

# Morphology and molecular phylogeny of the marine algal order Gelidiales (Rhodophyta) from New South Wales, including Lord Howe and Norfolk Islands

Alan J. K. Millar<sup>A,C</sup> and D. Wilson Freshwater<sup>B</sup>

<sup>A</sup>Royal Botanic Gardens Sydney, Mrs Macquaries Rd, Sydney, NSW 2000 Australia.

<sup>B</sup>Centre for Marine Science, University of North Carolina at Wilmington, 5600 Marvin Moss Lane, Wilmington, NC 28409, USA.

<sup>C</sup>Corresponding author. Email: alan.millar@rbgsyd.nsw.gov.au

**Abstract.** Fifteen species in seven genera of the marine benthic red algal order Gelidiales are reported from the New South Wales coast including Lord Howe Island and Norfolk Island. Critical sampling, a re-examination of herbarium specimens filed in the Royal Botanic Gardens Sydney and the University of Melbourne, and molecular sequencing of most of the species has determined that many of the previous identifications from this region of the Pacific were incorrect. *Gelidium pusillum* (Stackhouse) Le Jolis, once widely reported from this coast, is shown not to occur here and the specimens on which these misidentifications were made have proved to represent either new species or previously described species. Similarly, records of *Gelidium australe* J. Agardh have been found to represent misidentification of the formerly New Zealand endemic *Gelidium allanii* V.J.Chapman, and specimens identified as *Gelidium caulacanthum* J. Agardh actually represent the new species *Gelidium hommersandii* sp. nov. Previously recorded species verified in this study are *Capreolia implexa* Guiry & Womersley, *Gelidiella acerosa* (Forsskål) Feldmann & G.Hamel, *Gelidium maidenii* Lucas, *Pterocladia lucida* (Turner) J. Agardh, *Pteroclatiella caerulea* (Kützinger) Santelices & Hommersand [as *Pterocladia caerulea* (Kützinger) Santelices], *Pteroclatiella capillacea* (Gmelin) Santelices & Hommersand [as *Pterocladia capillacea* (Gmelin) Bornet], and *Ptilophora pectinata* (A. & E.S. Gepp) R.E.Norris. These species are described and illustrated in detail along with previously unreported reproductive structures. Three species are newly recorded for the New South Wales mainland [*Parviphycus antipae* Celan, *Gelidium crinale* (Turner) Gaillon, and *Pteroclatiella caloglossoides* (Howe) Santelices], and two species (*Gelidium isabellae* W.R.Taylor and *Gelidium allanii* V.J.Chapman) represent new records for the Australian continent. In addition, three new species are described: *Gelidium bernabei* sp. nov., *Gelidium declerckii* sp. nov., and *Gelidium hommersandii* sp. nov.

## Introduction

Given the common intertidal habitat of some of the species of this economically important group of algae [i.e. *Pteroclatiella capillacea* (Gmelin) Santelices & Hommersand and *Gelidium isabellae* W.T. Taylor], it is surprising that William Henry Harvey (1858; 1863), in his six-week sojourn in New South Wales (1 May–15 June 1855), did not collect many members of this group. In his five-volume set *Phycologia Australica*, he lists only five species and illustrates three [*Pteroclatiella lucida* (Turner) J. Agardh, *Gelidium asperum* (C. Agardh) Greville and *Ptilophora prolifera* (Harvey) J. Agardh], and there are only two specimens of *Pteroclatiella capillacea* collected by Harvey from Kiama on the southern coast of New South Wales (Harvey's Australian Algal Exsiccatae No. 333N). Published records from New South Wales

did not appear until 1906 when the Gepps reported several species sent to them by A.H.S. Lucas, the then Curator of Algae at the Royal Botanic Gardens in Sydney. *Pteroclatiella capillacea*, *Pteroclatiella lucida* and the new species now known as *Ptilophora pectinata* (A.Gepp & E.S.Gepp) R.E.Norris were reported. May (1949) reported on several species of *Gelidium* Lamouroux from the New South Wales coast, including the new record of *G. caulacanthum* J. Agardh for Australia. This latter record actually represents a new species (*G. hommersandii*) that is described in this paper. Lucas (1935) recorded several species from Lord Howe Island, including the then newly described and endemic *G. maidenii* Lucas. Millar (1990) described and illustrated *Ptilophora pectinata*, *Pteroclatiella capillacea* and *Pteroclatiella lucida* from the Coffs Harbour area.

The widespread red algal order Gelidiales has been the subject of several recent studies (Kraft and Abbott 1998; Rodríguez de Rios 1992; Shimada *et al.* 2000a, 2000b; Thomas and Freshwater 2001), including the regional monographic treatment of the group from southern Australia by Womersley and Guiry (1994). Only non-descriptive and non-illustrative lists of species exist from other coastlines of Australia, such as northern Australia (Lewis 1984), New South Wales (Millar and Kraft 1993) and Western Australia (Huisman and Walker 1990; Kendrick *et al.* 1990; Huisman 1993, 1997), and many of the identifications within these regions have not been critically challenged, especially with modern techniques such as molecular sequencing. At last count, some seven genera and 19 species of Gelidiales have been recorded from Australian waters, of which seven {*Gelidiella minima* Guiry & Womersley [= *Pterocladia minima* (Guiry & Womersley) Santelices & Hommersand], *Gelidiella ramellosa* (Kützinger) Feldmann & Hamel, *Ptilophora prolifera* (Harvey) J. Agardh, *Gelidium australe* J. Agardh, *Gelidium maidenii* Lucas, *Gelidium asperum* (C. Agardh) Greville, *Pterocladia rectangularis* (Lucas) Womersley & Guiry}}, are considered endemic. Only one species, *Gelidium maidenii* from Lord Howe Island, was considered to be endemic to NSW waters.

Millar and Kraft (1993), in their catalogue of red algae from New South Wales including Lord Howe Island, listed 11 species in the genera *Gelidiella* Feldmann & Hamel, *Gelidium*, *Pterocladia* J. Agardh (including *Pterocladia* Santelices & Hommersand) and *Ptilophora* Kützinger. During the past 10 years, there have been several taxonomic and systematic changes to this order of red algae (Santelices and Hommersand 1997; Shimada *et al.* 1999; Rico *et al.* 2002; Santelices and Rico 2002; Tronchin *et al.* 2002, 2003; Santelices 2004). We have therefore undertaken a revision of the members of the Gelidiales from New South Wales (NSW), including Lord Howe Island and Norfolk Island.

## Materials and methods

Subtidal collections made by SCUBA were preserved in 4% formalin-seawater. Vouchers were also dried with silica gel crystals for DNA analysis. Slide material was stained in an aniline blue solution made according to the recipe of Millar and Wynne (1992). Photographs were taken on either a Wild Photomakroscope M400, a Wild Leitz MPS51 Ortholux II system with Kodak EPY (Ektachrome 64T Professional) positive film, an Olympus CH-2 with Nikon Coolpix 4500 digital camera, or an Olympus BH2 microscope with a Spot RT digital camera. Images were produced electronically following the methods of Millar and Kraft (2001). Vouchers are deposited in NSW, WNC and the silica gel dried collection at CMS-UNCW. Herbarium abbreviations follow Holmgren *et al.* (1990).

Specimens included in DNA sequence analyses are listed in Table 1. Total genomic DNA was extracted from new specimens following the protocol of Hughey *et al.* (2001). Amplifications of chloroplast-

encoded *rbcL* and the nuclear-encoded 28S rRNA gene followed the methods of Thomas and Freshwater (2001). Sequencing reactions were performed using the Big Dye sequencing kit and protocol (Applied Biosystems, Foster City, CA) and analysed on an ABI 3100 Genetic Analyser (DNA Analysis Facility, Center for Marine Science, University of North Carolina Wilmington), or at the University of Sydney and the Prince Alfred Molecular Analysis Centre, Sydney, Australia. The sequences of *rbcL* and 28S rRNA gene amplification and sequencing primers are found in Freshwater and Rueness (1994) and Freshwater *et al.* (1999) respectively. Sequence data were compiled and aligned with Sequencher (Gene Codes, Ann Arbor, MI) and MacClade version 4.0 (Maddison and Maddison 2000). Characteristics of the aligned sequence data and models of molecular evolution were determined, and phylogenetic analyses were performed using MacClade, Modeltest version 3.06 (Posada and Crandall 1998), MrBayes version 2.01 (Huelsenbeck and Ronquist 2001) and PAUP version 4.0 (Swofford 2002).

Sequences of the 28S rRNA gene were only generated for two species as molecular vouchers. Sequences of *rbcL* were generated for specimens of all species newly collected in this study and herbarium specimens of *Ptilophora pectinata* as molecular vouchers and for phylogenetic analyses. The original *rbcL* dataset included sequences from 95 taxa. Multiple taxa of the same species that were identical or only varied at one or two sites were removed so that the analysed dataset included 74 *rbcL* sequences. The first 67 base pairs (bp) of the 1467 bp gene were excluded from analyses because a majority of sequences were incomplete at the 5' end. Maximum-likelihood and neighbour-joining distance analyses were run using the GTR+I+G model with the following settings: Base = (0.3532 0.1354 0.1639) Nst = 6 Rmat = (1.1213 8.9394 1.4415 1.9450 13.9113) Rates = gamma Shape = 1.5375 Pinvar = 0.5566. The maximum-likelihood analyses consisted of 10 separate searches of random sequence addition and tree bisection-reconnection (TBR) branch swapping. Preliminary bayesian analyses were run to determine a 'burnin' value based on the convergence of likelihoods. Two final bayesian analyses of 1 000 000 generations and a 1000-tree burnin were run. One of these analyses utilised the same model of evolution and parameters as described for the maximum-likelihood and distance analyses, while the other allowed separate models of evolution for the three different codon positions. Parsimony analysis of the data was done using a heuristic search of 1000 random sequence additions, MULTREES, and TBR branch swapping. Parsimony bootstrap analyses consisted of 1000 replications of 10 random sequence additions, MULTREES, and TBR swapping. Distance bootstrap values were derived from 1000 replications of neighbour-joining tree building with the previously described base substitution model.

## Results and observations

Genus *Capreolia* Guiry & Womersley, *Phycologia* 32: 267 (1993)

In studying many intertidal *Gelidium* species, Guiry and Womersley (1993) realised that what was being regularly misidentified as *Gelidium pusillum* (Stackhouse) LeJolis from southern Australia and New Zealand, was in actual fact a completely separate genus that lacked female plants in the wild. Only in culture was it demonstrated that fertilised carpogonia developed directly into tetrasporophytes, thus, displaying a biphasic, rather than the typical triphasic, life history. Only one species, *C. implexa*, is presently credited for the genus.

**Table 1. Species, collection locality (collector), and GenBank accession numbers for taxa included in *rbcL* sequence analyses**

Species	Collection location	Accession number
<i>Acanthopeltis japonica</i>	Shimoda, Shizuoda Pref., Japan (Shimada <i>et al.</i> 1999)	AB017673
<i>Capreolia implexa</i>	Port Philip Bay, Victoria, Australia (M. Guiry)	L22456
<i>Gelidiella acerosa</i>	Cahuita, Limón, Costa Rica (D. Thomas & W. Freshwater)	AF305812
<i>Gelidiella acerosa</i>	Ned's Beach, Lord Howe I. (A. Millar & W. Freshwater)	AY352424
<i>Gelidiella acerosa</i>	O'ahu, Hawaiian Is (W. Freshwater)	L22457
<i>Gelidiella acerosa</i>	Palm Cove, Queensland, Australia (M. Hommersand)	AF329822
<i>Gelidium allanii</i>	Doubtless Bay, North I., New Zealand (G. Knight & W. Nelson)	L22458
<i>Gelidium americanum</i>	Radio Island, Carteret Co., North Carolina, USA (W. Freshwater)	L22459
<i>Gelidium asperum</i>	Point Lonsdale, Victoria, Australia (M. Hommersand)	AY350782
<i>Gelidium australe</i>	Port McDonnell, South Australia, Australia (M. Hommersand)	AY350783
<i>Gelidium bernabei</i>	Long Reef, Collaroy Beach, New South Wales, Australia (A. Millar & W. Freshwater)	AY352418
<i>Gelidium canariensis</i>	Puerto de la Cruz, Tenerife, Canary Islands (J. Rico)	L22460
<i>Gelidium capense</i>	False Bay, Western Cape Prov., South Africa (J. Bolton)	L22461
<i>Gelidium caulacanthum</i>	Porirua Harbor, North I., New Zealand (G. Knight & W. Nelson)	U00103
<i>Gelidium corneum</i>	Aramar, Asturias, Spain (J. Rico)	L22071
<i>Gelidium coulteri</i>	Balboa Peninsula, Orange Co., California, USA (W. Freshwater)	U00105
<i>Gelidium crinale</i>	Fish Hook Bay, Rottneest I., Western Australia (J. Huisman)	AY350780
<i>Gelidium crinale</i>	Summer Cloud Bay, Jervis Bay, New South Wales, Australia (A. Millar & W. Freshwater)	AY350781
<i>Gelidium crinale</i>	Masonboro Inlet, New Hanover Co., North Carolina, USA (W. Freshwater)	U00981
<i>Gelidium crinale</i>	Awhai I., Hyogo Pref., Japan (Shimada <i>et al.</i> 1999)	AB017679
<i>Gelidium declerckii</i>	Nahoon Point, East London, Eastern Cape Prov., South Africa (E. Tronchin)	AY350775
<i>Gelidium declerckii</i>	Plantation Point, Jervis Bay, New South Wales, Australia (A. Millar & W. Freshwater)	AY350776
<i>Gelidium divaricatum</i>	Tokawa, Choshi, Chiba Pref., Japan (M. Yoshizaki)	U16828
<i>Gelidium floridanum</i>	Sebastian Inlet, Indian River Co., Florida, USA (W. Freshwater)	U00107
<i>Gelidium foliaceum</i>	Port Edward, KwaZulu-Natal, South Africa (E. Tronchin)	AF501284
<i>Gelidium hommersandii</i>	Piha, North I., New Zealand (G. Knight & W. Nelson)	U01043
<i>Gelidium hommersandii</i>	Woolloomooloo Bay, Sydney, New South Wales, Australia (A. Millar & W. Freshwater)	AY352420
<i>Gelidium isabelae</i>	KwaZulu-Natal, South Africa (M. Guiry & J. Rico culture)	AF305798
<i>Gelidium isabelae</i>	Long Reef, Collaroy Beach, New South Wales, Australia (A. Millar & W. Freshwater)	AY350779
<i>Gelidium isabelae</i>	Swartklip, False Bay, Western Cape Prov., South Africa (M. Hommersand)	AY350778
<i>Gelidium japonicum</i>	Keelung, Taiwan (S. Lin)	AF501287
<i>Gelidium koshikianum</i>	Nagahama, Shimo-Koshiki I., Koshiki I., Japan (Shimada <i>et al.</i> 2000a)	AB030626
<i>Gelidium latifolium</i>	Plouguerneau, Brittany, France (J. Cabioc'h & M. Hommersand)	U00112
<i>Gelidium microdenticum</i>	Cahuita, Limón, Costa Rica (D. Thomas & W. Freshwater)	AF305799
<i>Gelidium micropterum</i>	Kommetjie, Western Cape Prov., South Africa (J. Bolton)	U00446
<i>Gelidium pacificum</i>	Matsugahana, Amatsukominato, Chiba Pref., Japan (M. Yoshizaki)	U16832
<i>Gelidium pluma</i>	Hawai'i, Hawaiian Is (K. McDermid)	AF501288
<i>Gelidium pristoides</i>	Port Edward, KwaZulu-Natal, South Africa (E. Tronchin)	AF501282
<i>Gelidium pulchellum</i>	Graveyard Beach, Co. Galway, Ireland (M. Guiry)	U01969
<i>Gelidium pusillum</i>	Cancale, Brittany, France (J. Rueness & S. Fredriksen culture)	U01000
<i>Gelidium pusillum</i>	Fedje, Hordaland, Norway (J. Rueness & S. Fredriksen culture)	U00999
<i>Gelidium 'pusillum'</i>	Praia de Peruibe, Estado de Sao Paulo, Brazil (M. Cordeiro-Marino)	U01004
<i>Gelidium 'pusillum'</i>	Puerto de la Cruz, Tenerife, Canary Is (J. Rueness & S. Fredriksen culture)	U01003
<i>Gelidium 'pusillum'</i>	Solano Beach, San Diego Co., California, USA (M. Hommersand)	U00984
<i>Gelidium rex</i>	Tongoy Bay, Coquimbo, Chile (M. Edding)	AF305801
<i>Gelidium robustum</i>	Dana Point, Orange Co., California, USA (W. Freshwater)	U01041
<i>Gelidium serrulatum</i>	Mochimo, Sucre, Venezuela (W. Freshwater)	U01042
<i>Gelidium</i> sp.	Italy (M. Guiry & J. Rico culture # 1099, labelled <i>G. 'pusillum'</i> )	AY350774

**Table 1.** (continued)

Species	Collection location	Accession number
<i>Gelidium</i> sp.	Mallorca, Spain (J. Rueness & S. Fredriksen culture)	U00447
<i>Gelidium vagum</i>	Jodogahama, Iwate Pref., Japan (Shimada <i>et al.</i> 1999)	AB017680
<i>Gelidium vittatum</i>	Kommetjie, Western Cape Prov., South Africa (M. Hommersand)	U00112
<i>Parviphycus antipae</i>	Far Rocks, Lagoon, Lord Howe I. (A. Millar & W. Freshwater)	AY352425
<i>Parviphycus</i> sp.	Maloh, Siaton, Negros, Oriental, Philippines (J. West)	AF309386
<i>Parviphycus tenuissima</i>	La Garita, Gran Canaria, Canary Is (J. Rico)	AF320983
<i>Pterocladia lucida</i>	Ned's Beach, Lord Howe I. (A. Millar & W. Freshwater)	AY352423
<i>Pterocladia lucida</i>	Owhiro Bay, South Wellington, New Zealand (W. Nelson)	U01048
<i>Pterocladia lucida</i>	Wright I., Victor Harbor, South Australia (H. Womersley)	AF305808
<i>Pterocradiella bartlettii</i>	Port Aransas, Texas, USA (J. Jewett-Smith)	AF305807
<i>Pterocradiella beachiae</i>	Cahuita, Limón, Costa Rica (D. Thomas & W. Freshwater)	AF305811
<i>Pterocradiella caeruleascens</i>	Coconut I., Oahu, Hawaiian Islands (W. Freshwater)	AF305805
<i>Pterocradiella caloglossoides</i>	La Parouse, Botany Bay, New South Wales, Australia (A. Millar & W. Freshwater)	AY352422
<i>Pterocradiella capillacea</i>	Gordons Bay, Clovelly, New South Wales, Australia (A. Millar & W. Freshwater)	AY352421
<i>Pterocradiella capillacea</i>	Long Gully, south of Robe, South Australia (H. Womersley)	U01898
<i>Pterocradiella capillacea</i>	Owhiro Bay, South Wellington, New Zealand (W. Nelson)	U24156
<i>Pterocradiella capillacea</i>	Torre a Mare, Bari, Italy (E. Cecere)	U01888
<i>Pterocradiella melanoidea</i>	Mallorca, Spain (J. Rueness & S. Fredriksen culture)	U01046
<i>Pterocradiella nana</i>	Shimo-Koshiki I., Kagoshima Pref., Japan (Shimada <i>et al.</i> 2000 <i>b</i> )	AB023840
<i>Pterocradiella tenuis</i>	Tsuyazaki, Hukuoka Pref., Japan (Shimada <i>et al.</i> 2000 <i>b</i> )	AB023851
<i>Ptilophora diversifolia</i>	Protea Banks, KwaZulu-Natal, South Africa (E. Tronchin & W. Freshwater)	AF305803
<i>Ptilophora mediterranea</i>	Cape Matapan, Southern Peloponnesus, Greece (H. Huvé)	AF522360
<i>Ptilophora pectinata</i>	Collaroy Beach, New South Wales, Australia (V. May)	AY344043
<i>Ptilophora pinnatifida</i>	Sharks Bay, Port Alfred, Eastern Cape Prov., South Africa (M. Hommersand)	AF522361
<i>Ptilophora scalarimosa</i>	Bulusan, Luzon, Philippines (L. Liao)	AF305804
<i>Ptilophora subcostata</i>	Fujisawa, Kanagawa, Japan (M. Yoshizaki)	U16835

***Capreolia implexa*** Guiry & Womersley, *Phycologia* 32: 266–277, figs 1–7, 9–18 (1993). Womersley and Guiry 1994: 126, pl. 2, fig. 3; fig. 37

Figs 1–4.

