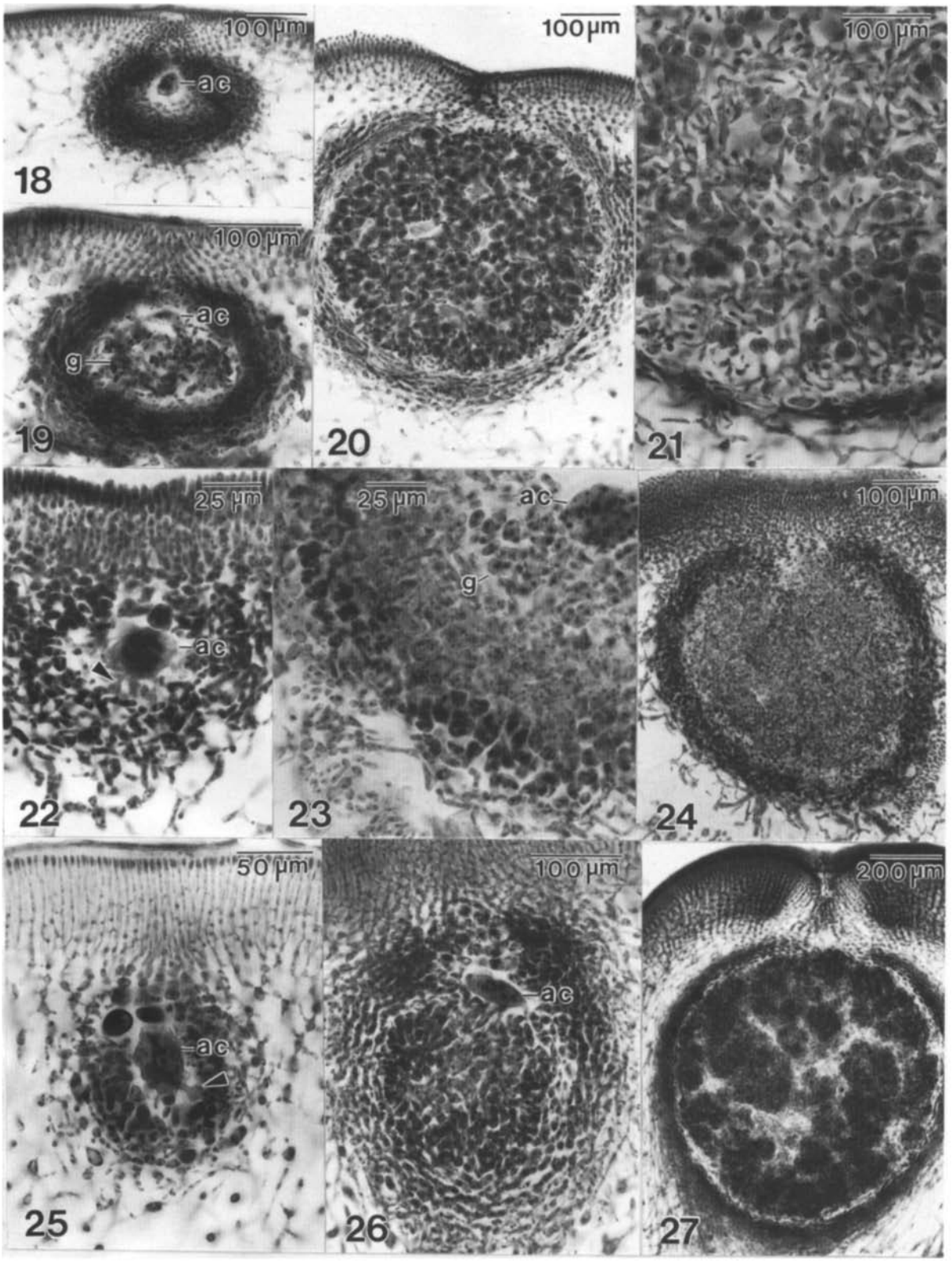
Growth by marginal and diffuse meristems; thalli foliose, smooth, entire or with marginal proliferation. Gametophytes dioecious; procarps and cystocarps scattered over thallus surface; auxiliary cell forming few protrusions and gonimoblast initials from inner side, surrounded by a compact envelope composed of rectangular cells; gonimoblasts irregularly branched, displacing envelope; inner gonimoblast cells enlarging, becoming multinucleate, the rest filiform, linked to one another by secondary pit connections forming an open network; carposporangia borne in small clusters separated by the gonimoblast network; terminal tubular cells short, fusing severally to envelope cells; ostiole present, small, formed by transverse division of surface cortical cells; carpospores released through ostiole and gaps formed by separation of surface cortical filaments. Tetrasporangial sori small, circular, nemathecial, forming crypts beneath wall; tetrasporangia in straight, unbranched chains formed by repeated transverse division of superficial cortical cells; tetraspores released by breakdown of outer wall.

Distribution: S. Australia, New Zealand, Is. Campbell Plateau. *Rhodoglossum lanceolatum* (Harvey) J. Agardh, 1876:186.

*Chondracanthus* Kützing, 1843:399. Figs 22–24, 38

Type: *Chondracanthus chauvinii* (Bory) Kützing, 1843:400; basionym: *Sphaerococcus chauvinii* Bory, 1828:165, pl. 20. [PC!]. [ = *C. chamissoi* (C. Agardh) Kützing, 1843:399; see Dawson *et al.*, 1964:66].

Growth by apical and marginal meristems; thalli pinnately branched or foliose, typically bearing numerous vegetative pinnules or papillae. Gametophytes dioecious or monoecious; procarps initiated near apex on ordinary branchlets, pinnules or papillae; auxiliary cell forming few protrusions and gonimoblast initials from inner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side, surrounded by a compact envelope divisible into inner vacuolate and outer cytoplasm-rich layers; gonimoblast filaments penetrating inner layer and linking to envelope cells by secondary pit connections late in cystocarp development; carposporangia in short chains interspersed among sterile gonimoblast and enlarged envelope cells; terminal tubular gonimoblast cells fusing with cells of outer envelope; pericarp and ostiole sometimes present, formed early in cystocarp development by resumed growth of cortical filaments. Tetrasporangial sori small to large, sometimes nemathecial, localized in inner cortex; tetrasporangia in branched chains, transformed from cells in primary cortical filaments; secondary tetrasporangial filaments absent; tetraspores released by gelatinous extrusion through pores in outer wall.

Distribution: Japan, Pacif. N. & S. America, N. & S. Atlantic Ocean.

*Chondracanthus tenellus* (Harvey) Hommersand comb. nov. (Japan, Korea, China)

Basionym: *Gigartina tenella* Harvey, Proc. Amer. Acad. Arts, Sci. 4:331. 1859. [TCD, Isotype BM!].

*Chondracanthus intermedius* (Suringar) Hommersand comb. nov. (Japan, Korea, China)

Basionym: *Gigartina intermedia* Suringar, Algae Japonicae, p. 30, pl. 17B. 1870. [L?].

*Chondracanthus tepidus* (Hollenberg) Guiry comb. nov. (Pacific N. Amer.)

Basionym: *Gigartina tepida* Hollenberg, Amer. J. Bot. 32:449, fig. 5. 1945. [US!].

*Chondracanthus canaliculatus* (Harvey) Guiry comb. nov. (Oregon to Baja Calif.)

Basionym: *Gigartina canaliculata* Harvey in W. J. Hooker and Arnott, The Botany of Captain Beechy's Voyage, p. 409. 1841. [TCD, Isotype L!]

*Chondracanthus harveyanus* (Kützing) Guiry comb. nov. (British Columbia to central Baja California)

Basionym: *Mastocarpus harveyanus* Kützing, Sp. Alg. 734.1849. [L!]

*Chondracanthus spinosus* (Kützing) Guiry comb. nov. (S.E. Alaska to Baja California)

Basionym: *Mastocarpus spinosus* Kützing, Bot. Zeit. 5:24. 1847. [L]

*Chondracanthus corymbiferus* (Kützing) Guiry comb. nov. (British Columbia to central Baja California.)

Basionym: *Mastocarpus corymbiferus* Kützing, Bot. Zeit. 5:24. 1847. [L!]

*Chondracanthus johnstonii* (Dawson) Guiry comb. nov. (Gulf of California.)

Basionym: *Gigartina johnstonii* Dawson, Allan Hancock Pac. Exped. 3:302. 1944. [LAM]

*Chondracanthus macdougalii* (Dawson) Guiry comb. nov. (Gulf of California.)

Basionym: *Gigartina macdougalii* Dawson, Allan Hancock Pac. Exped. 3:303, pl. 64, fig. 2. 1944. [LAM!]

*Chondracanthus glomeratus* (Howe) Guiry comb. nov. (Peru)

Basionym: *Gigartina glomerata* Howe, Mem. Torrey Bot. Club 15:103, pl. 39, pl. 40, figs 1–11. 1914. [NY!].