*Misapplied name: Gelidium pusillum sensu* May (in part), *Proc. Linn. Soc. N.S.W.* 74: 197 (1949); 1965: 371. May and Larkum 1981: 456 (in part). May *et al.* 1978: 387.

*Type:* MELU A37758., from Sandringham, Port Phillip Bay, Victoria, Australia, *M.D. Guiry*, 14.v.1988.

#### *Habitat and morphology*

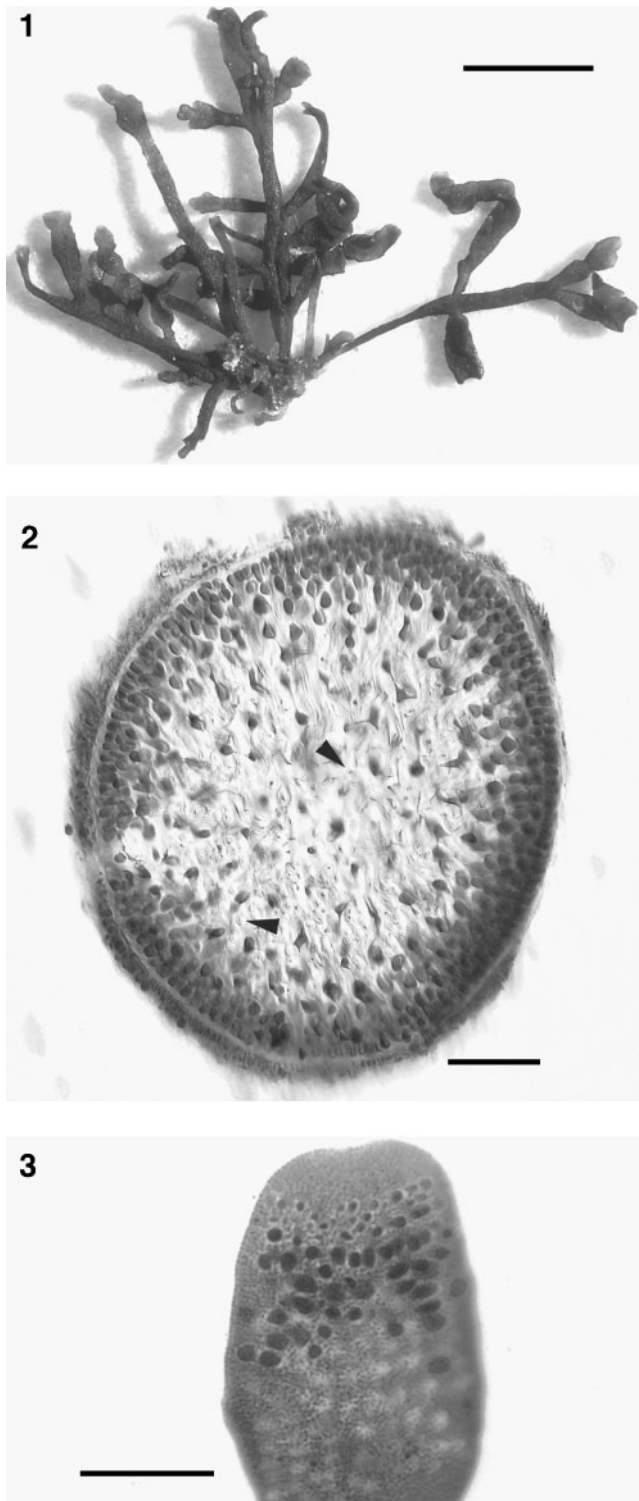
Plants grow intertidally on sandstone rocks in crevices forming dark (black) turf patches, and can also be found epizoically on limpets. Thallus dark red-brown to black, cartilaginous, consisting of terete prostrate branches with peg-like holdfast giving rise to terete to compressed erect branches (Figs 1, 4). Erect branches are 3–6(–10) mm in height and 150–350(–500) µm in width, with multiple orders of irregular to subdistichous branching, and they grow in a more or less repent fashion. Branch bases are not constricted and apices vary from acute to obtuse with prominent apical cells.

Thallus of prostrate branches composed of a 3–5-layer cortex of elliptical to globose cells surrounding a medulla of elongated thick-walled cells. Rhizines are numerous and concentrated in the outer medulla and inner cortex. The thallus construction of erect branches is similar to that of prostrate branches except that rhizines may be more numerous and are sometimes abundant in the central as well as outer medulla (Fig. 2).

Tetrasporangial sori may develop distally on main axes or secondary branches and have a narrow sterile margin. Tetrasporangia bearing secondary branches are sometimes strongly compressed and they may be slightly stipitate with retuse to truncate apices (Fig. 4). The tetrasporangia develop in capreolate to straight lines, mature acropetally and grow to lengths of 36 µm and diameters of 20 µm (Fig. 3).

#### *Distribution*

Wittelbee Point, South Australia to Broken Bay, NSW and Tasmania. Widespread in New Zealand. In the protologue, only Long Reef and Pearl Beach are listed as NSW localities. We suspect that it is more widespread along the NSW coast



**Figs 1–3.** *Capreolia implexa*. **Fig. 1.** Habit of herbarium specimen from Gordons Bay. NSW 614409. Scale = 2 mm. **Fig. 2.** Transverse section through terete portion of erect branch showing rhizines (arrowheads) in both the central and outer medulla. WNC Slide 2003-S076. Scale = 50  $\mu$ m. **Fig. 3.** Surface view of tetrasporangia developing in capreolate rows. WNC Slide 2003-S079. Scale = 200  $\mu$ m.

wherever there are rocky intertidal platforms and reefs. We did not locate it on Lord Howe or Norfolk Islands.

#### Remarks

Prior collections of this species from NSW had been made as early as 1921 but were misidentified as *Gelidium pusillum*. While both share superficially similar habits, *Capreolia implexa* exhibits acropetally developing, V-shaped to straight rows of tetrasporangia, whereas in *G. pusillum*, the tetrasporangia develop non-sequentially within rounded sori (Womersley and Guiry 1994). We have not discovered any reliable vouchers of *G. pusillum* in NSW and all previous records represent one or more of the *Gelidium* species described below. The V-shaped to straight rows of tetrasporangia distinguish *C. implexa* from all turfey New South Wales *Gelidium* species (Table 2).

Analyses of DNA sequence data from both nuclear and chloroplast loci indicate that *Capreolia implexa* is most closely related to *Gelidium caulacanthum* and *Gelidium hommersandii* [as *Gelidium* sp.] from New Zealand (Fig. 113; Freshwater *et al.* 1995; Freshwater and Bailey 1998; pers. obs.). Neither of these species exhibits the biphasic life history described for *Capreolia*, so this is not a synapomorphy for the clade. This group terminates one of the earliest diverging lineages within the large clade of Gelidiales taxa that have a *Gelidium*-type female reproductive and cystocarp development (Bailey and Freshwater 1997; Freshwater and Bailey 1998). Sequences of *rbcL* generated from *Capreolia implexa* specimens collected at Long Reef, Gordons Bay, Botany Bay and Jervis Bay in New South Wales were all identical and varied at only one site from the *rbcL* sequence generated from the Port Phillip Bay, Victoria isotype culture (Guiry and Womersley 1993; Freshwater *et al.* 1995).

#### Specimens examined

Long Reef, Collaroy, on upper intertidal rocks, barnacles and chitons, *A.J.K.Millar & D.W.Freshwater*, 4.ix.2002, NSW 615202 (NSW #16), NSW 615203 (NSW #17); Gordons Bay, Clovelly, intertidal rock shelves, *D.W.Freshwater & A.J.K.Millar*, 17.vii.2002, NSW 614409 (NSW #4); Bare Island, La Parouse, Botany Bay, east side of peninsular leading out to island, upper intertidal patches, *D.W.Freshwater & A.J.K.Millar*, 17.vii.2002, NSW 614410, WNC2003001 (NSW #2); Moe's Rock Bhewerre Peninsular, Jervis Bay, intertidal exposed oceanic rocks, *D.W.Freshwater & A.J.K.Millar*, 30.vii.2002, NSW 614411 (NSW #6).

#### Molecular vouchers

Specimen NSW #16, 1394 bp *rbcL* accession # AY350773; identical *rbcL* sequences from specimens NSW #2, NSW #4, NSW #6, NSW #17.

Genus *Gelidiella* Feldmann & Hamel, *Rev. Gen. Bot.* 46: 529 (1934)

A genus containing 20 or more species (Kraft and Abbott 1998) that traditionally have been separated from other Gelidiales by the absence of both rhizines and a

Table 2. Characteristics of Gelidiaceae species that grow as turfs in New South Wales, including Lord Howe Island

Character	<i>Gelidiella acerosa</i>	<i>Parviphycus antipae</i>	<i>Capreolia implexa</i>	<i>Gelidium bernabei</i>	<i>Gelidium crinale</i>	<i>Gelidium declerckii</i>	<i>Gelidium hommersandii</i>	<i>Gelidium isabellae</i>	<i>Pterocladia caloglossoides</i>
Height	10–25 mm	1–2 mm	3–6 (–10) mm	up to 4 mm	up to 18 mm	(2–) 3.5–10 (15) mm	10–40 mm	3.5–8 (10) mm	repent throughout
Branching pattern	irregular or distichous, second order branches short	simple, occasionally sub-dichotomous	irregular to subdistichous distally	mostly simple, but up to 3 orders of irregular branching	mostly simple or up to two orders of distichous, tri- to multifurcate tips sometimes present	irregular to distichous, up to five orders, sometimes twisted near apex, surface proliferations common	pinnate, up to four orders; turf form: profuse, irregular in multiple planes	simple to three orders of distichous branching	opposite or multiple divaricate-radiate
Erect branch shape	ligulate, terete, may form anastomoses	linear, terete to compressed	terete to slightly compressed, mostly stoloniferous, arise from upper side of prostrate branch	ligulate, terete at base becoming compressed, originate sub-dorsally from prostrate branch	linear to narrowly lanceolate, terete to compressed at base becoming compressed or flattened	sub-terete becoming flattened, clavate	terete to subterete but reproductive are compressed	flattened, lanceolate to clavate	linear, compressed to flattened
Erect branch width	0.5–0.7 (1.1) mm	0.04–0.09 mm	0.15–0.35 (–0.5) mm	0.12–0.28 (–0.36) mm	0.1–0.2 mm or 0.2–0.8 mm	50–100 µm at base, 200–450 µm distally	0.24–0.32 mm	0.3–0.8 mm	0.25–0.8 mm
Branch bases	not constricted	slightly to not constricted	not constricted	not constricted	not constricted	not constricted except for flattened secondary branches	not constricted	constricted (stipitate) or tapered	tapered
Branch apices	mostly obtuse	acute	acute to obtuse	initially acute becoming obtuse	mostly acute	obtuse	acute	obtuse	acuminate to acute

	4 or 5 cells	1 or 2 cells	3–5 cells	4 or 5 cells in prostrate; 3 or 4 cells in erect	3 or 4 cells	4 or 5 cells	4 or 5 cells	mostly 2 or 3 cells, thicker in some areas of blade	3 or 4 cells
Cortex width	4 or 5 cells	1 or 2 cells	3–5 cells	4 or 5 cells in prostrate; 3 or 4 cells in erect	3 or 4 cells	4 or 5 cells	4 or 5 cells	mostly 2 or 3 cells, thicker in some areas of blade	3 or 4 cells
Rhizine number and distribution	absent	absent	numerous to abundant, outer medulla to inner cortex, or throughout medulla	erect: abundant, medulla to inner cortex; prostrate: less, outer medulla and inner cortex	numerous throughout medulla and inner cortex	numerous throughout medulla and inner cortex	numerous throughout medulla and inner cortex	erect: abundant in medulla; prostrate: less numerous in medulla	numerous surrounding medullary cells
Tetrasporangia position	not observed	not observed	on terminal or lateral compressed stichidia	on multiple orders of irregular distal branching	not observed	subterminally on erect branches	distally on ordinary branches	distally in secondary branches	not observed
Tetrasporangial sori margin	not observed	not observed	narrow sterile margin	no sterile margin	not observed	sterile margin	no sterile margin	sterile margin	not observed
Tetrasporangia position	not observed	not observed	V-shaped to straight rows	irregular	not observed	irregular	irregular	irregular lines	not observed

gametophytic stage in the life history. Careful study of the type species, *G. acerosa* (Forsskål) Feldmann & Hamel, has confirmed that rhizines are totally absent from this species (Melo 1992), but their presence in *G. calcicola* Maggs & Guiry seemingly compromised this character at the generic level (Maggs and Guiry 1987). A recent study of *G. calcicola* has revealed it to be a species of *Pterocliadiella* Santelices & Hommersand (JM Rico and DW Freshwater unpublished data), and therefore lack of rhizines is a synapomorphy for *Gelidiella*.

Several studies have shown that gametophytes are present in the life history of *Gelidiella* species. Sreenivasa Rao (1974) observed meiotic divisions during tetraspore formation, and Kapraun *et al.* (1994) reported an alternation of diploid and haploid nuclear DNA amounts in tetrasporophytes and germlings grown from tetrasporangia (presumptive gametophytes) in *G. acerosa*. Santelices (1997a) described the first *Gelidiella* male gametophytes in *G. acerosa*, and subsequently male gametophytes were described from a second species, *G. tenuissima* Feldmann & Hamel (Rico *et al.* 2002). Absence of a gametophytic stage in the life history can no longer be considered a characteristic of this genus.

On a molecular level, separate and combined analyses of both nuclear and chloroplast DNA loci resolve species of *Gelidiella* as a monophyletic group occupying one of four major evolutionary lineages within the Gelidiales (Bailey and Freshwater 1997; Freshwater and Bailey 1998; Rico *et al.* 2002).

The identification of *Gelidiella* species is difficult due to their generally small size and simple habit, but a table of species characteristics has been compiled by Kraft and Abbott (1998). One species is known from New South Wales, but it occurs only on Lord Howe Island and Norfolk Island. It is entirely absent from the mainland.

***Gelidiella acerosa*** (Forsskål) Feldmann & Hamel, *Rev. Gen. Bot.* 46: 533 (1934). Abbott 1999: 202, figs 53A–C. Cribb 1996: 82, 83. Huisman 2000: 42. Millar and Kraft 1993: 11. Millar 1999: 499

Figs 5–6, 8–9.

*Basionym*: *Fucus acerosus* Forsskål, *Flora aegyptiaco-arabica* ... 190 (1775).

*Homotypic synonym*: *Echinocaulon acerosus* (Forsskål) Børgesen, *Dansk Botanisk Arkiv* 8(2): 5(1932).

*Misapplied name*: *Gelidium rigidum sensu* V.J. Chapman, *Botanica Marina* 20: 161 (1977).

*Type*: Herb. Forsskål in C, from Mokha, Yemen (*vide* Børgesen 1932; Price and Scott 1992).

#### *Habitat and morphology*

Plants form patches within the intertidal to shallow subtidal algal turf community. Thallus (Figs 5, 8) olive-yellow to dark red often variable along a single branch, cartilaginous, composed of arcuate, terete prostrate branches giving rise to

erect branches 1–5 cm in height, 0.5–0.7 (1.1) mm in width. Prostrate and erect branches may form anastomoses. Erect branches are ligulate, terete, with irregular or distichous branching. Second-order branches are generally short. Branch tips are mostly obtuse, occasionally acute with a prominent apical cell.

Thallus composed of a 4- or 5-cell-layer cortex grading into a densely packed medulla of thick-walled, longitudinally elongate cells (Fig. 9). Outermost cortical cells are mostly isodiametric in surface view, and radially elliptical in transverse sections. Inner cortical cells are more irregular in shape and become longitudinally elongate towards the medulla. Rhizines are absent.

Tetrasporangia to 36 µm long and 20 µm in diameter are borne in terminal to subterminal sori on lateral branches. Tetrasporangial sori are usually swollen relative to the bearing branch and have no sterile margin.

#### *Distribution*

Found throughout the tropical and subtropical Indian, Pacific and Atlantic oceans. In New South Wales, known only from Lord Howe Island and also from Norfolk Island.

#### *Remarks*

*Gelidiella acerosa* is the most common and easily recognisable *Gelidiella* species. It is an important component of the reef flat flora in tropical waters, and is harvested for food and agar extraction in Asian countries (Trono and Ganzon-Fortes 1988; Kapraun *et al.* 1994). Our Lord Howe Island collections came from the intertidal rock flats at Ned's Beach, where tangled, decumbent plants grow intermixed with other species. The *rbcL* sequence of *G. acerosa* specimens from Lord Howe Island, NSW and Palm Cove, Queensland were identical and resolved in a monophyletic clade with additional specimens from Hawaii and Costa Rica (Fig. 113). Unpublished analyses by Freshwater, Muhlstein and Bowman that include additional Pacific specimens indicate that *G. acerosa* from eastern Australia is sister to other Pacific populations.

#### *Specimens examined*

LORD HOWE ISLAND: *G.Kraft & A.J.K.Millar K11023* 17.xii.1986 (MELU); Neds Beach, intertidal rock platform, *A.J.K.Millar & D.W.Freshwater LHI #6*, 1.x.2002 (NSW 614402). NORFOLK ISLAND: probably Slaughter Bay, Kingston lagoon, *W.Laing*, no date, NSW 416720.

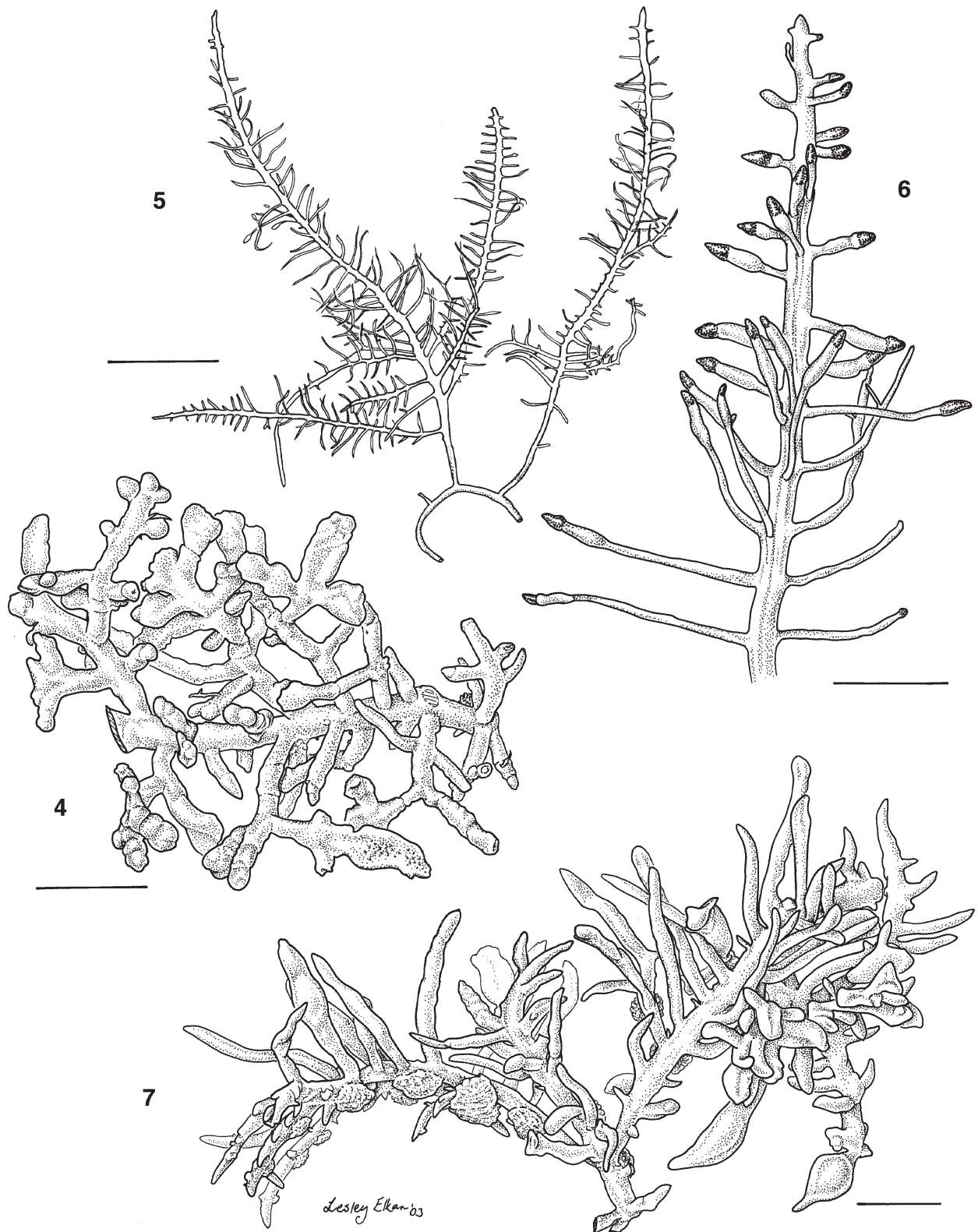
#### *Molecular vouchers*

Specimen LHI #6, 1386 bp *rbcL* accession # AY352424, 1131 bp 28S rDNA accession # AY359963.