*Chondracanthus chamissoi* (C. Agardh) Kützing, Phycologia generalis, p. 399. 1843. (Peru, Chile)

Basionym: *Sphaerococcus chamissoi* C. Agardh, Icones algarum ineditae, Fasc. 1, pl. 10. 1820. [LD!, Isotype E!].

*Chondracanthus teedii* (Roth) Kützing, Phycologia generalis, p. 399. 1843. (N. & S. Atlantic Ocean)

Basionym: *Ceramium teedii* Roth, Cat. Bot. 3:108, pl. 4. 1806. [BM-partim!]

*Chondracanthus elegans* (Greville in Saint-Hilaire) Guiry comb. nov. (Brazil, Uruguay)

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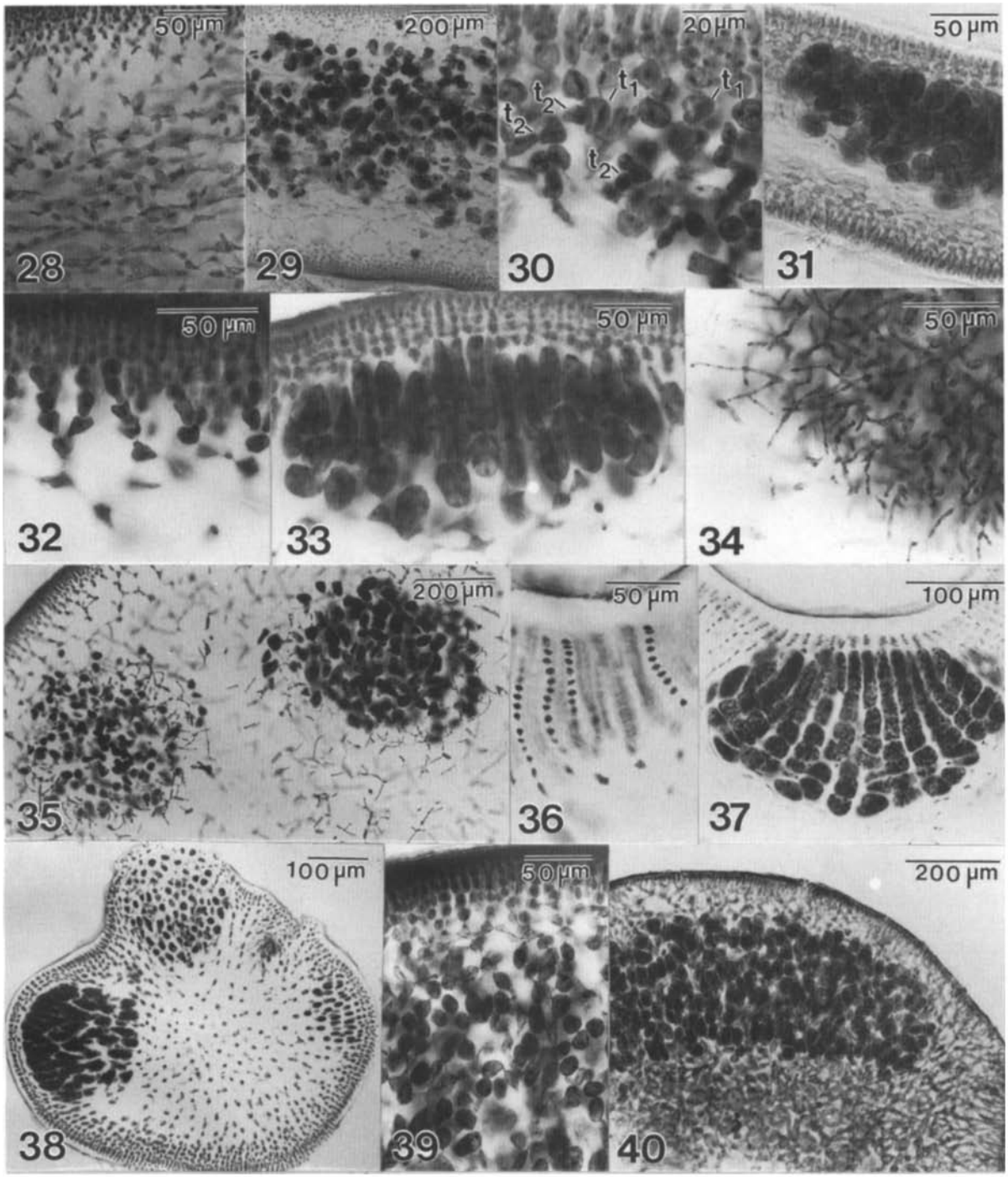
Female reproduction. *Figs 18–21. Rhodoglossum lanceolatum. Fig. 18.* Auxiliary cell (ac) surrounded by envelope. *Fig. 19.