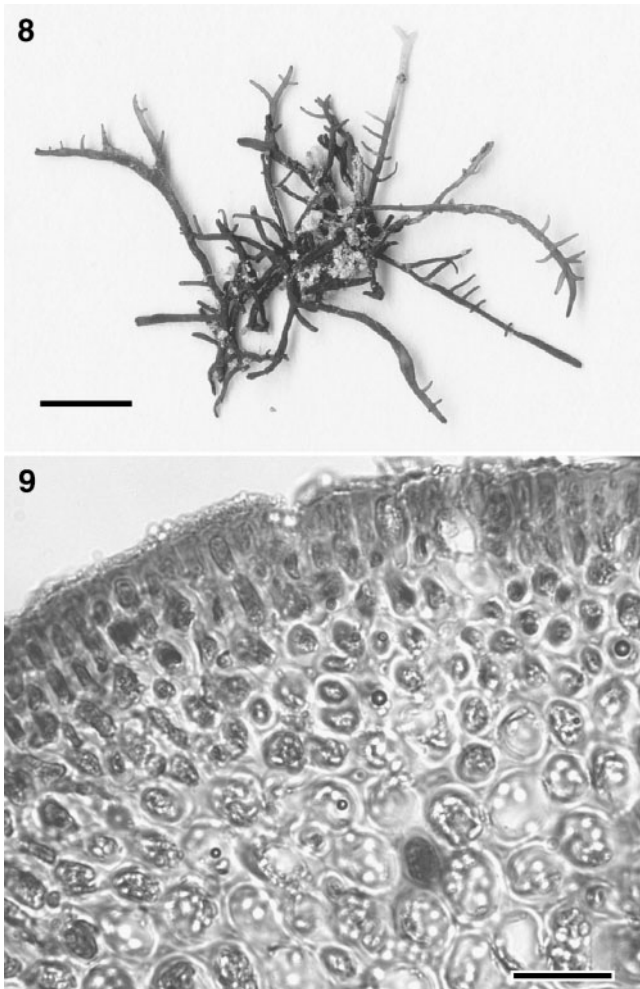
Genus ***Parviphycus*** Santelices *Cryptgamie, Algol.* 25: 313–326 (2004)

The genus *Parviphycus* was recently erected to accommodate *Gelidiella* species that differed by displaying a distichous





**Figs 4–7.** General habits. **Fig. 4.** *Capreolia implexa*. Habit of tetrasporangial specimen. NSW 614410. Scale = 2 mm. **Fig. 5.** *Gelidiella acerosa*. Habit of pressed specimen. MELU GK9052a. Scale = 1 cm. **Fig. 6.** *Gelidiella acerosa*. Detail of tetrasporangia branches. NSW 292560. Scale = 2 mm. **Fig. 7.** *Gelidium bernabei*. Habit of cystocarpic specimen. NSW 615573. Scale = 1 mm.



**Figs 8–9.** *Gelidiella acerosa*. **Fig. 8.** Habit of pressed specimen. NSW 614402. Scale = 5 mm. **Fig. 9.** Transverse section of erect branch showing radially elliptical outer cortical cells and gradual transition from medulla to cortex. WNC Slide 2003-S011. Scale = 25  $\mu$ m.

pattern of apical cell division in both erect and prostrate axes, axial and periaxial cells that are in distinctive rows in transverse sections, and tetrasporangia that are produced by periaxial cells in regularly arranged rows (Santelices 2004).

At present there are four species that have been included within this genus, the type *P. adnatus*, and *P. antipae*, *P. tenuissimus*, and *P. womersleyanus*. However, many more *Gelidiella* species remain poorly studied and it is likely that that genus will be restricted to the type *G. acerosa* and a few other species.

Only the one species, *P. antipae*, occurs in NSW waters and at this stage it is known only from Lord Howe Island.

***Parviphycus antipae*** (Celan) Santelices *Cryptogamie Algol.* 25: 324, figs 9, 15, 20, 25

Figs 10–14.

*Basionym:* *Gelidiella antipae* Celan, *Bull. Sect. Sci. Acad. Roum.* 19: 77–78, figs A–F (1938). Norris 1992: 35, fig. 21. Womersley & Guiry 1994: 123, figs 34K–N.

*Misapplied name:* *Gelidiella bornetii sensu* Millar and Kraft, *Aust. Syst. Bot.* 6: 11 (1993).

*Type:* presumably in PC, from Cape Caliacra, Romanian coast of the Black Sea.

#### *Habitat and morphology*

Thalli forming a dark red to black turf on upper-intertidal rocks of terete prostrate branches that produce many erect branches (Fig. 10), 1–2 mm in height and 40–90  $\mu$ m in width. Holdfasts of unconsolidated, single-cell rhizoids that form a fringe (Fig. 11), sometimes fasciculate along the ventral surface of prostrate branches (Fig. 10). Erect branches are linear, terete to compressed, and simple but occasionally proximally subdichotomous. Branch tips are acute with a prominent apical cell (Fig. 12).

Surface cortical cells of prostrate branches tend to be transversely elongated while surface cells of erect branches are irregular in shape and arrangement (Fig. 13). Medullary cells are elongated (Fig. 12), but there is little difference between the appearance of medullary and cortical cells in transverse sections (Fig. 14). Cells of the central axial filament and second-order branch filaments are generally recognisable, and rhizines are absent. All specimens examined were sterile.

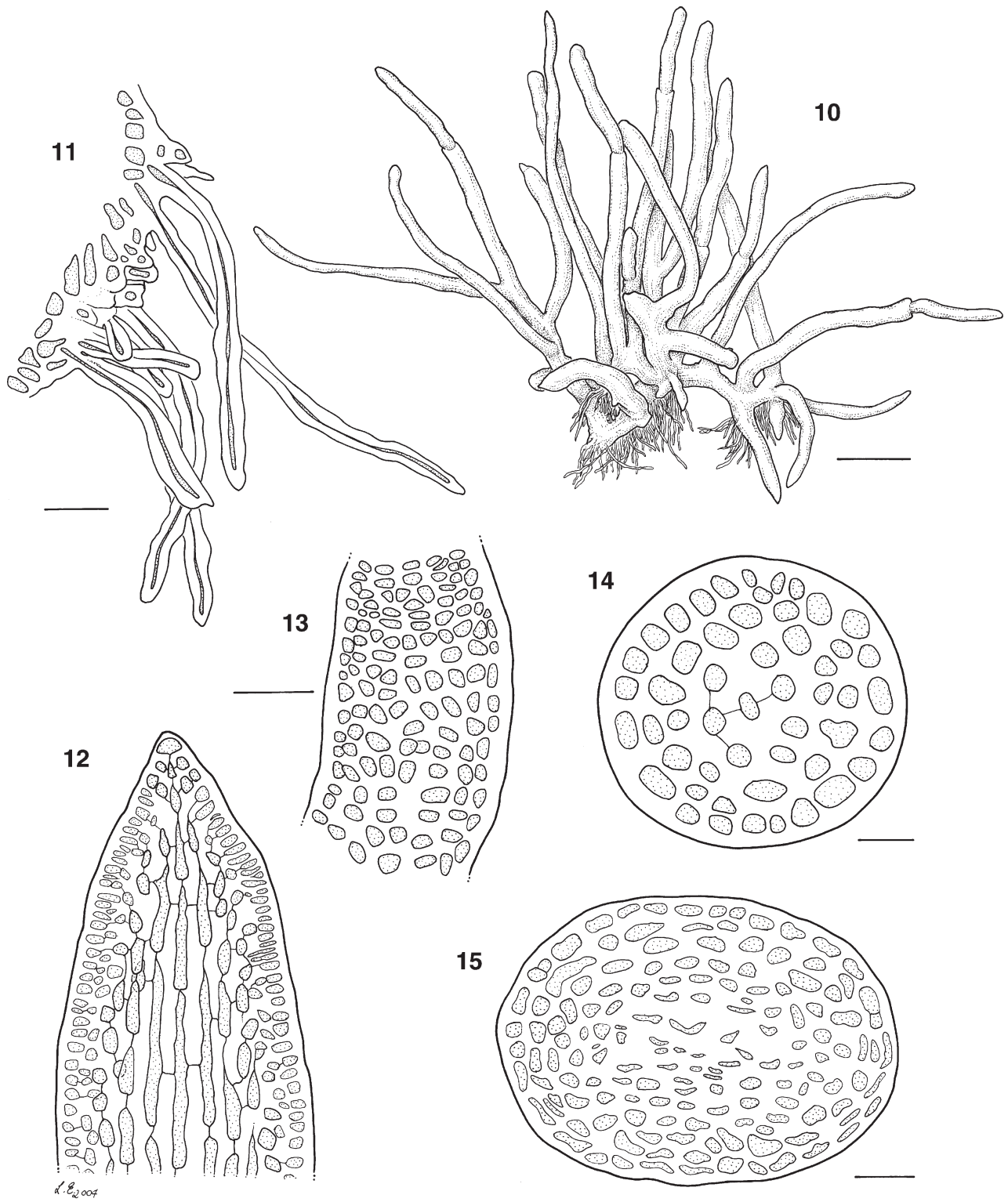
#### *Distribution*

Mediterranean, Baja California, KwaZulu-Natal (South Africa). In Australia, from Elliston to Kangaroo Island in South Australia. In New South Wales, known only from Lord Howe Island.

#### *Remarks*

The Lord Howe Island specimens are characterised by an extensive system of terete prostrate branches that give rise to terete to compressed, mostly simple but occasionally proximally subdichotomous upright branches (Fig. 10). The range of widths (40–90  $\mu$ m) and heights (1–2 mm) of upright branches in combination with the observed habit identifies these specimens as *P. antipae*. *Parviphycus antipae* has also been reported from intertidal pools and the subtidal of southern Australia (Womersley and Guiry 1994 as *G. antipae*). Our Lord Howe Island collections of this species were from high-intertidal rocks.

The first Lord Howe Island collections of this species were incorrectly identified as *Gelidiella bornetii* (Weber van Bosse) Feldmann & Hamel by



**Figs 10–14.** *Parviphycus antipae*. **Fig. 10.** Habit of Lord Howe Island specimen. NSW 615209. Scale = 250  $\mu$ m. **Fig. 11.** Rhizoids emanating from lower surface of prostrate branch. NSW 615209. Scale = 25  $\mu$ m. **Fig. 12.** Longitudinal section showing apical cell and elongate medullary cells. NSW 615209. Scale = 25  $\mu$ m. **Fig. 13.** Surface cortical cells near apical tip showing an irregular arrangement. NSW 615209. Scale = 25  $\mu$ m. **Fig. 14.** Transverse section of an erect branch. WNC Slide 2003-S002. Scale = 10  $\mu$ m. **Fig. 15.** *Gelidiella lubrica*. Transverse section of an erect branch. L. # 989.241 827, WNC Slide 2003-S001. Scale = 10  $\mu$ m.

Millar and Kraft (1993), but the original description for this species states that its fronds are flattened; erect branches are up to 5 mm in height and surface cortical cells are aligned (Weber-van Bosse 1926). As noted above, the Lord Howe Island specimens neither have the axis symmetry nor attain the height described for *G. bornetii*, and surface cortical cells were often found to have an irregular arrangement, even near the apical tips (Fig. 13). The concept of *G. bornetii* has been confused because the Rijksherbarium specimen labelled as the Holotype (L 941,27–296) does not fit Weber-van Bosse's protologue. Observations on the Holotype, which is terete to compressed throughout, led Hatta and Prud'homme van Reine (1991) to propose that *G. bornetii* is a synonym of *G. lubrica* (Kützinger) Feldmann & Hamel. Although the basic habit of *G. lubrica* and the designated Holotype specimen of *G. bornetii* is the same as that of the Lord Howe Island *Parviphycus antipae*, we have observed a distinct difference in holdfast morphology. Rhizoidal cells in the *G. bornetii* holotype are consolidated into discrete, peg-like holdfasts whereas those of *P. antipae* are not consolidated and may occur over large areas of the lower surface of prostrate branches (Fig. 10). *Gelidiella lubrica* also is larger in size than *P. antipae* (Fig. 15).

*Parviphycus adnata* (E.Y. Dawson) Santelices is another morphologically similar species that has been proposed as a synonym of *P. antipae* (Norris 1992, as *Gelidiella antipae*). Santelices (2002) defined three characters that distinguish these two species (as *G. antipae* and *G. adnata*): (1) differences in the size and arrangement of surface cortical cells between erect and prostrate branches, (2) number and pattern of tetraspore production, and (3) disposition of tetrasporangial stichidia on the thalli. Although the absence of tetrasporangial plants in the Lord Howe Island collections precludes the use of the last two characters, surface cortical cell characters differ from that described for *Parviphycus adnata*. Surface cortical cells of *P. adnata* prostrate branches are transversely elongated and approximately twice as large as the longitudinally elongated surface cells of erect branches. In the Lord Howe Island specimens surface cortical cells of prostrate branches do tend to be transversely elongated, but they are similar in size and not larger than erect-branch surface cells. Surface cells of erect branches are also irregular in shape rather than longitudinally elongated.

Analyses of *rbcL* sequences resolved *P. antipae* within a clade of *Parviphycus* species that includes *P. tenuissima* (Feldmann & Hamel) Santelices and an unidentified *Parviphycus* species from the Philippines (Fig. 113). This clade is sister to the clade of *Gelidiella acerosa* populations as was previously determined by Rico *et al.* (2002). Our addition of *Parviphycus antipae* into this analysis further supports the heterogeneity of the *Gelidiella* complex and hence the genus *Parviphycus*.

### *Specimens examined*

*Parviphycus antipae* (Celan) Santelices: Lord Howe Island, Neds Beach, high intertidal pools, *G.Kraft & R.Ricker*, 3.xii.1978, MELU A40024–A40026; Far Rocks, lagoon, *D.W.Freshwater & A.J.K.Millar*, 4.x.2002, NSW 615209 (LHI #5). *Gelidiella bornetii* (Weber van Bosse) Feldmann & Hamel: Indonesia, *Weber van Bosse* L.10264 No. 55, bar code L0054067. *Gelidiella lubrica* (Kützinger) Feldmann & Hamel: Indonesia, *Weber van Bosse* No. 941.27 295, L. 10264 No. 56; *Sep 1984* No. 991.028 776, L. 10264 No. 58; *Oct 1984* No. 989.241 827, L. 10264 No. 57.

### *Molecular vouchers*

Specimen LHI #5, 1116 bp *rbcL*, accession # AY352425.

Genus *Gelidium* Lamouroux, *Ann. Mus. Hist. Nat. [Paris]* 20: 128 (1813)

This is the largest and the name-bringing genus of the order. Species are found in subtropical to temperate coasts of every continent. Prized for their commercial value in producing agar (e.g. Jensen 1993), the genus has been studied extensively over the last two centuries but especially within the last few decades. Four species of *Gelidium*, viz. *G. australe*, *G. caulacanthum*, *G. maidenii*, and *G. pusillum*, were reported from NSW before this study (Millar and Kraft 1993; Table 3). All but *G. maidenii* were based on misidentifications. Three additional species are newly described, bringing to seven the number of species now known from this coast.

*Gelidium allanii* Chapman, *The Marine Algae of New Zealand, Part III: Rhodophyceae: Issue 1*; 98, plate 33A (1969)

Figs 16–31.

*Misapplied name: Gelidium australe sensu Lewis, Department of Defence Materials Research Laboratories Report MRL-R-912: 9 (1984). Lucas 1935: 218. May 1949: 197; 1965: 371.*

*Type: AKU 47, from Waitata Rocks, Russell, Bay of Islands, New Zealand, 20.xi.1937, V.W. Lindauer Algae of New Zealand Exsiccatae No. 137. (Isotypes in NSW).*

### *Habitat and morphology*

Plants grow both intertidally and subtidally on rocks and consist of erect branches (Fig. 16) with short rhizoidal branchlets extending from the base of tufts (Fig. 17). The prostrate rhizoidal branches are attached to the substratum by peg-like holdfasts of consolidated rhizoidal cells (Fig. 17). Erect branches are ligulate and shallowly zigzag, up to 6 cm in length and to 1–1.5 mm in width, and have 3–5 orders of subopposite to alternate pinnate marginal branching (Figs 16, 18). Ultimate branches are often clavate (Fig. 19). Main axes and marginal branches taper towards the base but are not constricted. Apices are acute to obtuse with a point (Fig. 20). Vegetative branches are compressed to flattened, but terminal branches in small specimens

**Table 3. Previous (Guiry and Womersley 1993; Millar and Kraft 1993) and currently (this study) reported New South Wales Gelidiales species and their distributions (mainland v. Lord Howe Island)**  
Revised identifications of previously reported species are shown in bold

Species	Previous		Species	Current	
	Mainland	LHI		Mainland	LHI
<i>Capreolia implexa</i>	+		<i>Capreolia implexa</i>	+	
<i>Gelidiella acerosa</i>		+	<i>Gelidiella acerosa</i>		+
<i>Gelidiella bornetii</i>		+	<b><i>Parviphycus antipae</i></b>		+
<i>Gelidium australe</i>	+	+	<b><i>Gelidium allanii</i></b>	+	+
<i>Gelidium caulacanthum</i>	+		<b><i>Gelidium hommersandii</i></b>	+	
<i>Gelidium maidenii</i>		+	<i>Gelidium maidenii</i>		+
<i>Gelidium pusillum</i>	+	+	<b><i>Gelidium bernabei</i></b>	+	
			<b><i>Gelidium crinale</i></b>	+	+
			<b><i>Gelidium declerckii</i></b>	+	
			<b><i>Gelidium isabelae</i></b>	+	+
<i>Pteroclatiella caerulescens</i>		+	<i>Pteroclatiella caerulescens</i>		+
<i>Pteroclatiella caloglossoides</i>		+	<b><i>Pteroclatiella caloglossoides</i></b>	+	
<i>Pteroclatiella capillacea</i>	+	+	<i>Pteroclatiella capillacea</i>	+	+
<i>Pterocladia lucida</i>	+	+	<i>Pterocladia lucida</i>	+	+
<i>Ptilophora pectinata</i>	+		<i>Ptilophora pectinata</i>	+	

may be subterete. Thalli are uniaxial with generally distinct apical cells (Fig. 20). Longitudinal and transverse sections show a cortex containing 4–5 layers of cells (Figs 21–23). Cells in the outer cortical layer are elliptical to ovate; inner cortical cells are globose to transversely elliptical and somewhat elongate. Medullary cells are thick-walled and longitudinally elongated. Rhizines are abundant in the outer medulla and inner cortex (Figs 21, 23), are sometimes present in the central medulla but never as abundant as in the outer medulla.

Cystocarps are bilocular and develop singly at the tips of ultimate branchlets (Figs 24, 25). Cystocarpic branchlets are generally simple and compressed to flattened. Carpogonia develop from intercalary cells of third-order branch filaments (Fig. 26). Files of nutritive filament cells develop from the basal cells of third-order branch filaments and surround cells of the second-order branch filaments (Fig. 27). Gonimoblast filaments develop from fertilised carpogonia and grow among the nutritive filaments forming a placental tissue. Carposporangia are formed from gonimoblast cells (Fig. 28). Third-order branch cells elongate during formation of the cystocarp cavities maintaining connections between the pericarp and central placental tissues (Figs 24, 25). At maturity cystocarps have a pericarp of five or six layers of cortical cells and ostioles with peristomes.

Tetrasporangial sori develop predominantly on the distal portions of compressed ultimate branchlets (Fig. 29). The sori may become elongated in older fertile branches where growth has continued (Fig. 30), and they have slightly swollen sterile margins that contain many rhizine cells (Fig. 31). Tetrasporangia are arranged irregularly and initially develop acropetally, are mostly isodiametric (to 28 µm). Older

portions of sori contain tetrasporangia in various stages of development. Mature tetrasporangia are cruciately divided with decussate longitudinal cleavages (Fig. 31).

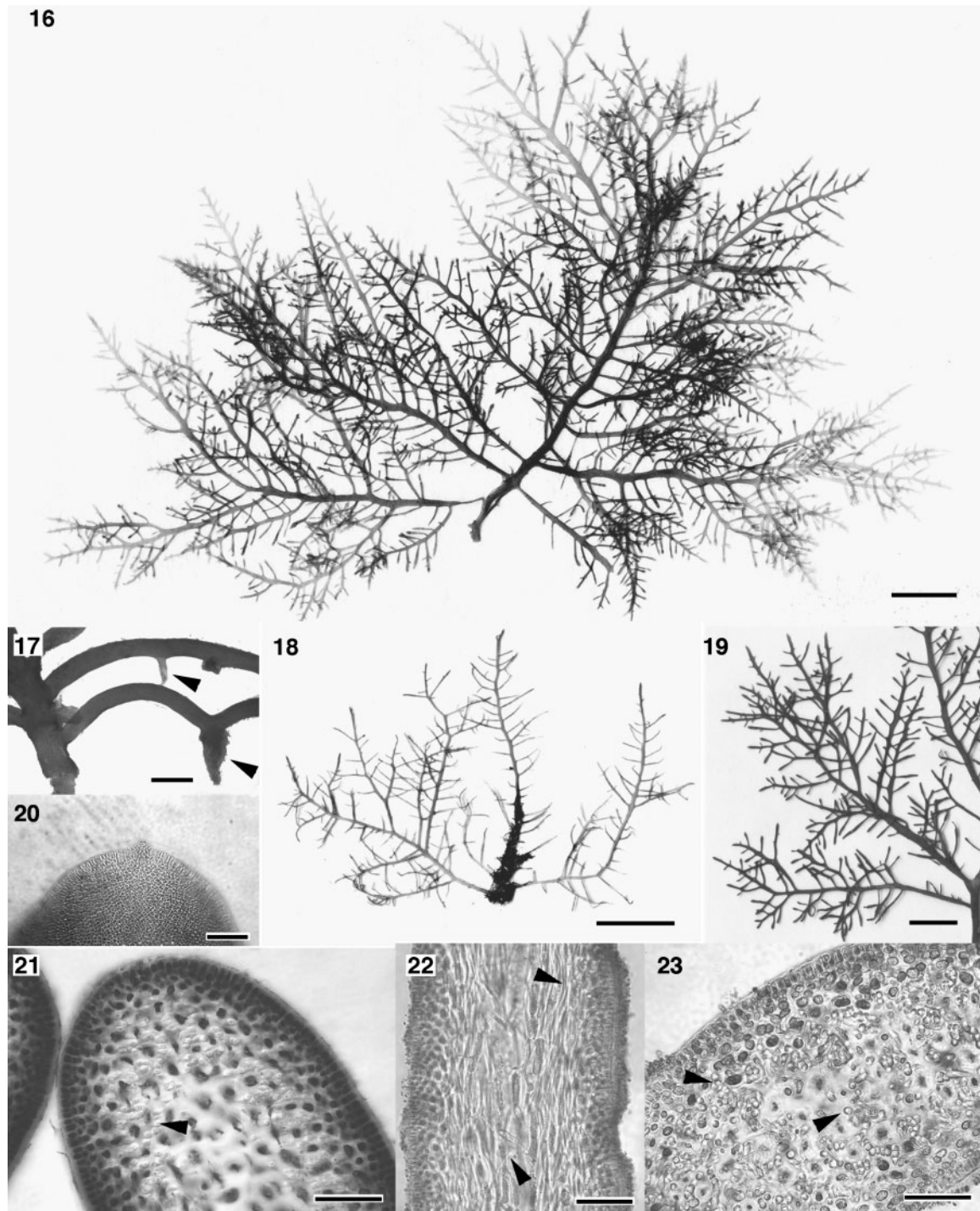
Spermatangial sori have not been observed.

#### Distribution

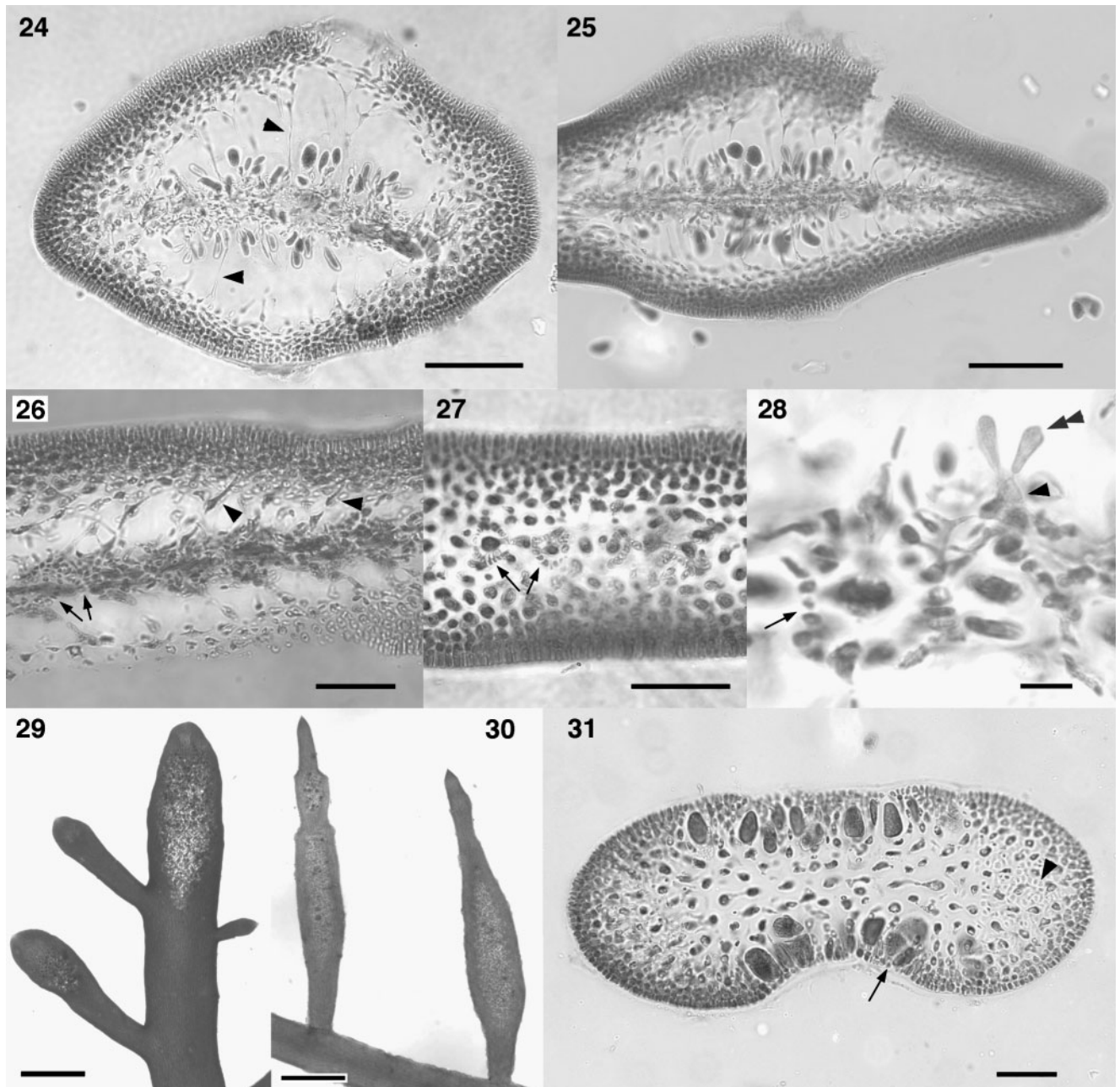
New South Wales coast, Lord Howe Island, Norfolk Island and New Zealand.

#### Remarks

Specimens of this species collected in New South Wales have previously been misidentified as either *Gelidium australe* or *Pteroclatiella capillacea*. Careful comparisons of the NSW populations, additional New Zealand (NZ) specimens (including isotypes) and Chapman's (1969) original descriptions of *G. allanii* and *G. allanii* var. *atro-purpurea* V.J. Chapman reveal several minor morphological differences between these specimens and the original descriptions. New Zealand plants may be larger (up to 13 cm) and have multiple branches arising from close to the base of erect axes, a tendency not seen in NSW plants. The upper parts of New Zealand plants identified as var. *atro-purpurea* have a profusion of ultimate pinnae giving thalli a fasciculate appearance, but this branching pattern is not observed in NSW plants. Chapman describes the main axes of *G. allanii* and var. *atro-purpurea* as being up to 0.5 and 1.0 mm respectively, but NZ specimens observed in this study are up to 1.5 mm wide. Ultimate branches of NSW and NZ specimens were often clavate (Fig. 19) with strongly compressed bases, but they are reported to be linear with subterete bases in the original description. Finally, slight differences are also found



**Figs 16–23.** *Gelidium allanii*. **Fig. 16.** Habit of specimen from Doubtless Bay, New Zealand showing shallowly zig-zag branches. NSW 614407. Scale = 1 cm. **Fig. 17.** Proximal branchlets with peg-like holdfasts (arrowheads). WNC Slide 2003-S050. Scale = 500  $\mu$ m. **Fig. 18.** Specimen from Old Gulch, Lord Howe Island. NSW 614408. Scale = 1 cm. **Fig. 19.** Portion of specimen from Doubtless Bay, New Zealand showing clavate ultimate branches. WNC2003004. Scale = 5 mm. **Fig. 20.** Obtuse apex showing extended apical cell. WNC Slide 2003-S066. Scale = 50  $\mu$ m. **Fig. 21.** Transverse section showing a cortical layer of four or five cells, thick-walled medullary cells, and rhizines (arrowheads) concentrated in the outer medulla and inner cortex, but absent from the central medulla. WNC Slide 2003-S065. Scale = 50  $\mu$ m. **Fig. 22.** Longitudinal section showing rhizines (arrowheads) concentrated in the outer medulla and inner cortex, but also present in the central medulla. WNC Slide 2003-S060. Scale = 50  $\mu$ m. **Fig. 23.** Transverse section showing rhizines (arrowheads) concentrated in the outer medulla and inner cortex, but also present in the central medulla. WNC Slide 2003-S061. Scale = 50  $\mu$ m.



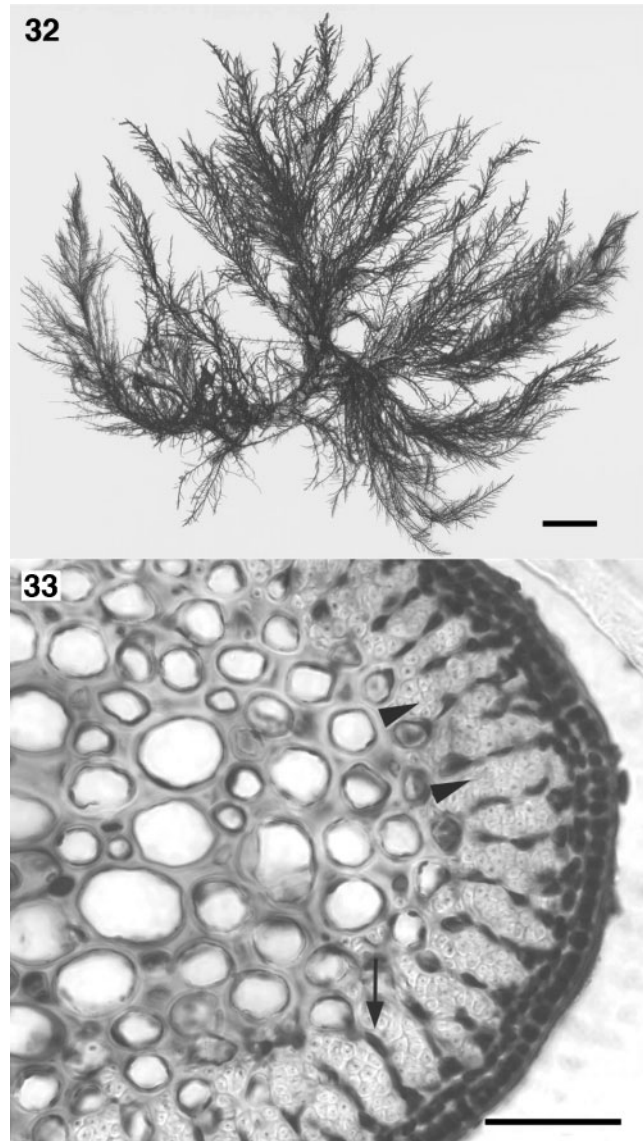
**Figs 24–31.** *Gelidium allanii*. **Fig. 24.** Transverse section of cystocarp. Elongated third-order branch cells are indicated by arrowheads. WNC Slide 2003-S053. Scale = 100  $\mu\text{m}$ . **Fig. 25.** Longitudinal section of cystocarp. WNC Slide 2003-S053. Scale = 100  $\mu\text{m}$ . **Fig. 26.** Longitudinal section of fertile female branchlet showing carpospores (arrowheads) and nutritive cell filaments (arrows). WNC Slide 2003-S055. Scale = 50  $\mu\text{m}$ . **Fig. 27.** Transverse section of fertile female branchlet showing nutritive cell filaments (arrows) growing around second order branch cells. WNC Slide 2003-S055. Scale = 50  $\mu\text{m}$ . **Fig. 28.** Transverse section of placental network in a mature cystocarp showing a gonimoblast cell (arrowhead) giving rise to two carposporangia (double arrowheads), and nutritive cell filaments (arrow) surrounding second order branch cells. WNC Slide 2003-S053. Scale = 10  $\mu\text{m}$ . **Fig. 29.** Tetrasporangial sori on the distal portion of branches. WNC Slide 2003-S066. Scale = 500  $\mu\text{m}$ . **Fig. 30.** Elongate tetrasporangial sori on branches that have continued growing after initial sori development. WNC Slide 2003-S069. Scale = 500  $\mu\text{m}$ . **Fig. 31.** Transverse section through a tetrasporangial sorus showing rhizines (arrowhead) concentrated in the sterile margin and a mature tetrasporangium with decussate cleavages (arrow). WNC Slide 2003-S059. Scale = 50  $\mu\text{m}$ .

between the rhizine positions, which Chapman describes as extremely abundant in the medulla and extending into the inner cortex, whereas they were observed to be abundant in the outer medulla and inner cortex, but are always fewer, and sometimes absent, in the central medulla of the NSW and NZ plants examined (Figs 21–23). One feature, which is consistent with Chapman's description and our observations, is that the tetrasporangial sori are in compressed ultimate branches with swollen margins (Fig. 31).

*Gelidium allanii* does not attain the size of *G. australe*, which can be 10–25 cm long (Fig. 32). Axes of *G. allanii* taper from the base to upper parts, but there is only slight tapering in *G. australe*. *Gelidium australe* is very distinct in transverse section. Immediately below the outer cortical cells there is a dense, inner-cortical rhizine layer transected by filaments of cortical cells (Fig. 33). Few to no rhizines are found in the medulla of elongated cells with relatively large diameter lumens, and little to no intercellular space. Rhizines are concentrated within the outer medulla and inner cortex of *G. allanii* and medullary cells have much smaller diameter lumens (Figs 21–23).

Analyses of *rbcL* sequences indicate that *G. allanii* is closely related to the recently described Japanese species, *G. koshikianum* Shimada, Horiguchi & Masuda (Fig. 113; Shimada *et al.* 2000a, fig. 23). Specimens of *G. allanii* from Lord Howe Island and Doubtless Bay, New Zealand varied from each other at two *rbcL* sites and from *G. koshikianum* at only four sites. These two species are part of a clade of predominantly east-Asian *Gelidium* species represented by only *G. pacificum* Okamura in this study (Fig. 113), but that also includes *G. elegans* Kützinger, *G. linoides* Kützinger, and *G. tenuifolium* Shimada, Horiguchi & Masuda (Shimada *et al.* 2000a).

The small amount of *rbcL* sequence divergence between *G. allanii* and *G. koshikianum* falls within the intraspecific divergence range reported for some *Gelidium* species (Freshwater and Rueness 1994), but the time since speciation and mutation rate will have an effect on the amount of fixed mutations that accumulate between any two taxa. There are distinct morphological differences that distinguish *G. allanii* and *G. koshikianum* despite their similar *rbcL* sequences. Main axes of *G. koshikianum* become wider (up to 2.5 mm *v.* 1–1.5 mm) and are not shallowly zigzag as in *G. allanii*. The pattern of branching in *G. koshikianum* is opposite with the lengths of second- and third-order branches being generally short and varying little along the main axes. By contrast, *G. allanii* has a sub-opposite to alternate branching pattern with second and higher order branches varying in length. The description of tetrasporangial sori in *G. koshikianum* mentions that they occur at the apices of short determinate branches, but in *G. allanii* sori bearing branches are not always determinate (Fig. 30).



**Figs 32, 33.** *Gelidium australe*. **Fig. 32.** A typical specimen from Port MacDonnell, Victoria, Australia. UNC herbarium (unnumbered), coll. M.H. Hommersand, 11 xi 1995. Scale = 2 cm. **Fig. 33.** Transverse section showing dense concentrations of rhizines (arrowheads) transected by cortical cell filaments (arrow). WNC Slide 2003-S018. Scale = 50  $\mu$ m.

Smaller specimens of *Gelidium allanii* could perhaps be confused with large specimens of *G. hommersandii* or lax specimens of *Pterocladia capillacea* in New South Wales. *Gelidium hommersandii* is different in having terete to subterete vegetative axes that are not shallowly zigzag, numerous rhizines throughout the medulla and inner cortex, and tetrasporangial sori with no sterile margin. The Lord Howe Island collection of *G. allanii* was made within the large intertidal band of mainly *P. capillacea* at Old Gulch. Although *P. capillacea* collected at Lord Howe Island is more lax and has narrower axes than mainland specimens, there are



several differences distinguishing it from *G. allanii*. There is a marked decrease in the width and length of branches with increasing branch order in *P. capillacea* giving specimens a generally pyramidal appearance not seen in *G. allanii*. Main axes of *P. capillacea* are also not bent or shallowly zig-zag as they often are in *G. allanii*.

#### *Specimens examined*

NEW SOUTH WALES: Port Stephens, Fly Point, *A.J.K. Millar & P.G. Richards*, 22.xi.1991 (NSW 290673 tetrasporic, NSW 290674 cystocarpic); West side Boondelbah Island, 6 m deep on large boulders, *A.J.K. Millar & P.G. Richards*, 23.xi.1991 (NSW 290668); Fingal Bay, *K. Harada* 2837, 8.vii.1976 (NSW 614550); Port Jackson, *V. May* #1195, 20.i.1946 (NSW 209167); Botany Bay, *V. May* #254A, 14.xii.1944 (NSW 209160); Kallymenia Flats, off Hole-in-the-wall, Jervis Bay, *A.J.K. Millar & P.G. Richards*, cystocarpic, 3.vi.1990, NSW 290086—NSW 290089. LORD HOWE ISLAND: *F.A. McNeil* v.1932 (NSW); The Crevice, near The Arch, at lagoon edge, *A.J.K. Millar & P.G. Richards*, 8.iii.1993 (NSW 292626); North side of South Passage, *A.J.K. Millar & P.G. Richards*, 10.iii.1993 (NSW 292624); Old Gulch, east side upper intertidal rocks, *A.J.K. Millar & D.W. Freshwater* LHI #2, 4.x.2002 (NSW 614408, WNC 2003003). NORFOLK ISLAND: *I. McComish*, 1937 (NSW 484996). NEW ZEALAND: Waitata Rocks, Russell, Bay of Islands, New Zealand, by *V.W. Lindauer* Algae of New Zealand Exsiccatae No. 13, 20.xi.1937, NSW 484990, NSW 484993—NSW 484995, NSW 484984 (all isotypes); Doubtless Bay, *G. Knight & W.A. Nelson*, 23.xi.1992 (NSW 614407, WNC 2003004).