* Auxiliary cell (ac) bearing irregularly branched gonimoblast filaments (g). *Figs 20–21.* Mature cystocarp with gonimoblast network bearing carposporangia. *Figs 22–24. Chondracanthus chamissoi. Fig. 22.* Auxiliary cell (ac) with protrusions (arrowhead), surrounded by envelope. *Fig. 23.* Auxiliary cell (ac) with gonimoblast filaments (g). Note lighter inner and darker outer layers of envelope. *Fig. 24.* Mature cystocarp. *Figs 25–27. Gigartina pistillata. Fig. 25.* Auxiliary cell (ac) with protrusions (arrowhead) surrounded by envelope. *Fig. 26.* Auxiliary cell (ac) bearing mixture of gonimoblasts (g) and vegetative cells surrounded by envelope. *Fig. 27.* Mature cystocarp.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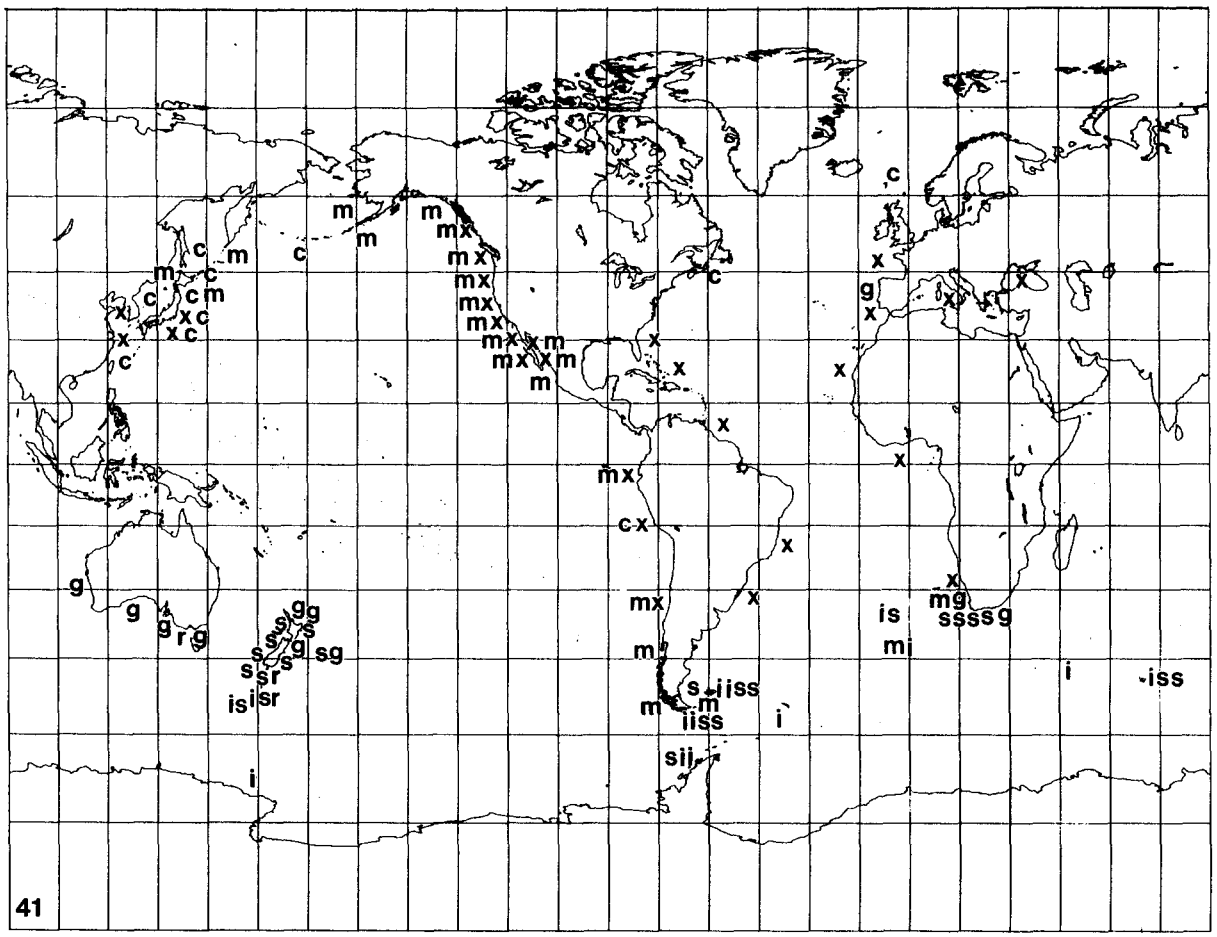