#### *Molecular vouchers*

Specimen LHI #2, 1390 bp *rbcL* accession #AY350777; specimen from Doubtless Bay, New Zealand, 1431 bp *rbcL* accession # L22458.

***Gelidium bernabei*** A.J.K. Millar & D.W. Freshwater, *sp. nov.*

Figs 7, 34–44.

*Holotype*: NSW 605631 (including NSW Slide 28–1), 17.vii.2002, *D.W. Freshwater & A.J.K. Millar* (Fig. 34).

#### *Description*

Thallus ex ramis prostratis teretibus hapteris parvis obtusisque compositus, et ramis erectis teretibus-compressis ex pagina subdorsali ramorum prostratorum orientibus. Rami erecti usque 4 mm alti, ligulati, plerumque simplices autem interdum ramificatione irregulari usque ad 3 ordines; apices primo acuti, postea obtusi. Rami prostrati cortice 4–5 stratis cellularum et rhizinis aggregatis in medulla exteriore et cortice interiore; rami erecti cortice 3–4 stratis cellularum et rhizinis abundantibus per medullam et corticem interiorem. Rami feminei juvenes depressione in medio; cystocarpia bilocularia, subterminalia, ostiolis sine peristomiis. Rami tetrasporangiferi multis ordinibus ramificationis irregularis vel palmatae; tetrasporangia irregulariter disposita in soris sine marginibus sterilibus, cruciatim divisa, 25–28  $\mu\text{m}$  longa, 22–28  $\mu\text{m}$  lata aspectu superficiali.

Thallus composed of terete prostrate branches with peg-like holdfasts, and terete to compressed erect branches originating from the sub-dorsal surface of prostrate branches. Erect branches up to 4 mm tall, ligulate, mostly simple, but sometimes with up to three orders of irregular branching; apices initially acute, becoming obtuse. Prostrate branches with cortex of 4 or 5 cell layers and rhizines concentrated in outer medulla and inner cortex; erect branches with cortex of 3 or 4 cell layers and rhizines abundant throughout medulla and inner cortex. Young female branches with median depression; cystocarps bilocular, subterminal, with ostioles without peristomes. Tetrasporangial branches with multiple orders of irregular or palmate branching; tetrasporangia arranged irregularly in sori without sterile margins, cruciately divided 25–28  $\mu\text{m}$  long and 22–28  $\mu\text{m}$  in surface view.

#### *Type locality*

Gordons Bay, Clovelly, Sydney metropolitan region of NSW.

#### *Etymology*

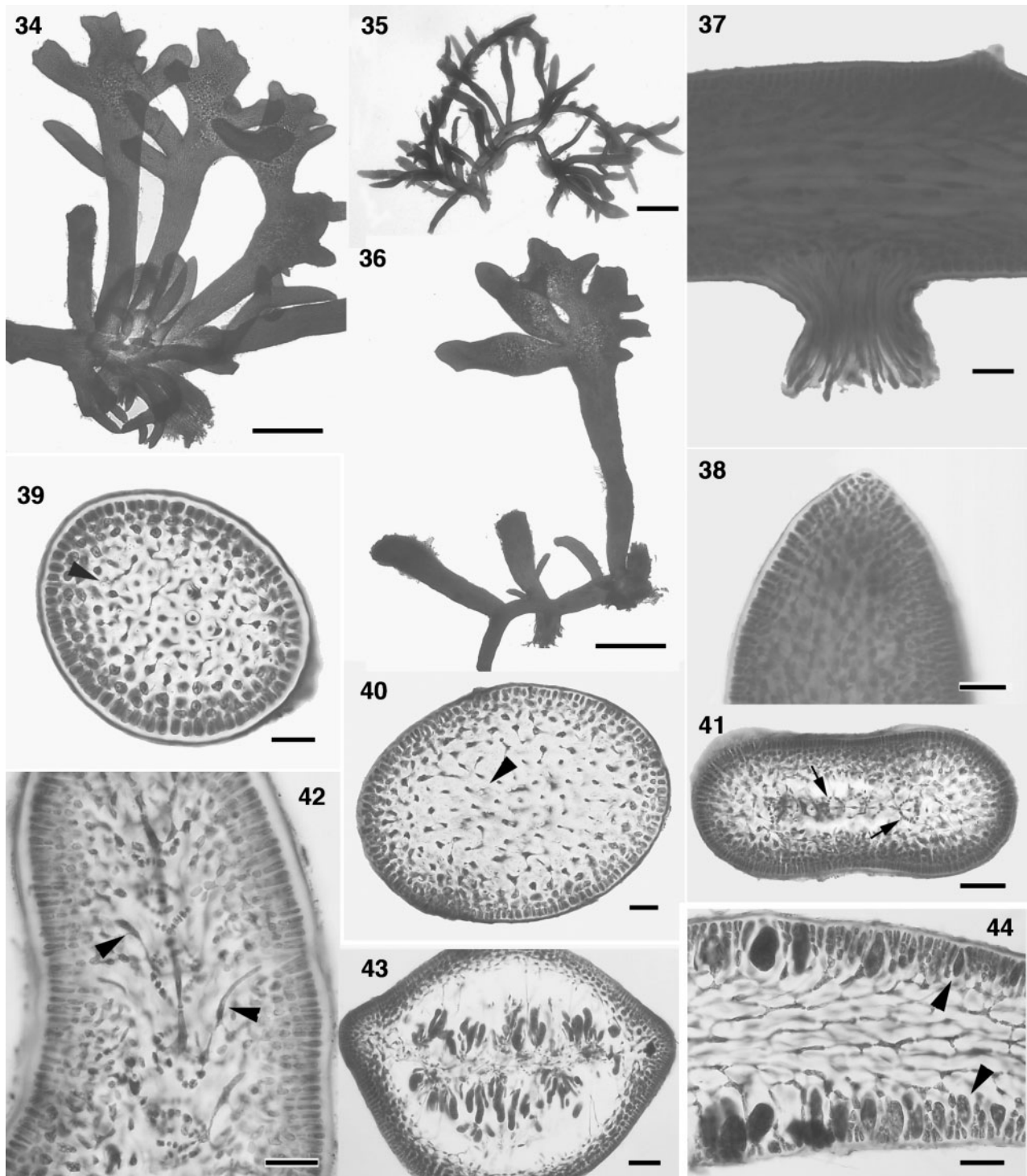
Named in honour of our good friend and colleague, Professor Bernabé Santelices (Pontificia Universidad Católica de Chile), who has spent the better part of several decades studying the order Gelidiales.

#### *Distribution*

From Byron Bay in the north to at least the Sydney metropolitan area of the NSW coastline, but probably more widespread along the coast.

#### *Habitat and morphology*

Specimens growing as small clumps or turfs on barnacles and rocks in the upper intertidal zone. Plants consist of a system of terete prostrate branches and terete to compressed erect branches up to 4 mm in height (Figs 7, 34–36). The prostrate branches are attached to the substratum by peg-like holdfasts of consolidated rhizoidal cells that develop into discoid pads (Fig. 37). Erect branches most often originate from the sub-dorsal surfaces of prostrate branches and may be prolific. Erect branches are ligulate and mostly simple but may have up to three orders of irregular marginal branching (Figs 34, 35). Main axes and marginal branches are not basally constricted and have apices that are acute during initial development but later become obtuse (Fig. 38). Branches are cylindrical at their bases, and gradually become compressed. Thalli are uniaxial with distinct apical cells (Fig. 38). Transverse sections through prostrate (Fig. 39) and erect (Fig. 40) branches show a cortex containing four or five and three or four layers of cells, respectively. Cells in the outer cortical layer are anticlinally elongated. Inner cortical cells are cuboidal but become more irregular and also elongated parallel to the branch axis near the medulla. Medullary cells are thick-walled and elongated in a direction



**Figs 34–44.** *Gelidium bernabei*. **Fig. 34.** Habit of specimen from holotype clump of plants. NSW 605631, NSW Slide 28-1. Scale = 500  $\mu$ m. **Fig. 35.** Habit of paratype from Long Reef. NSW 615573. Scale = 1 mm. **Fig. 36.** Habit of plant with secondarily attached branches. NSW Slide 28-1. Scale = 500  $\mu$ m. **Fig. 37.** Rhizoidal pad typical of attachment holdfasts. NSW Slide 28-2. Scale = 25  $\mu$ m. **Fig. 38.** Young branch apex showing apical cell. NSW 28-2. Scale = 25  $\mu$ m. **Fig. 39.** Transverse section of prostrate branch showing cortical cells and rhizine (arrowhead) distribution. NSW Slide 28-3. Scale = 25  $\mu$ m. **Fig. 40.** Transverse section of erect branch showing cortical cells and rhizine (arrowhead) distribution. NSW Slide 28-4. Scale = 25  $\mu$ m. **Fig. 41.** Transverse section of cystocarp showing nutritive cell filaments (arrows) growing around second order branch cells. NSW Slide 28-6. Scale = 50  $\mu$ m. **Fig. 42.** Longitudinal section of fertile branch showing carpegonia (arrowheads). NSW Slide 28-5. Scale = 25  $\mu$ m. **Fig. 43.** Transverse section of mature cystocarp. NSW Slide 28-6. Scale = 50  $\mu$ m. **Fig. 44.** Longitudinal section showing tetrasporangial initials (arrowheads) and mature tetrasporangia. NSW Slide 28-8. Scale = 25  $\mu$ m.

parallel to the branch axis. Rhizines are abundant throughout the medulla and extend into the inner cortex of erect branches (Fig. 40). Rhizines are less abundant and predominantly located within the outer medulla and inner cortex of prostrate branches (Fig. 39).

Reproductive structures occur on erect axes that may be simple or branched, sometimes in multiple planes (Figs 7, 34, 36). Early development of female reproductive structures occurs terminally on main axes and branches. Young fertile areas have a median depression on each side of the branch (Fig. 41). Nutritive filaments are borne on basal cells of the third-order cell rows on both sides of the central plane of the blade, and grow around cells of the second-order cell rows (Fig. 41). Carpogonia develop from intercalary cells of third-order cell rows (Fig. 42). Mature cystocarps are bilocular and located subterminally (Fig. 43). Carposporangia are produced singularly or in clusters from gonimoblast cells that with the nutritive cell filaments form a placental tissue layer that surrounds the second-order cell rows in the centre of the cystocarp cavity (Fig. 43). Some cells of the third-order cell rows elongate during expansion of the cystocarp cavities maintaining a connection between the central placental tissue and the pericarp. At maturity the pericarp is composed of six or seven layers of cortical cells. Ostioles lacking peristomes are formed on both sides of the cystocarps.

Tetrasporangia-bearing axes have multiple orders of irregular to palmate branching (Figs 34, 36). Tetrasporangial sori have no sterile margin. Tetrasporangia are arranged irregularly and initially develop acropetally (Fig. 44). Older portions of sori contain tetrasporangia in various stages of development. Mature tetrasporangia are cruciately divided (Fig. 44). Spermatangial sori have not been observed.

#### Remarks

*Gelidium bernabei* can be distinguished from all other New South Wales turfey Gelidiales by a combination of characters (Table 2). The subdorsal emergence of erect branches from prostrate branches is generally diagnostic and specimens observed in this survey did not attain the height of other turf species. *Gelidium bernabei* can be distinguished from *Capreolia implexa* by its predominantly simple branching, abundant rhizines throughout the medulla, absence of sterile margin around tetrasporangial sori and an irregular arrangement of tetrasporangia within sori. It differs from *G. declerckii* in its predominantly simple, non-flattened erect branches and tetrasporangial sori with no sterile margin. The basally terete to distally compressed erect branches of *G. bernabei* also separate it from *G. isabellae*, which has flat, stipitate erect branches. *Gelidium bernabei* differs from *G. crinale* in having irregular branching, terete bases of erect axes, and obtuse apices.

The *rbcL* sequences of *G. bernabei* specimens collected at Gordon Bay and Long Reef varied at two sites and are

highly divergent from those for other New South Wales *Gelidium* species. Phylogenetic analyses indicate that *G. bernabei* represents an isolated lineage within the large clade of Gelidiales taxa that have the 'Gelidium-type' reproductive development (Bailey and Freshwater 1997). There is strong bootstrap and Bayesian clade-probability support for *G. bernabei* diverging within the 'Gelidium-type' reproductive lineage after the two clades containing *Capreolia* and *Ptilophora* species. Although *G. bernabei* is resolved as the next lineage to diverge after the *Capreolia* and *Ptilophora* clades in the maximum-likelihood tree, there is no support for this exact position (Fig. 113).

#### Specimens examined

Broken Head, South of Byron Bay, intertidal rocks on beach at northern side of headland, tetrasporophyte, *A.J.K.Millar & P.G.Richards*, 26.vii.1992, NSW 292721, NSW 292722. North side of Gordons Bay, Clovelly, upper intertidal rocks, *D.W.Freshwater & A.J.K.Millar*, 17.vii.2002, NSW 605631(NSW #5). Long Reef, Collaroy, upper intertidal rocks and on chitons, *D.W.Freshwater & A.J.K.Millar*, 4.ix.2002, NSW 615573 (NSW #14).

#### Molecular vouchers

Specimen NSW #5, 1396 bp *rbcL* accession # AY352419; NSW #14, 1389 bp *rbcL* accession # AY352418.

***Gelidium crinale* (Turner) Gaillon**, Dictionnaire des Sciences Naturelles 53: 362 (1828). Harvey 1846: pl. 53, fig. 5; Okamura 1937: 195, pl. 146, figs 1–10; Womersley & Guiry 1994: 133, figs 35D, 39A–D

Figs 47–52.

*Basionym:* *Fucus crinalis* Turner, *Fuci sive Plantarum Fucorum* ..... 4: 198 (1819).

*Homotypic synonyms:* *Gelidium corneum* var. *crinalis* (Turner) Greville, *Algae britannicae* ... 145 (1846).

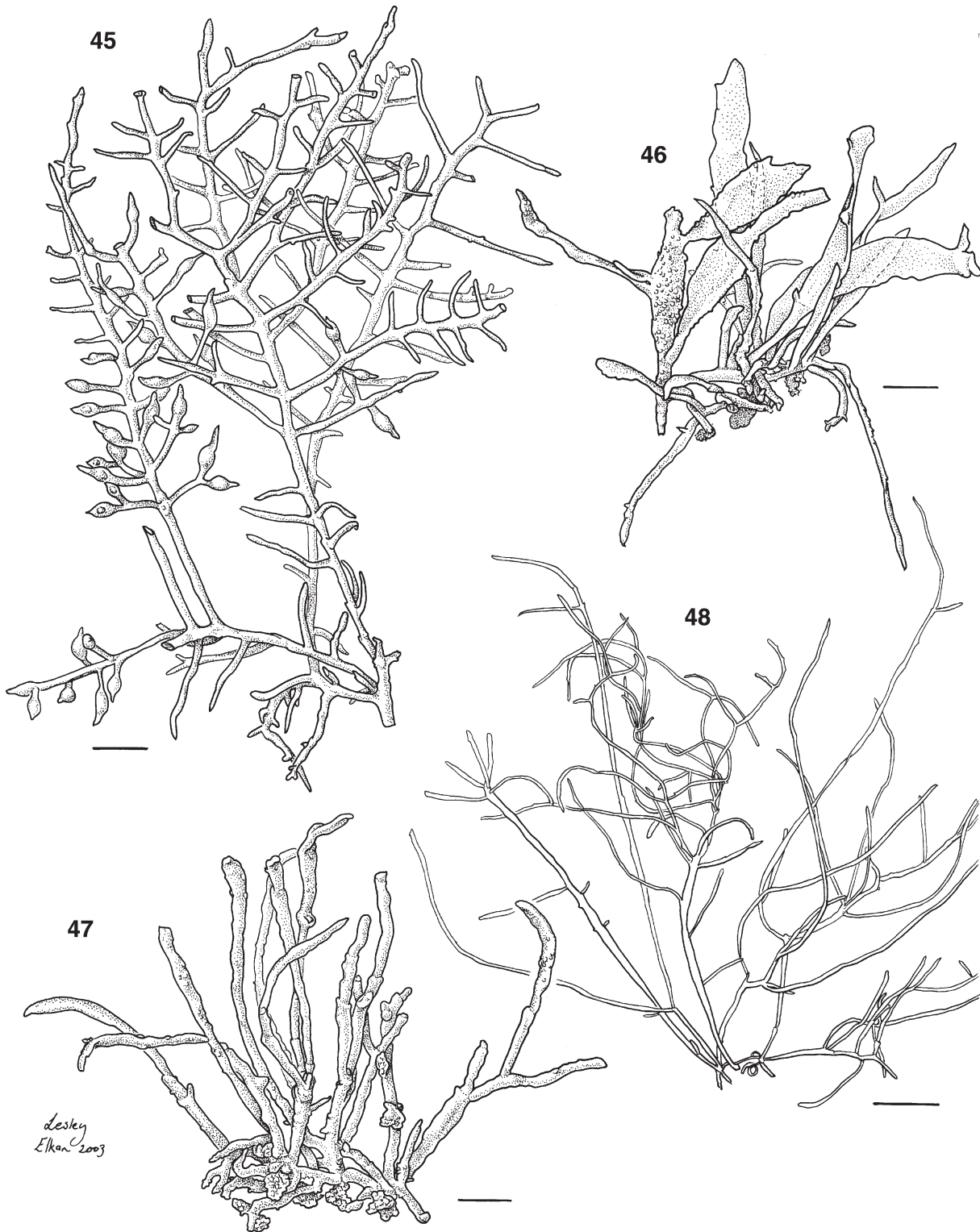
*Acrocarpis crinalis* (Turner) Kützinger, *Phycologia generalis* ... 405 (1843).

*Misapplied name:* *Gelidium pusillum* sensu Millar and Kraft (in part), *Aust. Syst. Bot.* 6: 11 (1993).

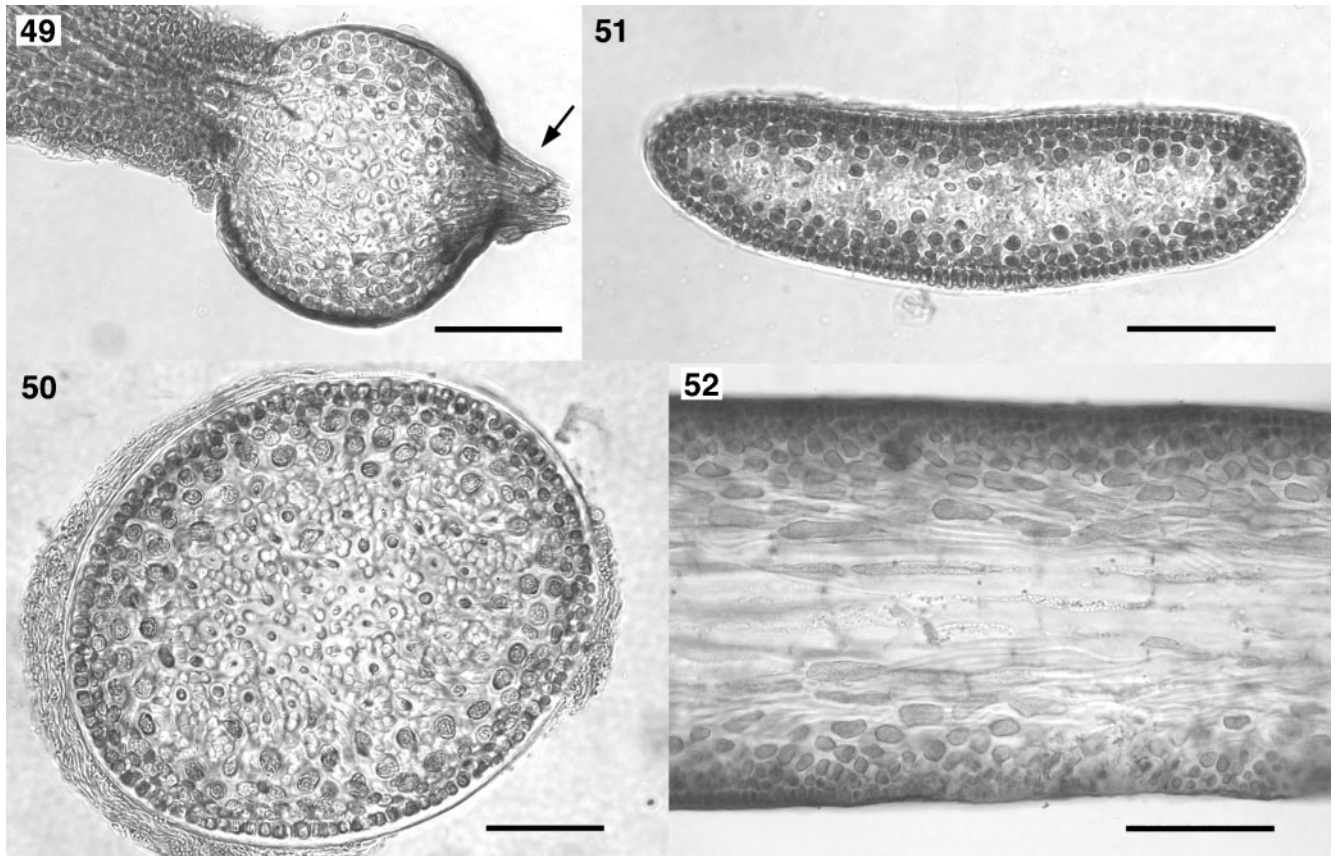
*Type:* in BM from near Ilfracombe, Devon, England (Dixon and Irvine 1977: 140).

#### Habitat and morphology

Two morphological forms (Figs 47, 48), differing predominantly by size, were found growing as intertidal turfs. Erect branches of the short, wiry form are 0.1–0.2 mm in width and 2–5 mm in height, while those of the larger form are 0.2–0.8 mm in width and 9–18 mm in height. Thallus colour dark red to black. Thallus cartilaginous, composed of terete prostrate branches giving rise to proximally terete to compressed erect branches that become compressed to flattened distally. Erect branches are linear to narrowly lanceolate, and may be mostly simple (short form, Fig. 47) or have up to two orders of distichous branching (large form, Fig. 48). Many specimens have tri- to multifurcate



**Figs 45–48.** *Gelidium* habits. **Fig. 45.** *Gelidium hommersandii*. Portion of holotype from Sydney Harbour. NSW 126946. Scale = 1 mm. **Fig. 46.** *Gelidium isabelae*. Habit of specimens from Lord Howe Island. NSW LHI #4. Scale = 1 mm. **Fig. 47.** *Gelidium crinale*. Habit of short, turf-like specimen. NSW 605635. Scale = 1 mm. **Fig. 48.** *Gelidium crinale*. Habit of large, wiry specimen. NSW 605636. Scale = 3 mm.



**Figs 49–52.** *Gelidium crinale*. **Fig. 49.** Transverse section through a prostrate branch showing a holdfast of consolidated cells (arrow) opposite of the attachment point of an erect branch. NSW 701609. Scale = 100  $\mu\text{m}$ . **Fig. 50.** Transverse section through subterete portion of erect branch. WNC Slide 2003-S049. Scale = 50  $\mu\text{m}$ . **Fig. 51.** Transverse section through compressed portion of erect branch. NSW 701610. Scale = 50  $\mu\text{m}$ . **Fig. 52.** Longitudinal section through an erect branch. NSW 701609. Scale = 50  $\mu\text{m}$ .

tips. Branch bases are unstricted and apices are mostly acute with a prominent apical cell. Holdfasts of consolidated cells forming a cylindrical peg or brush (Fig. 49). Thallus composed of a cortex of three or four cell layers surrounding a medulla of elongated, thick walled cells (Figs 50, 51). Outer cortical cells are globose to elliptical, but inner cortical cells become elongated in the direction of the axis near the medulla (Fig. 52). Rhizines abundant and filling intercellular space throughout the medulla and inner cortex (Figs 50, 51).

Tetrasporangia, spermatangia and cystocarps not observed.

#### Distribution

Known throughout the Indian Ocean (Silva *et al.* 1996), northern Atlantic (Thomas 2000) and Pacific Oceans (Thomas 2000). On the New South Wales mainland, we have collected this species from Montague Island in the south to Broken Bay in the Sydney Metropolitan region. It occurs extensively on Lord Howe Island, but has not been discovered on Norfolk Island.

#### Remarks

*Gelidium crinale* has been previously reported from Western Australia and South Australia (Huisman 1993; Womersley and Guiry 1994). This is the first record of *G. crinale* from New South Wales, previous collections having been referred to *G. pusillum* (Millar and Kraft 1993). *Gelidium crinale* was first described by Turner (1819) based on specimens from Britain. This species, as well as *G. pulchellum* (Turner) Kützing, were included by Dixon and Irvine (1977) in an expanded concept of *G. pusillum*. Fredriksen *et al.* (1994) included breeding and isoenzyme studies to show that *G. pulchellum* and *G. pusillum* were separate entities, and this was further supported by Freshwater and Rueness (1994). Current research by Rico, Thomas and Freshwater (Thomas 2000; JM Rico DT Thomas and DW Freshwater unpubl. data) has likewise shown that *G. crinale* is indeed a separate species from *G. pusillum*.

Morphological variability in *G. crinale* collected from different environments has been previously noted and has led to some taxonomic confusion (e.g. Kapraun 1980).

Young or short specimens may resemble other turfy *Gelidium* species, and this was probably a factor in Dixon and Irvine's (1977) proposed synonymy of *G. crinale* and *G. pusillum*, which they based in part on following the growth of marked plants in nature. Larger, more profusely branched specimens have also been identified as *G. pulchellum* (e.g. Williams 1948). Many erect branches of *G. crinale* will generally be tri- or multifurcate giving the tips a fork-like appearance. Although present in the studied New South Wales specimens, this characteristic was not as prevalent as in specimens examined from other regions of the world. New South Wales specimens of *G. crinale* can be distinguished from other turfy *Gelidium* species in the area by several characters (Table 2). Short-form specimens are similar to *G. bernabei* but can be identified by their having more narrow erect branches that originate from the dorsal, v. subdorsal, surface of prostrate branches. *Gelidium crinale* differs from the turf form of *G. hommersandii* in its less profuse, distichous branching and having compressed to flattened distal portions of erect branches. *Gelidium declerckii* is more profusely branched than *G. crinale* and has clavate shaped erect branches. The larger form of *G. crinale* collected at Lord Howe Island is somewhat similar to *G. isabellae* but does not have erect branches that are constricted at the base with obtuse tips. *Gelidium crinale* erect branches are also not as flattened, nor do they show the decussate lines in surface view that are often visible in *G. isabellae*.

*Gelidium crinale* has been reported from many localities around the world (e.g. Silva *et al.* 1996; Shimada *et al.* 1999), and *rbcL* sequence analyses confirm that this species is widely distributed (Thomas 2000). We have collected *G. crinale* from Summer Cloud Bay, Jervis Bay, on mainland NSW and Lord Howe Island. Analyses of *rbcL* sequences from these samples showed that they were identical and sister to that from a Western Australian sample collected by John Huisman (Table 1; Fig. 113). *Gelidium crinale* is resolved within the '*G. coulteri*' clade of Freshwater *et al.* (1995) in analyses of both *rbcL* and LSU sequences (Freshwater and Bailey 1998; Shimada *et al.* 1999).

#### *Specimens examined*

NEW SOUTH WALES mainland: Summer Cloud Bay, Bherwerre Peninsula, Jervis Bay, intertidal rocks, *A.J.K.Millar*; *N.Yee & D.W.Freshwater*, 30.vii.2002, NSW 614404, NSW 605635 (NSW #7); South side of North West Trench, Montague Island, 29 m deep forming turf on rocks, *A.J.K.Millar*; *P.G.Richards & N.Yee*, 28.ii.2000, NSW 605636 (NSW Slide 25–3); Barrenjoey Head, Broken Bay, *V.May* #516B, 25.ii.1945, NSW 209105, NSW 209103. LORD HOWE ISLAND: Far Rocks, Signal Point, forming a band above the *Corallina officinalis* belt, *G.Kraft*, *C.O'Brien & R.Wetherbee*, 11.v.1977 (MELU K10016); Signal Point, *G.Kraft & C.O'Brien*, 2.x.1976 (MELU GK9145); Old Gulch, tall intertidal turf, *A.J.K.Millar & D.W.Freshwater*, 4.x.2002, NSW 614405, NSW 605637, NSW 701609, NSW 701610, (LHI #1); Neds Beach, high intertidal

pools, *G.Kraft*, 3.xii.1978 (MELU). WESTERN AUSTRALIA: Rottnest Island, Fish Hook Bay, *J.M.Huisman*, 28.iii.1999, MURU and WNC.

#### *Molecular vouchers*

Specimen NSW #7, 1396 bp *rbcL* accession # AY350781; identical *rbcL* sequence from specimen LHI #1.

#### *Gelidium declerckii* Tronchin *sp. nov.*

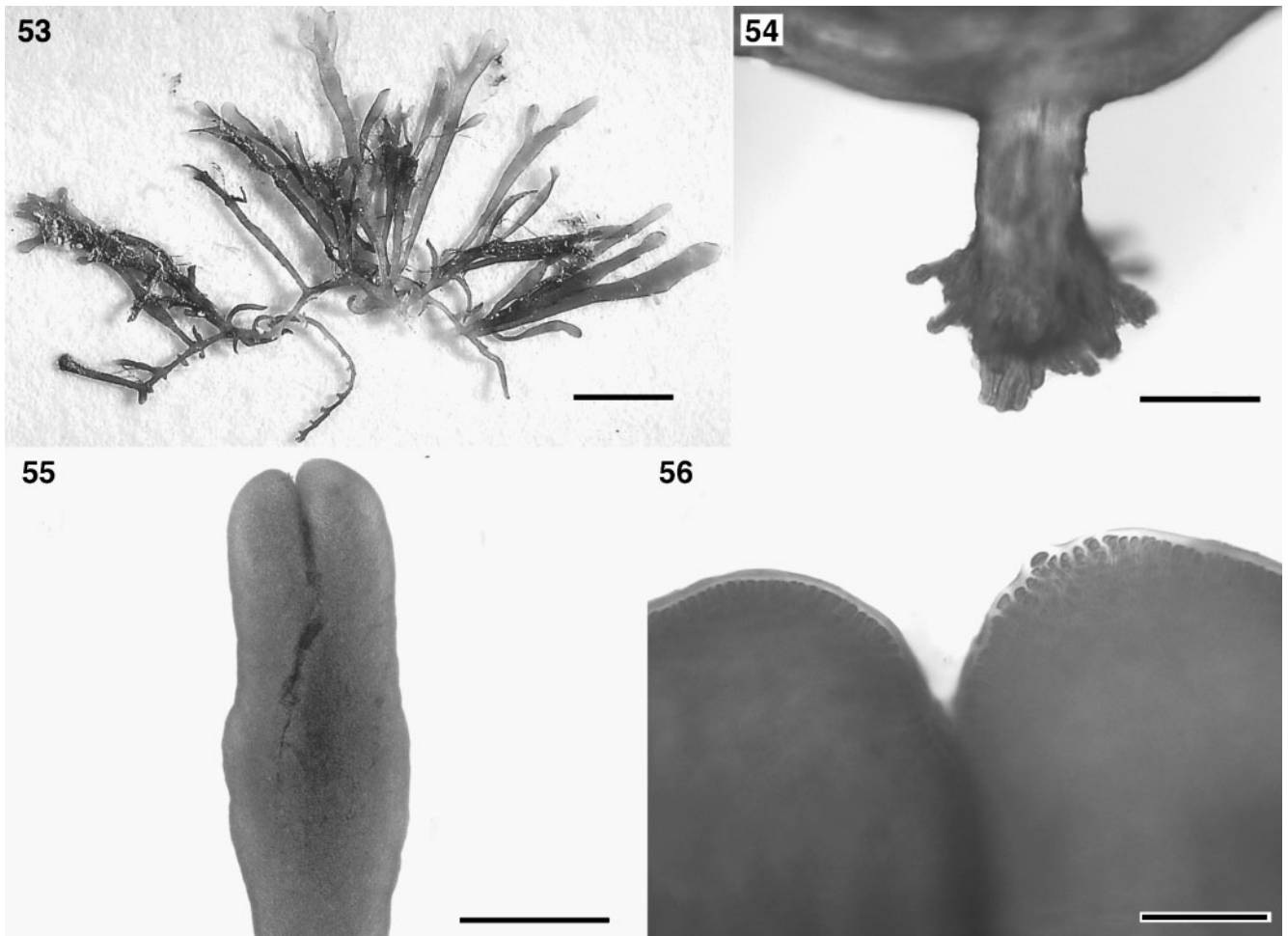
Figs 53–65.

*Holotype*: NSW 614429, 20.vi.2002, *D.W. Freshwater & A.J.K.Millar*. NSW-9 (Fig. 53).

#### *Description*

Thalli erecti (2–)3.5–10(–15) mm alti. Stolones prostrati teretes ca. 125 µm diametro. Axes erecti cylindracei ad subcylindracei in parte basali, sursum complanati [50–100(–140) µm crassi et 200–450(–600) µm lati] in parte distali. Apices ramorum obtusi, bipartiter vel tripartiter. Ramificatio irregularis et disticha. Prolifcationes superficiares ramorum frequentes. In partibus distalibus ramulorum complanatis, usque ad ordines 5 ramorum genitos, crispatos, irregulariter curvatos tortosque. Lacerae apicalitè et in margines distales. In sectione transversa, cellulæ corticales externae quadratae usque ad 8 µm longitudine 5 µm latitudine multus angustiore, cum ratione longitudinis/latitudinis 1–1.5. Cellulæ interaneae corticales globosae protoplastis angulosis, 6–10 µm (pro parte maxima ca. 8 µm) diametro. Filamenta rhizoidalia inter cellulæ corticales interaneas, pro parte maxima < 3 µm diametro omnino medulla dispersa. Cellulæ medullosae ovoideae usque ad 17 µm diametro. Sori spermatangiales subterminales, in superficiebus ambabus laminarum, circumcincti angusto margine sterili. Sori tetrasporangiales subterminales, initio evoluti acropetalitè. Tetrasporangia cruciatim divisa, 22–34 µm longa, 22–30 µm lata aspectu superficiali, cum ratione longitudinis/latitudinis 1–1.5. Cystocarpia ignota.

Uprights (2–)3.5–10(–15) mm in height. Prostrate stolons terete, ~125 µm in diameter. Uprights cylindrical to subcylindrical becoming flattened [50–100(–140) µm thick], broadening distally [200–450(–600) µm wide]. Apices blunt, bi- or tripartite. Irregularly and distichously branched. Surface proliferations common. In the flattened distal parts up to five orders of branches produced, crisped, irregularly curled and twisted. Lacerations occur apically and on distal margins. In transverse section, outer cortical cells quadrangular, up to 8 µm in length, as narrow as 5 µm in width, with a length/width ratio of 1–1.5. Inner cortical cells are globose with angular protoplasts, 6–10 µm (mostly approximately 8 µm) in diameter. Rhizines occur between inner cortical cells, mostly < 3 µm in diameter, and scattered throughout the medulla. Medullary cells ovoid, up to 17 µm in diameter. Spermatangial sori subterminal, on both blade surfaces,



**Figs 53–56.** *Gelidium declerckii*. **Fig. 53.** Habit of holotype. NSW 614429. Scale = 2 mm. **Fig. 54.** Cylindrical attachment holdfast (issuing from prostrate stolon) terminating in brush-like hapteron of elongate, acetate cells. BOL wet collection 510. Scale = 100 µm. **Fig. 55.** Distal region of upright developing an apical bifurcation. BOL wet collection 510. Scale = 400 µm. **Fig. 56.** Magnification of apex in Fig. 55 showing initial stages of bifurcation. Note only one branch has an apical cell. BOL wet collection 510. Scale = 100 µm.

surrounded by narrow sterile margin. Tetrasporangial sori subterminal, initially acropetally developed. Tetrasporangia cruciately divided, 22–34 µm long and 22–30 µm wide in surface view, with length/width ratio of 1–1.5. Cystocarps unknown.

#### *Type locality*

Plantation Point, Jervis Bay, NSW.

#### *Etymology*

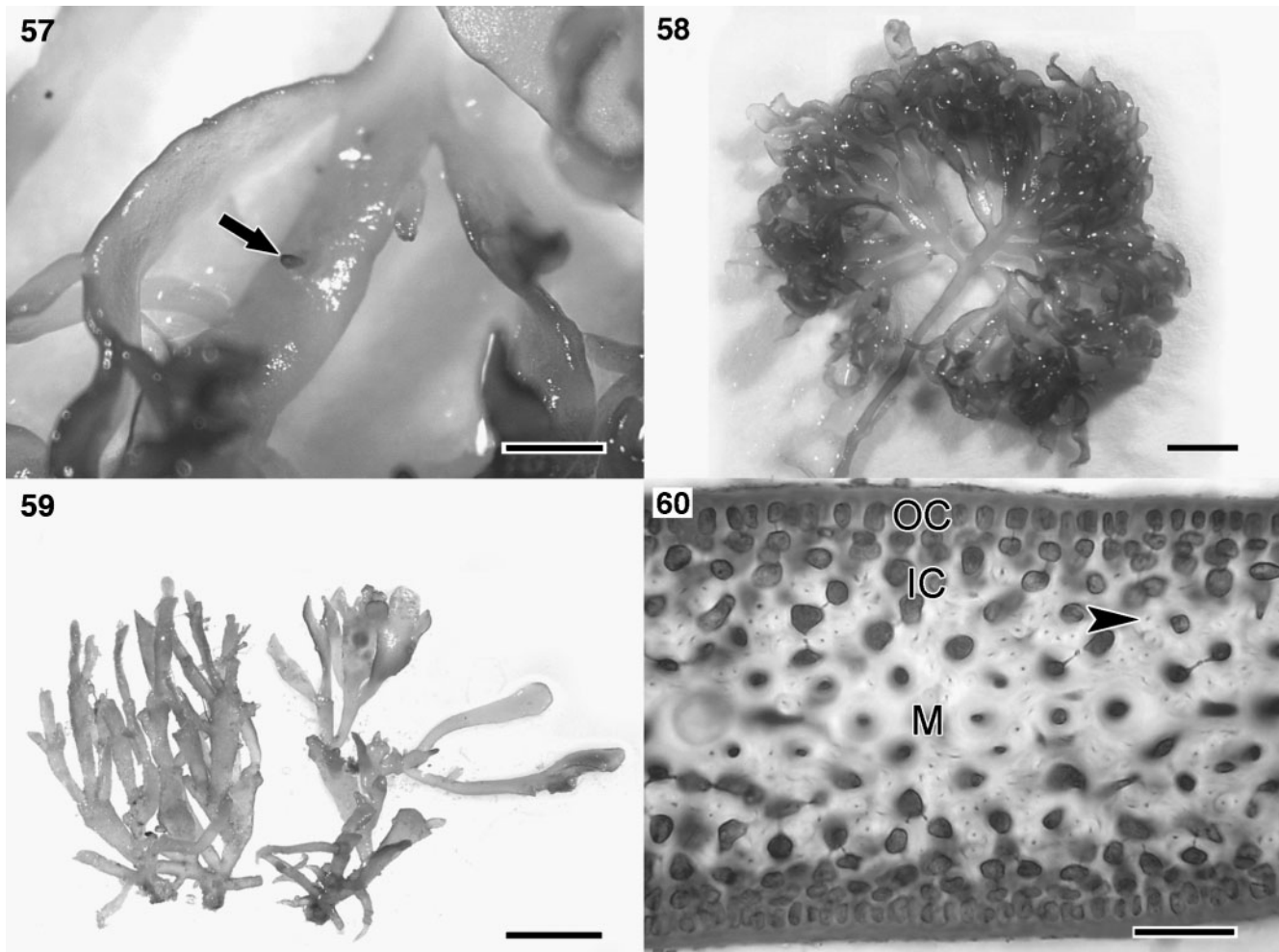
This species is named after Dr Olivier De Clerck (University of Gent, Belgium) in recognition of his passion and enthusiasm for algal taxonomy and his wonderful ability to communicate it. Dr Enrico Tronchin contemporaneously and collaboratively discovered and sequenced this species from South Africa, but recommended that the NSW populations be made the type locality based on their reproductive state.