*Fig. 41.* Map showing the distribution of genera of the Gigartinaceae: *Chondrus* (C), *Mazzaella* (M), *Iridaea* (I), *Sarcothalia* (S), *Rhodoglossum* (R), *Chondracanthus* (X), *Gigartina* (G). The number of letters corresponds roughly to the number of species in each area.

Basionym: *Gigartina elegans* Greville in Saint-Hilaire, Voyage distr. diam... Brésil, 2:449. 1833. [E,PC].

*Chondracanthus acicularis* (Roth) Fredericq comb. nov. (N. & S. Atlantic Oceans and Mediterranean Sea)

Basionym: *Ceramium aciculare* Roth, Cat. Bot. 3:114–116. 1806.

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*Figs 28–40.* Tetrasporangial reproduction. *Figs 28–29. Chondrus crispus. Fig. 28.* Tetrasporangial filaments initiated from medullary cells. *Fig. 29.* Mature tetrasporangial sorus. *Figs 30–31. Mazzaella californica. Fig. 30.* Maturing sorus showing primary ($t_1$) and secondary ($t_2$) tetrasporocytes. *Fig. 31.* Mature sorus. *Figs 32–33. Iridaea cordata. Fig. 32.* Transformation of existing intercalary subcortical cells into tetrasporocytes. *Fig. 33.* Mature sorus. *Figs 34–35. Sarcothalia stiriata. Fig. 34.* Portion showing young tetrasporangial filaments initiated from medullary filaments radiating from a single center. *Fig. 35.* Maturing (left) and mature (right) tetrasporangial sori. *Figs 36–37. Rhodoglossum lanceolatum. Fig. 36.* Nemathecial development: chains of young tetrasporocytes initiated by apical growth of surface cortical cells. *Fig. 37.* Mature sorus. *Fig. 38. Chondracanthus chamissoi.* Transformation of intercalary subcortical cells into tetrasporocytes (right), and mature sorus (left). *Figs 39–40. Gigartina pistillata. Fig. 39.* Young sorus showing mostly secondary tetrasporangial filaments. *Fig. 40.* Mature sorus.

*Gigartina* Stackhouse, 1809:55. Figs 25–27, 39–40
Type: *Gigartina pistillata* (S. G. Gmelin) Stackhouse, 1809:74; basionym: *Fucus pistillatus* S. G. Gmelin, 1768:159, pl. 18, fig. 1. [taxonomic synonym: *Chondrodictyon* Kützing, 1843:396; type *C. capense* Kützing, 1843:396] [L!]

Growth by apical or marginal meristems; thalli cylindrical, compressed or flattened, dichotomously branched or foliose, often bearing adventitious marginal or superficial branchlets, pinnules, or papillae. Gametophytes dioecious or monoecious; procarps formed near apex on adventitious branchlets, pinnules or papillae; cystocarps large, subterminal; auxiliary cell forming protrusions bearing gonimoblast initials from inner side, surrounded by a compact envelope; gonimoblast filaments penetrating between cells of envelope, linking to them progressively by cell fusions or secondary pit connections; carposporangial chains derived from uninucleate gonimoblast cells and multinucleate, heterokaryotic envelope cells, and linked to sterile cells and other carposporangia forming an extensive network; mature carposporangia in clusters, separated by cells of the sterile network and surrounded by a common outer envelope; terminal tubular gonimoblast cells fusing with envelope cells; carposporangia, gonimoblast cells, and envelope cells interconnected with broadened pit connections between cells; external pericarp and ostiole present, formed by resumed growth of the outer cortical filaments; carpospores released through ostiole. Tetrasporangial sori raised, elliptical to linear, formed progressively at boundary between inner cortex and medulla; tetrasporangia transformed from inner primary cortical cells and lateral secondary filaments, forming short chains linked to neighboring cells by secondary pit connections; tetraspores released by excision and gelatinous extrusion of sorus.

Distribution: Tethyan (Australia, N. New Zealand, S. Africa, Atlantic Europe).

*Gigartina pistillata* (S. G. Gmelin) Stackhouse, 1809:74 (Atlantic Europe) [see Hommersand *et al.*, 1992]

*Gigartina disticha* Sonder, 1845:55 [HBG, Isotypes L!, LD!] (W. Australia)

*Gigartina muelleriana* Setchell et Gardner, 1933:294 (S. Australia) substitute name for *Gigartina flabellata* J. Agardh, Sp. Alg. 2(1):265. 1851. [LD!]

*Gigartina crassicaulis* (C. Agardh) Setchell et Gardner, 1933:294 [LD!] (S. Australia)

*Gigartina wehliae* Sonder, 1871:62, pl. 4 [MEL?, Isotype LD!] (S. Australia)

*Gigartina clathrata* (Decaisne) Rabenhorst, 1878:71, including *Chondrodictyon capense* Kützing, 1843:396. [see Parkinson, 1981, pp. 19–21] (Cape Province, S. Africa).

*Gigartina macrocarpa* J. Agardh, 1876:683 [LD!] (N. New Zealand)

*Gigartina chapmanii* J. D. Hooker et Harvey in Harvey, 1855:251, pl. 119, B [BM!] (N. New Zealand)

*Gigartina clavifera* J. Agardh, 1876:194 [LD!] (S. New Zealand)

*Species incertae sedis*

*Gigartina alveata* (Turner) J. Agardh, 1851:271. [BM!]

*Gigartina ancistroclada* Montagne, 1845:121. [PC!, Isotype L!]

*Gigartina pachymenioides* Lindauer, 1949:350. [AK!]

*Gigartina skottsbergii* Setchell et Gardner, 1936:472. [UC!]

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## References


Agardh, C. A.,1820. Icones Algarum Ineditae. Fasc. I. Berling, Lund, [2] pp., pls. 1–10.

Agardh, C. A., 1821. Icones Algarum Ineditae. Fasc. II. Eckstein, Stockholm, [3] pp., pls. 11–20.

Agardh, C. A., 1822. Species Algarum...Vol. 1. Pt.2, Florideae. Lund, 169–398.

Agardh, J. G., 1847. Öfver de Capska arterna af slaget Iridaea. Köngl. Svensk. Vetensk. Acad. Handl. 1847: 81–97, pl. 1. [issued 1849].

Agardh, J. G., 1851. Species genera et ordines algarum. Vol. 2(1). Gleerup, Lund, xii + 351 pp.

Agardh, J. G., 1872. Bidrag till Florideernes systematik. Lunds Univ. Årsskr., 8(6): 1–60.

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

Agardh, J. G., 1885. Till algernes systematik. Afd. 4. Lunds Univ. Årsskr., Afd. 3. 21(8): 1–117.

Agardh, J. G., 1899. Analecta Algologica. Cont. V. Lunds Univ. Årsskr. N. F., Afd. 2. 35(4): 1–160, pls 1–3. [Issued 1903?]

Bory de Saint-Vincent, J. B. G. M., 1826. Iridea. Dict. Class. Hist. Nat. 9: 15–16.

Bory de Saint-Vincent, J. B. G. M., 1827–1829. Vol. I, pts 1–6 Cryptogamie. In L. I. Duperrey (ed.), Voyage autour du monde,..., La Coquille. A. Bertrand, Paris. Pts 1–2:[iii]–96 pp. (1827), pts 3–4:97–200 (1828); pts 5–6:201–301 (1829).

Brodie J., M. D. Guiry & M. Masuda, 1991. Life history and morphology of Chondrus nipponicus (Gigartinales, Rhodophyta) from Japan. Brit. Phycol. J. 26: 33–50.

Dawson, E. Y., 1944. The marine algae of the Gulf of California. Allan Hancock Pac. Exped. 3: 189–453, pl. 31–77.

Dawson, E. Y., 1961. Marine red algae of Pacific Mexico. IV. Gigartinales. Pacific Naturalist 2: 191–343, pl. 1–63.

Dawson, E. Y., C. Acleto & N. Foldvik, 1964. The seaweeds of Peru. Beih. Nova Hedwigia: 13: [vi] + 111, pl. 1–81.

DeToni f., G. B., 1936. Noterella di nomenclatura algologica, VII. Primo elenco di Floridee omonime. Brescia, 8 pp. (unnumbered).

Fredericq, S., J. Brodie & M. H. Hommersand, 1992. Developmental morphology of Chondrus crispus (Gigartinaceae, Rhodophyta). Phycologia 31: 542–563.

Gmelin, S. G., 1768. Historia Fucorum. Academia Scientarium, St. Petersburg, [8] + 239 + [6], 33 pls.