#### *Distribution*

Known from the south-eastern coasts of South Africa and Australia. South African plants have been recorded from Nahoon Point (East London) and Kidd's Beach, two localities ~50 km apart along the coast of the Eastern Cape Province of South Africa. Australian plants have only been recorded from Plantation Point, Jervis Bay, New South Wales.

#### *Habitat and morphology*

Plants may either occur in small patches on mollusc shells and rock surfaces or may form a more expansive turf on intertidal rock platforms. Plants are dark purple in colour, occurring in dense tufts of uprights (2–)3.5–10(–15) mm in height united by terete prostrate stoloniferous branches ~125 µm in diameter (Fig. 53). Rhizoids issue irregularly along prostrate stolons and are cylindrical, either tapering



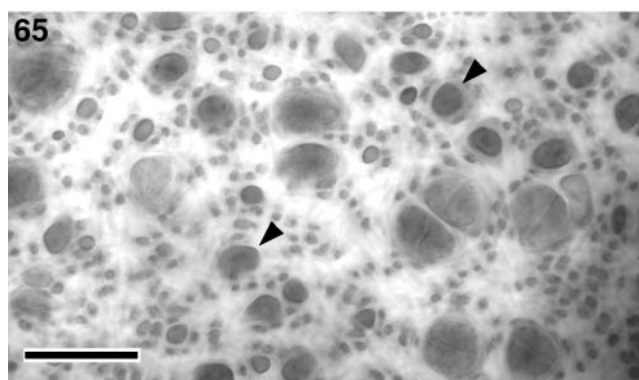
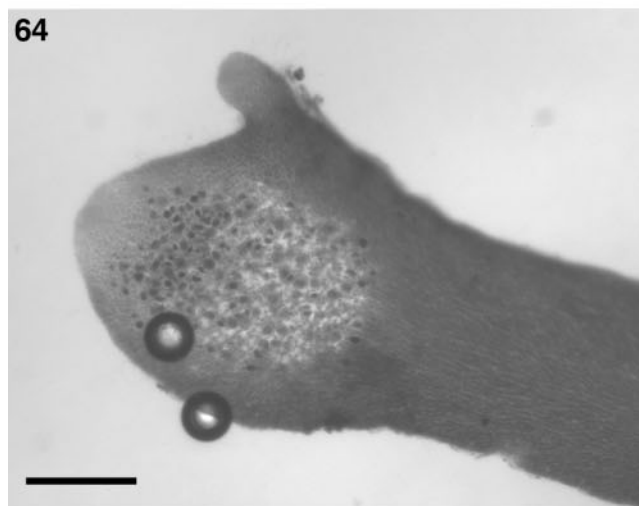
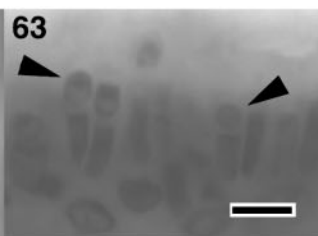
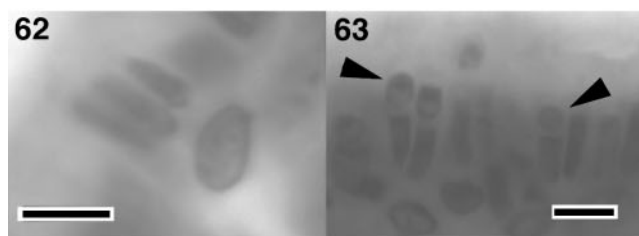
**Figs 57–60.** *Gelidium declerkii*. **Fig. 57.** Papillate proliferation issuing from surface of flattened distal branch. BOL 510. Scale = 1 mm. **Fig. 58.** Distichously branched upright with irregularly curled and twisted branches. BOL 510. Scale = 2 mm. **Fig. 59.** Presumably grazed specimen displaying more robust, rigid and branched habit with only a few distal branch portions retaining bi- and tri-furcate apices. BOL 509. Scale = 2 mm. **Fig. 60.** Transverse section showing an outer cortex (OC), inner cortex (IC) with interspersed rhizines (arrowhead), and thick-walled, filamentous medulla (M). BOL 110878, Slide 170. Scale = 50  $\mu\text{m}$ .

to an abrupt point or producing at their ends brush-like attachment haptera (Fig. 54), composed of thick-walled, acetate cells, when they contact the substratum. Uprights are cylindrical to subcylindrical basally (50–100  $\mu\text{m}$  in diameter) becoming flattened [50–100(–140)  $\mu\text{m}$  thick], broadening distally [200–450(–600)  $\mu\text{m}$  wide] and terminating in blunt apices that may be bi- or tripartite (Fig. 53), sometimes pseudodichotomous and often lacerated. Lacerations may occur terminally (Fig. 55), on either side of the apical cell (Fig. 56), or marginally, running longitudinally down the upright. Surface proliferations are common and range from small papillae (Fig. 57) to flattened, adventitious branches. Apical cells are dome-shaped and may be flush with the outer cortical layer of cells or may be slightly protuberant. Branching is irregular and distichous, occurring mostly basally on the uprights and close to the

apices. In the flattened, distal reaches of the thallus up to five orders of branches may be produced that are crisped and irregularly curled and twisted (Fig. 58). Presumably grazed thalli lack the abovementioned extensively branched and irregularly curled distal regions, but may still bear a few uprights that are slightly twisted and curled distally (Fig. 59). These thalli are generally more robust, rigid and prolifically branched proximally. Nonetheless, their uprights are still subcylindrical basally (up to 175  $\mu\text{m}$  thick) becoming quickly flattened distally and producing tripartite apices on occasion.

In transverse section, thalli have an outer cortex of quadrangular cells that are up to 8  $\mu\text{m}$  in length and as narrow as 5  $\mu\text{m}$  in width, with a length/width ratio of 1–1.5 (Fig. 60). Inner cortical cells are variably shaped, mostly globose and 8  $\mu\text{m}$  in diameter (ranging from 6 to 10  $\mu\text{m}$ ), with





angular protoplasts. Rhizines are numerous, mostly  $< 3 \mu\text{m}$  in diameter, and occur in clusters between inner cortical cells and scattered throughout the medulla. In branch apices rhizines are few and instead occur individually and scattered throughout the internal tissue. Medullary filaments are round to ovoid in transverse section, thick-walled and up to  $17 \mu\text{m}$  in diameter. Cells in the stoloniferous branches can become somewhat larger: outer cortical cells may be up to  $10 \mu\text{m}$ , inner cortical cells up to  $12.5 \mu\text{m}$  and rhizines up to  $5 \mu\text{m}$  in diameter.

Rounded to obovate spermatangial sori occur subterminally on erect branches. Sori are found on both blade surfaces and are surrounded by a narrow sterile margin (Fig. 61). Outer cortical cells undergo two anticlinal cell divisions giving rise to four elongated spermatangial initials (Fig. 62). Spermatangia are formed by transverse divisions of the spermatangial initials (Fig. 63). Tetrasporangia develop acropetally in young portions of sori that occur subterminally on erect branches (Fig. 64). Both mature and developing tetrasporangia are present in older portions (Fig. 65). Tetrasporangia are cruciately divided and when viewed from the surface are  $22\text{--}34 \mu\text{m}$  long,  $22\text{--}30 \mu\text{m}$  wide, with a length/width ratio of  $1\text{--}1.5$ . Cystocarpic plants have not been found.

#### Remarks

*Gelidium declerckii* has features in common with numerous descriptions of *Gelidium pusillum* and its varieties from the world over, but none have exactly the same complement of thallus proportions and cell dimensions. No gelidialean turf-forming species has previously been described to regularly develop uprights with irregularly curled and twisted distal ends, such as are produced by *G. declerckii*. It should be noted, however, that uprights of *Gelidium reptans* (Suhr) Kylin may become twisted and Womersley and Guiry (1994) describes the uprights of *G. pusillum* from southern Australia as having slightly undulate distal margins.

When grazed, this species most closely resembles *Gelidium arenarium* Kylin recorded from two localities in the KwaZulu-Natal Province of South Africa. Compared to

**Figs 61–65.** *Gelidium declerckii*. **Fig. 61.** Transverse section of fertile branch showing spermatangial sori (arrows) on both blade surfaces, and narrow sterile margins. WNC Slide 2003-S036. Scale =  $100 \mu\text{m}$ . **Fig. 62.** Elongated spermatangial initials formed by the anticlinal division of an outer cortical cell. Three of four spermatangial initials visible in plane of focus. WNC Slide 2003-S044. Scale =  $10 \mu\text{m}$ . **Fig. 63.** Spermatangia (arrowheads) formed by the transverse divisions of the spermatangial initials. WNC Slide 2003-S044. Scale =  $10 \mu\text{m}$ . **Fig. 64.** Tetrasporangial sorus. WNC Slide 2003-S038. Scale =  $250 \mu\text{m}$ . **Fig. 65.** Surface view of older portion of tetrasporangial sorus showing both fully developed and developing (arrowheads) tetrasporangia. Distal end = top of figure. WNC Slide 2003-S038. Scale =  $50 \mu\text{m}$ .

the lectotype of *G. arenarium* (Isipingo, T. A. Stephenson, 13 viii 1935, LD, s.n.) and the descriptions of this species (Kylin 1938; Norris 1992), it differs primarily in size: axes being consistently thicker and cells consistently smaller, particularly in the outer cortex where the range in cell size overlaps that of *G. arenarium* by only 1  $\mu\text{m}$ . *G. arenarium* also has mostly cylindrical axes, and it lacks the characteristic curled and twisted distal parts, although Norris (1992, fig. 2) appears to illustrate two slightly curled apices.

Some uprights of *G. declerckii* appear to experience a sudden onset of apical proliferation (Fig. 58). It is likely that this is promoted by the longitudinal laceration of the flattened apices. Of the two branches resulting from a laceration, only one bears an apical cell early on (Fig. 56), the second branch developing an apical cell later and resuming apical growth.

This species can be distinguished from other turfey New South Wales *Gelidium* species by a combination of morphological characters (Table 2). It has clavate erect branches that become flattened unlike *G. bernabei* and the turf form of *G. hommersandii*. Its apical tips are obtuse unlike the acute tips found in *G. crinale* and *G. hommersandii* and it lacks the constricted or stipitate erect branches found in *G. isabelae*, and also the decussate lines that are often visible when viewing the surface of *G. isabelae* branches.

South African samples of *G. declerckii* from Kidd's Beach and Nahoon Point have identical *rbcL* sequences and only vary at four-nucleotide sites (< 0.3%) from the Jervis Bay, mainland NSW sample. It is strongly supported as the sister taxon to an unnamed *Gelidium* species from the Mediterranean (Fig. 113). Both these species are resolved within the 'European-Clade' of Freshwater *et al.* (1995). This is the first species with a distribution outside of the north-east Atlantic to be resolved in this clade. *Gelidium declerckii* is only distantly related to other Indo-Pacific Gelidiales species.

#### *Specimens examined*

SOUTH AFRICA: Kidd's Beach, Eastern Cape Province; *E.M. Tronchin*, 6.v.2001, BOL 110878 & BOL 510 (wet preserved); Nahoon Point, Eastern Cape Province, *E.M. Tronchin*, 7.v.2001, BOL 99067 and BOL 509 (wet preserved); NEW SOUTH WALES: Plantation Point, Jervis Bay, *A.J.K. Millar & D.W. Freshwater* 30.vii.2002, NSW 614429 (NSW #9).

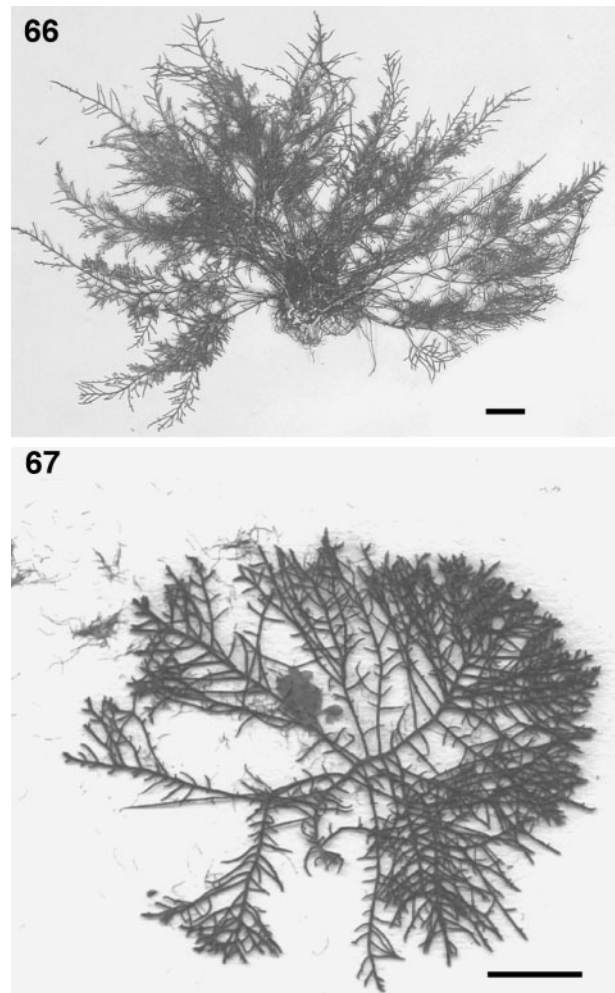
#### *Molecular vouchers*

Specimen NSW #9, 1393 bp *rbcL* accession # AY350776; BOL 99067, 1434 bp *rbcL* accession # AY350775; identical *rbcL* sequence from BOL 110878.

***Gelidium hommersandii*** A.J.K. Millar & D.W. Freshwater *sp. nov.*

Figs 45, 66–74.

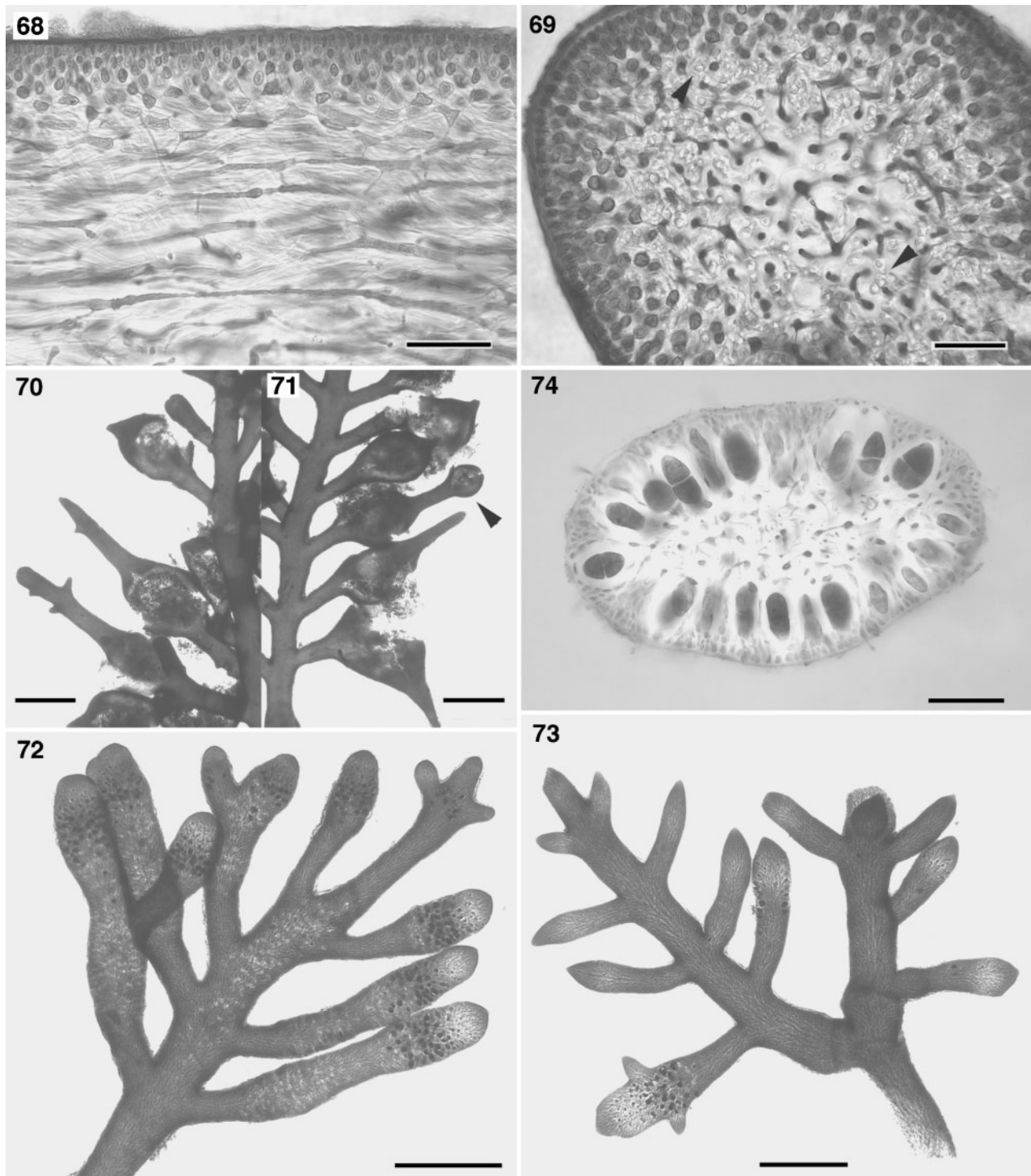
*Holotype*: NSW 126946, 12.vii.1969, *R. Coveny* (Fig. 67).



**Figs 66, 67.** *Gelidium hommersandii*. **Fig. 66.** Habit of subtidal specimen from Pahia, New Zealand. NSW 614406. Scale = 5 mm. **Fig. 67.** Habit of intertidal holotype specimen from Sydney Harbour, Australia. NSW 126946. Scale = 5 mm.

#### *Description*

Thallus ex ramis prostratis teretibus hapteris parvis obtusisque compositus, et ramis erectis teretibus fortasse compressis ubi reproductivis. Rami erecti 10–40 mm alti, lineares, usque 4 ordinibus ramificationis pinnatae vel profuse irregularis; apices acuti; cortex 4–5 stratis cellularum, et rhizinis abundantibus per medullam et corticem interiorem. Rami feminei reproductivi teretes, 2-plus ordinibus ramificationis plerumque distichae; cystocarpia bilocularia, ostiolis sine peristomiis. Rami tetrasporangiferi teretes-compressi multis ordinibus ramificationis distichae vel irregularis; tetrasporangia irregulariter disposita in soris sine marginibus sterilibus, cruciatim divisa, 30–40  $\mu\text{m}$  longa, 25–30  $\mu\text{m}$  lata aspectu superficiali.



**Figs 68–74.** *Gelidium hommersandii*. **Fig. 68.** Longitudinal section showing a four- or five-celled cortex and periclinally elongated medullary cells. WNC Slide 2003-S087. Scale = 50  $\mu$ m. **Fig. 69.** Transverse section showing cortical layer and thick-walled medullary cells. Rhizines (arrowheads) are abundant within the medulla and inner cortex. WNC Slide 2003-S086. Scale = 50  $\mu$ m. **Fig. 70.** Whole mount of cystocarp bearing branchlets showing acute and acuminate tips. NSW 485004. WNC Slide 2003-S097. Scale = 500  $\mu$ m. **Fig. 71.** Whole mount showing fertile branchlet (arrowhead) bearing two cystocarps. NSW 485004. WNC Slide 2003-S096. Scale = 500  $\mu$ m. **Fig. 72.** Whole mount of New Zealand specimen showing tetrasporangial branchlets. WNC Slide 2003-S088. Scale = 500  $\mu$ m. **Fig. 73.** Whole mount of Australian specimen showing tetrasporangial branchlets. WNC Slide 2003-S082. Scale = 500  $\mu$ m. **Fig. 74.** Transverse section of tetrasporangial sorus showing no sterile margin and tetrasporangia at different stages of development. WNC Slide 2003-S083. Scale = 50  $\mu$ m.