Greville, K. 1830. Algae britannical. MacLachlan & Stewart, Edinburgh, lxxxviii + 218 pp., 19 pls.

Greville, K., 1833. Algae. In A. F. C. P. de Saint-Hilaire, Voyage dans le district des diamans et sur le littoral du Brésil... Vol. 2, A. Bertrand, Paris: 423–424, 436, 447–450.

Guiry, M. D. & D. J. Garbary, 1990. A preliminary phylogenetic analysis of the Phyllophoraceae, Gigartinaceae and Petrocelidaceae (Rhodophyta) in the North Atlantic and North Pacific. In D. J. Garbary & G. R. South (eds.), Evolutionary Biogeography of the Marine Algae of the North Atlantic, NATO Advanced Science Inst. Series G: Ecological Sc, Vol. 22, Springer Verlag: 349–410.

Harvey, W. H., 1855. Algae. In J. D. Hooker, The Botany of the Antarctic Voyage...Pt. 2, Flora Novae-Zelandiae. Vol. 2, Pt. 2, Flowerless Plants. Lovell Reeve, London: 211–266, pl. 107–121.

Harvey, W. H., 1859. Characters of new algae, chiefly from Japan and adjacent regions, collected by Charles Wright in the North Pacific Exploring Expedition under Captain John Rodgers. Proc. Am. Acad. Arts & Sci. 4: 327–334.

Harvey, W. H., 1860. Algae. In J. D. Hooker, The Botany of the Antarctic Voyage...Pt. 3, Flora Tasmaniae. Vol. 2, Pt. 2, Monocotyledones and Acotyledones Lovell Reeve, London: 282–343, pl. 185–196.

Harvey, W. H. & J. D. Hooker, 1845. Algae. In J. D. Hooker, The Botany of the Antarctic Voyage...Vol. 1, Flora Antarctica, Pt. 1, Botany of Lord Auckland's group and Campbell's Island. Reeve Bros., London: 175–193, pl. 69–78.

Hering, D., 1841. Diagnoses algarum novarum a cl. Dr. Ferdinand Krauss in Africa australi lectarum. Ann. Mag. Nat. Hist. 8: 90–92.

Hollenberg, G. J., 1945. New marine algae from Southern California, III. Am. J. Bot. 32: 447–451.

Holmes, E. M., 1895. New marine algae from Japan. J. Linn. Soc., Bot. 31: 248–260, pl. 7–12.

Holmgren, P. K., N. H. Holmgren N. H. & L. C. Barnett, 1990. Index Herbariorum, I. The herbaria of the world. 8th edn. Bohn, Scheltema & Holkema, Utrecht, [Regnum Vegetabile Vol. 120], 693 pp.

Hommersand, M. H., S. Fredericq & J. Cabioch, 1992. Developmental morphology of Gigartina pistillata (Gigartinaceae, Rhodophyta). Phycologia 31:300–325.

Hooker, W. J. & G. A. W. Arnott, 1841. The Botany of Captain Beechy's Voyage... Bohn, London, ii + 485 pp., 99 pls.

Hooker, J. D. & W. H. Harvey, 1845. Algae antarcticae. J. Bot., Lond. 4: 249–276, 293–298.

Hooker, J. D. & W. H. Harvey, 1845. Algae Novae Zelandiae. J. Bot., Lond. 4: 521–551.

Howe, M. A., 1914. The marine algae of Peru. Mem. Torrey Bot. Club 15: 1–185, pl. 1–66.

Hudson, W., 1762. Flora Anglica, 1st edn. Nourse & Moran for the author, London, viii + [7] + 506 + [22] pp.

Kim, D. H., 1976. A study of the development of cystocarps and tetrasporangial sori in Gigartinaceae (Rhodophyta, Gigartinales). Nova Hedwigia 27: 1–93.

Kützing, F. T., 1843. Phycologia Generalis... Brockhaus, Leipzig, xxxii + 458 pp., 80 pls.

Kützing, F. T., 1847. Diagnosen und Bemerkungen zu neuen oder kritischen Algen. Bot. Zeit. 5: 1–5, 22–25, 33–38, 52–55, 164–167, 177–180, 193–198, 219–223.

Kützing, F. T., 1849. Species Algarum. Brockhaus, Leipzig, vi + 922 pp.

Kylin, H., 1941. Californische Rhodophyceen. Lunds Univ. Årsskr., N. F., Avd. 2, 37(2): 1–51, pl. 1–13.

Kylin, H., 1956. Die Gattungen der Rhodophyceen. Gleerup, Lund, xv + 673 pp.

Leister, G. L., 1977. Taxonomy and reproductive morphology of Iridaea cordata (Turner) Bory and Iridaea crispata Bory (Gigartinaceae, Rhodophyta) from southern South America. Unpublished Ph. D. dissertation, Duke University: xvii + 186.

Lindauer, V. W., 1949. Notes on Marine Algae of New Zealand. I. Pacif. Sci. 3: 340–352.

Linnaeus, C., 1767. Mantissa Plantarum, 142 + [2] pp. (Supplement to Systema naturae. Vol. 2. Regnum Vegetabile. 12th ed., Stockholm).

Mikami, H., 1965. A systematic study of the Phyllophoraceae and Gigartinaceae from Japan and its vicinity. Sci. Papers Inst. Algol. Res., Fac. Sci., Hokkaido Univ. 5: 181–285, pl. 1–11.

Montagne, [J. F.] C., 1845. Plantes cellulaires. Voyage au Pole Sud...sur...l'Astrolabe et la Zélée...pendant ... 1837–1838–1839–1840... Botanique. Vol. 1, Paris, xiv + 349 pp. and atlas of 20 pls.

Nuttall, T., 1817. Description of Collinsia, a new genus of plants. J. Acad. Nat. Sci. 1: 189–192.

Okamura, K., 1929–1932. Icones of Japanese algae. VI. Kazamashobo, Tokyo: 1–96, pl. 251–300.

Papenfuss, G. F., 1950. Review of the genera of algae described by Stackhouse. Hydrobiologia 2: 181–208.

Parkinson, P. G., 1981. Iridea. Phyc. Hist. Anal. Autodid. fasc. III. Pettifogging Press, Auckland, 28 pp.

Postels, A. P. & F. J. Ruprecht, 1840. Illustrationes algarum... Pratz, St. Petersburg: iv + 22 + [2] pp., 40 + [1] pl. [Latin Edition].

Rabenhorst, L., 1878. Beitrag zur Meeresalgen-Flora der Auckland-Inseln. Hedwigia 17: 65–77.

Roth, A. W., 1806. Catalecta Botanica, Fasc. 3. Gleditschiano, Leipzig, viii + 350 + [9] pp., 12 pls.

Setchell, W. A. & N. L. Gardner, 1933. A preliminary survey of Gigartina, with special reference to its Pacific North American species. Univ. Calif. Publ. Bot. 17: 255–340, pl. 43–55.

Setchell, W. A. & N. L. Gardner, 1936. Iridophycus Gen. Nov. and its representation in South America. Proc. Nat. Acad. Sci. USA 22: 469–473.

Setchell, W. A. & N. L. Gardner, 1937. Iridophycus in the Northern Hemisphere. Proc. Nat. Acad. Sci. USA 23: 169–174.

Simons, R. H., 1983. The genus Trematocarpus (Sarcodiaceae, Rhodophyta) in southern Africa and the exclusion of Sphaerococcus (Chondrus) scutellatus. Bothalia 14: 803–808.

Sonder, O. G., 1845. Nova algarum genera et species, quas in itinere ad oras occidentales Novae Hollandiae, collegit L. Preiss, Ph.D.Dr. Bot. Zeit. 3: 49–57.

Sonder, O. G., 1871. Die Algen des tropischen Australiens. Abh. Naturwiss. Verein Hamburg 5: 33–74, pl. 1–6.

Stackhouse, J., 1797. Nereis Britannica. Fasc. 2. Hazard, Bath; White, London, ix–xxiv, 31–70 pp., pls. 9–13.

Stackhouse, J., 1809. Tentamen marino-cryptogamicum... Mem. Soc. Imper. Naturalistes Moscou 2: 50–97.

Suringar, W. F. R., 1870. Algae japonicae musei botanici Lugduno-Batavi. Haarlem, 39 + viii pp., 28 pls.

Turner, D., 1808. Fuci... Vol. 1, Arch, London, [1]–164 pp., pl. 1–71.

Turner, D., 1809. Fuci... Vol. 2, Arch, London, [1]–162 pp., pl. 72–134.

Turner, D., 1819. Fuci... Vol. 4, Arch, London, [1]–153 pp., pl. 197–258.

Yendo, K., 1920. Novae Algae Japoniae. Decas I–III. Bot. Mag. [Tokyo] 34: 1–12.

Wittmann, W., 1965. Aceto-iron-haematoxylin-chloral hydrate for chromosome staining. Stain Technol. 40: 161–164.