Thallus composed of terete prostrate branches with peg-like holdfasts, and terete erect branches possibly compressed when reproductive. Erect branches 10–40 mm tall, linear with up to four orders of pinnate or profuse irregular branching; apices acute; cortex with four or five cell layers, and rhizines abundant throughout medulla and inner cortex. Female reproductive branches terete with two or more orders of mostly distichous branching; cystocarps bilocular, with ostioles without peristomes. Tetrasporangial branches terete to compressed with multiple orders of distichous or irregular branching; tetrasporangia arranged irregularly in sori with no sterile margins, cruciately divided, 30–40 µm long, 25–30 µm wide in surface view.

#### *Type locality*

Mrs Macquaries Point, northern point of Woolloomooloo Bay, Sydney Harbour.

#### *Etymology*

This name honours our good friend, colleague and mentor Professor Max H. Hommersand (University of North Carolina, Chapel Hill, USA), who has devoted a lifetime to the study of red algae including the order Gelidiales.

*Misapplied names:* *Gelidium caulacanthum sensu* May (in part) *Proc. Linn. Soc. N.S.W.* 74: 196 (1949). *Contr. N.S.W. Natn. Herb.* 3: 371 (1965).

*Gelidium pusillum sensu* May (in part) *Proc. Linn. Soc. N.S.W.* 74: 196 (1949).

#### *Distribution*

South-east Australia and New Zealand.

#### *Habitat and morphology*

Specimens found from the mid-intertidal in rock crevices and irregularities, down into the subtidal zone. Plants consist of a system of terete rhizoidal and erect branches. The prostrate rhizoidal branches are attached to the substratum by peg-like holdfasts of consolidated rhizoidal cells. Erect axes to 10–40 mm in length with up to four orders of profuse (Fig. 66) or distichous (Fig. 67) laterals that are either at 45-degree angles to main axes (Fig. 66) or are patent (90-degree angles, Figs 45, 67). Main axes and marginal non-fertile branches have mostly acute apices and with no, to slight, basal constrictions. Sterile branches are terete throughout, but fertile branchlets may be compressed (Fig. 74). Thalli are uniaxial with distinct apical cells. Longitudinal (Fig. 68) and transverse (Fig. 69) sections show a cortex containing four or five layers of cells. Cells in the outer cortex are elliptical to rectangular; inner cortical cells are globose to irregular. Medullary cells are thick-walled and elongated in a direction parallel to the branch axis. Rhizines are abundant throughout the medulla and inner cortex (Fig. 69).

Cystocarps are bilocular and develop in the middle to distal portions of branchlets that have two or more orders of predominantly distichous branching (Figs 70, 71). Branchlets are terete with acute or acuminate tips and may bare multiple cystocarps (Fig. 71). At maturity cystocarps have a pericarp of five to seven layers of cortical cells and ostioles lacking peristomes.

Tetrasporangia bearing branchlets are terete to compressed and have multiple orders of distichous to irregular branching (Figs 72, 73). Tetrasporangial sori have no sterile margin (Fig. 74). Tetrasporangia are arranged irregularly and initially develop acropetally. Older portions of sori may contain tetrasporangia in various stages of development. Mature tetrasporangia are cruciately divided 30–40 µm long and 25–30 µm wide in surface view. Spermatangial sori have not been observed.

#### *Remarks*

Specimens of *G. hommersandii* were found to have two superficially different morphological forms that vary in size and the amount and arrangement of distal branching and subtidal v. intertidal habitat. Erect axes of subtidal non turf-forming specimens are up to 40 mm in height and have pinnate marginal branching (Fig. 66). The erect axes of intertidal turf-forming specimens are shorter and although proximally they have pinnate marginal branching, their distal branching is irregular and profuse (Figs 45, 67). The distal branches of adjacent erect axes form a nearly solid, tangled canopy. The turf specimens observed in this study formed thick patches on intertidal rocks along the shoreline of many Sydney Harbour localities. It was observed that the proximal portions of thalli under the tangled canopy of branches in these patches were continuously moist, even after long periods of desiccation/exposure.

Larger NSW specimens of *G. hommersandii* have been previously misidentified as *G. caulacanthum* (May 1949). *Gelidium caulacanthum* is generally larger (up to 80 mm) than *G. hommersandii*, with blunt apices, and predominantly irregular branching that sometimes becomes pinnate in distal regions (Chapman 1969). Irregular branching does occur in the turf form of *G. hommersandii*, but only in the distal v. proximal regions.

The turf form of *G. hommersandii* can be distinguished from other NSW turf species of by various combinations of characters (Table 2), but it differs from all others in having vegetative axes that are uniformly terete to subterete throughout.

Analyses of *rbcL* sequence data resolve *G. hommersandii* within a strongly supported clade that also includes *G. caulacanthum* and *Capreolia implexa* (Fig. 113). Sequences of the Woolloomooloo Bay turf specimen and the larger-form New Zealand specimen varied by 0.6%, while the range of variation between these two specimens

and *G. caulacanthum* and *C. implexa* was 2.69–4.28%. This strongly supported clade of species is sister to *G. divaricatum* Martens and all four species form a clade that is also well supported in these analyses. This larger clade is sister to the *Ptilophora* clade in the maximum likelihood tree presented in Fig. 113, but there is no bootstrap support for this relationship. Analyses of sequence data from additional loci have also been unable to resolve the relationships of the clade containing *Capreolia* and *G. hommersandii*, the *Ptilophora* clade, and the remaining species with a *Gelidium*-type cystocarp, suggesting that these lineages may have diverged over an evolutionarily short time period (Bailey and Freshwater 1997; Freshwater and Bailey 1998).

#### Specimens examined

NEW SOUTH WALES: Careel Head, Whale Beach, *V May* 1186, 1.i.1946, NSW 209122; Newport, north Headland, *V May* 707, iv.1945, NSW 209114; Narrabeen Headland, *V May* 2482, 6.xii.1947, NSW 209134; Port Jackson, Sydney Harbour, Bradleys Head, *V May* 1196, 20.i.1946, NSW 485004; *V May* 2344, 23.vi.1947, NSW 484999; Mrs Macquaries point, intertidal rocks on the Woolloomooloo side, *R. Coveny*, 12.vii.1969, NSW 126946; on the very end of the point, *A.J.K. Millar*, 12.i.1990, NSW 288452–288454, 289723–289725; *D.W. Freshwater*, 7.viii.2002, NSW #13; 8.ix.2002, NSW 605630; Fairy Bower, Manly, *V May* 2407, 31.viii.1947, NSW 209130; Botany Bay, Sans Souci, *V May*, 5.v.1946, NSW 209125; Ulladulla, *V May* 23.xii.1975, NSW 209095. NEW ZEALAND: Pahia, *G. Knight*, 25.xi.1995, NSW 614406, CMS-UNCW silica collection.

#### Molecular vouchers

Specimen NSW #13, 1352 bp *rbcL* accession # AY352420; specimen from Pahia, New Zealand, 1395 bp *rbcL* accession # U01043.

***Gelidium isabelae*** Taylor, *Allan Hancock Pacific Expeditions* 12: 154, pl. 5, figs 8–12 (1945)

Figs 46, 75–80.

*Heterotypic synonym: Gelidium pusillum* f. *pseudointricata* (Skottsberg & Levring) May, *Proc. Linn. Soc. N.S.W.* 74: 198 (1949).

*Misapplied names: Gelidium pusillum sensu* May (in part), *Proc. Linn. Soc. N.S.W.* 74: 197 (1949); 1965: 371. May and Larkum 1981: 456.

*Gelidium reptans sensu* Thomas and Freshwater, *Phycologia* 40: 344, fig. 1 (2001). Tronchin *et al.* 2002: 550, fig. 1.

*Type*: MICH from Ecuador, Archipiélago de Colón, on rocks at Pta. Albermarle, Isla Isabela, *W.R. Taylor* no. 34–121, 12.i.1934.

#### Habitat and morphology

Forming a conspicuous turf on the intertidal rocks, the thallus (Fig. 46) is light to dark red, composed of narrow, terete prostrate branches giving rise to lanceolate to clavate, flattened erect branches 0.3–0.8 mm wide and 3.5–8 (10) mm in height (Fig. 75). Holdfasts of consolidated cells forming cylindrical ‘pegs’. Bases of erect branches are terete to compressed but most quickly taper to flattened blades giving a constricted or stipitate appearance. Branches simple or with

up to three orders of distichous branching. Erect branches may convert to the narrow terete morphology of prostrate branches and begin producing holdfast and additional erect branches where they contact the substratum (Fig. 76). Apices of erect branches are mostly obtuse with a prominent apical cell. Apices of prostrate branches and some newly forming erect branches are acute.

Thallus of prostrate branches composed of a three-cell-layered cortex of irregularly globose cells surrounding a medulla of elongated, thick-walled cells with narrow lumens (Fig. 77). The thallus of erect branches is composed of a cortex of irregularly globose to elliptical cells that is 3–5 layers thick where branches are terete to compressed (Fig. 78) and 2 or 3 layers thick where flattened (Fig. 79). The cortical layer may be thicker and files of cortical cells may extend through the medulla in the areas between the secondary cell filaments. The medulla is narrow in flattened portions of branches and consists of elongated thick walled cells with narrow lumens. Rhizines are abundant within erect branches (Fig. 78), and are found within the medulla and inner cortex of terete to compressed proximal regions, but are restricted to the medulla of flattened distal regions. Rhizines are less numerous and not present in all sections of prostrate branches (Fig. 77).

Tetrasporangial sori develop on secondary branches and have a sterile margin (Fig. 80). Tetrasporangia (which grow up to 28 µm in diameter) develop in irregular lines and mature mostly acropetally.

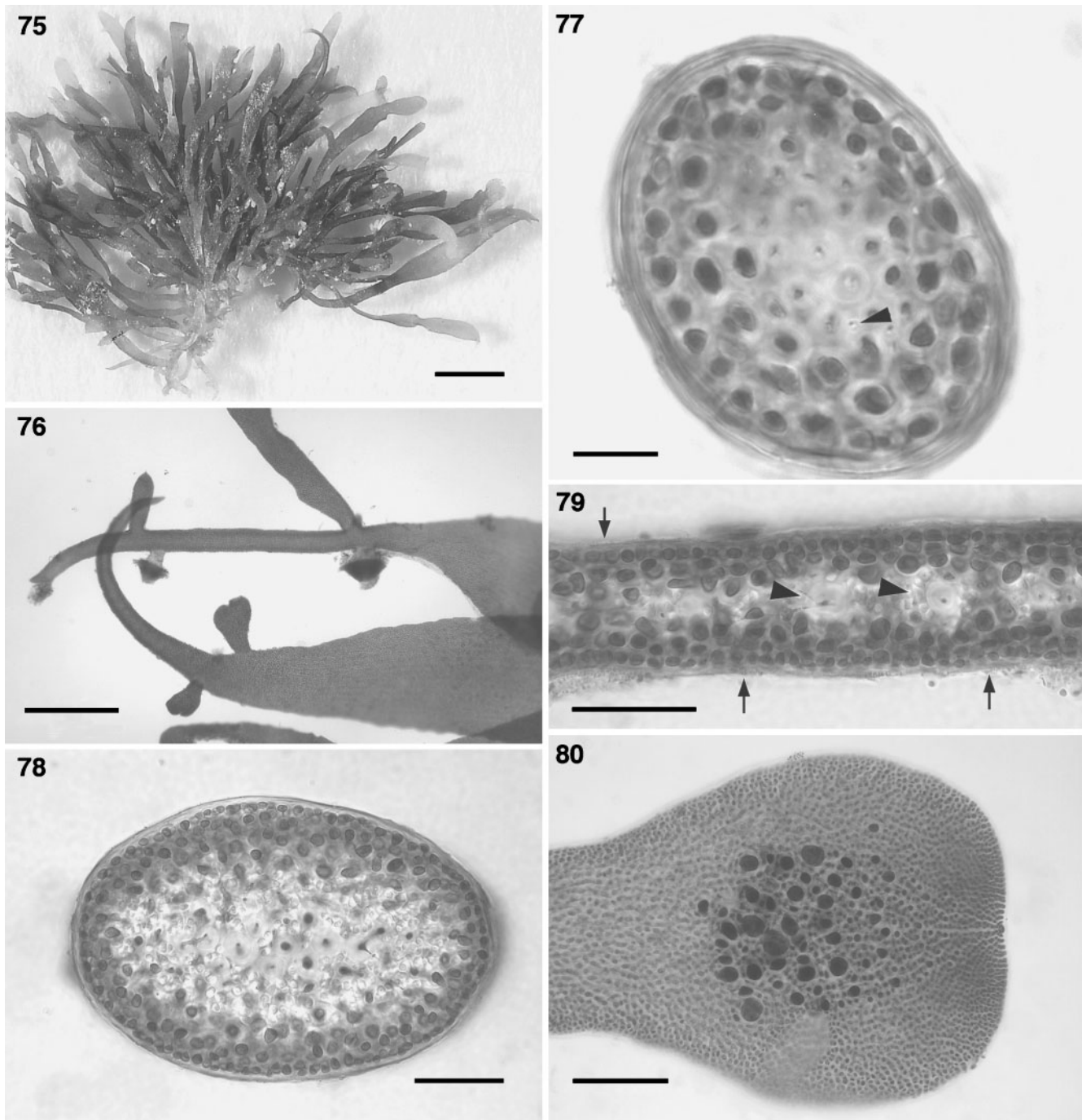
Cystocarpic and spermatangial plants have not been observed during this study.

#### Distribution

Pacific Colombia (Taylor 1945); Ecuador (Taylor 1945); South Africa, {Tronchin *et al.* 2002 [as *G. ‘reptans’* (Suhr) Kylin]}, Western Australia (DW Freshwater and AJK Millar unpubl. data); New Caledonia (DW Freshwater and AJK Millar unpubl. data); New South Wales: Plantation Point, Jervis Bay; Long Reef, Collaroy; Lord Howe Island.

#### Remarks

*Gelidium isabelae* is a common element of the intertidal turf flora of New South Wales and is the dominant Gelidiales turf species at Lord Howe Island. The *rbcL* sequences from nine different samples collected at three sites along the New South Wales mainland and two sites on Lord Howe Island were identical (Fig. 113). Sequence analyses also indicate that this species is present in South Africa. Two samples, one collected at Swartklip, False Bay, South Africa and one from KwaZulu-Natal, South Africa (Table 1), have *rbcL* sequences that are different from each other at three base pairs, and they are only four or seven base pairs different from the New South Wales samples. Analyses of *rbcL* place this species in the ‘*Suhrria* clade’ of Tronchin *et al.* (2002). Within this group, *G. isabelae*



**Figs 75–80.** *Gelidium isabelae*. **Fig. 75.** Habit of specimen. NSW 614432. Scale = 1 mm. **Fig. 76.** Distal ends of erect flattened branches becoming terete, prostrate branchlets with holdfasts. NSW 701607. Scale = 0.5 mm. **Fig. 77.** Transverse section through prostrate branch showing 3 cell-layered cortex and few rhizines (arrowhead) in medulla. WNC Slide 2003-S072. Scale = 25  $\mu\text{m}$ . **Fig. 78.** Transverse section through the proximal region of an erect branch showing 3–5-cell-layered cortex and abundant rhizines filling the space between cells of the medulla and inner cortex. NSW 701608. Scale = 50  $\mu\text{m}$ . **Fig. 79.** Transverse section through flattened region of erect branch. The cortex adjacent to medullary cells that are part of the secondary cell filaments (arrowheads) is two or three cells thick, but it is thicker in areas between the secondary cell filaments (arrows). WNC Slide 2003-S070. Scale = 50  $\mu\text{m}$ . **Fig. 80.** Tetrasporangial sorus with sterile margin and tetrasporangia developing in irregular lines. NSW 701607. Scale = 100  $\mu\text{m}$ .

is resolved in a subclade of small, turfy *Gelidium* species that includes *G. microdenticum* Taylor and two other species that have been incorrectly identified as *G. 'pusillum'* (e.g. Freshwater and Rueness 1994).

The South African collections of *G. isabelae* had been tentatively referred to *Gelidium reptans* (Suhr) Kylin (Thomas and Freshwater 2001; Tronchin *et al.* 2002) or *Gelidium minusculum* (Weber-van Bosse) R.E. Norris. Recent analyses of a *rbcL* sequence from a Sodwana Bay, South Africa specimen that has been morphologically matched to the type of *G. reptans* has shown that the Swartklip specimen is not this species (EM Tronchin and DW Freshwater unpublished). Morphological comparisons of the Swartklip and New South Wales materials with the original (Weber-van Bosse 1921) and later descriptions of *G. minusculum* (Hatta and Prud'homme van Reine 1991; Norris 1992) also show that this species is not *G. minusculum*. Morphologically the South African and New South Wales taxon is most closely allied with *G. isabelae*, a species described by Taylor (1945) based on collections from Isla Isabela, Ecuador (Type) and Bahía Utria, Chocó, Colombia. Although our numerous collections demonstrate a greater range of variation than that described by Taylor, they closely match the description in having terete to compressed prostrate branches giving rise to flattened, stipitate erect branches that are ligulate, lanceolate or spatulate, simple to occasionally pinnately branched with mostly obtuse apices. Many of the New South Wales specimens also have the decussate lines visible when observing the blade surface that Taylor (1945, pg. 155) explicitly mentions. These 'lines' are a result of the sometimes-uneven thickness of the pigmented cortical cell layer in the flattened, distal portions of erect branches (Fig. 79).

The presence of visible decussate lines in the blades of *G. isabelae* distinguishes this species from other turfy New South Wales *Gelidium* species. None of the other turfy species also produce erect branches that are stipitate nor as flat as those in *G. isabelae*.

#### *Specimens examined*

NEW SOUTH WALES mainland: Collaroy, Long Reef, upper intertidal rocks and channels, *D.W.Freshwater & A.J.K.Millar*, 4.ix.2002 (NSW 700189, NSW #15); Jervis Bay, Plantation Point, *D.W.Freshwater & A.J.K.Millar*, 30.vii.2002, (NSW 614431, NSW 701608, NSW #10, WNC2003002-H); Summer Cloud Bay, Bhowerre Peninsular, Jervis Bay, intertidal rocks, *D.W.Freshwater & A.J.K.Millar*, 30.vii.2002 (NSW 700190, NSW #8); Potato Point near Coila, *V.May* #2465, 26.x.1947 (NSW 209132); Green Cape, *A.J.K.Millar & P.G.Richards*, 8.ii.1992, NSW 291033, NSW 291034. LORD HOWE ISLAND: Neds Beach, high intertidal pools, *G.Kraft*, 3.xii.1978 (MELU); Far Rocks, *G.Kraft*, 1.x.1976 (MELU); *G.Kraft & C.O'Brien* 2.x.1976 (MELU K9145); Old Gulch, west side, *G.Kraft & A.J.K.Millar*, 17.xii.1986 (MELU K11040); Neds Beach, outer intertidal rocks, *D.W.Freshwater & A.J.K.Millar*, 1.x.2002 (NSW 614432, LHI #3)(NSW 614435, LHI #4, WNC2003002-B) (NSW 614438, LHI #8, WNC2003002-C, WNC2003002-E); Old Gulch, east side at the mouth of the

gulch, *D.W.Freshwater & A.J.K.Millar*, 4.x.2002, (NSW 614437, LHI #7) (NSW 614439, LHI #10, WNC2003002-D)(NSW 614440, LHI #11, WNC2003002-F, WNC2003002-G), NSW 701607. WESTERN AUSTRALIA: Rottneest Island, west end of Stricklands Bay, *D.W.Freshwater WA-13*, 18.viii.2002 (CMS-UNCW silica gel collection). NEW CALEDONIA: Noumea, Anse Vata, Aroyo de L'Hippodrome (near Racehorse track), *D.W.Freshwater NC-2*, 15.ix.2002 (CMS-UNCW silica gel collection). SOUTH AFRICA: Swartklip, False Bay, Western Cape Prov., *M.H.Hommersand*, 15.vii.1993 (CMS-UNCW silica gel collection); KwaZulu-Natal Prov., *M.Guiry & J.Rico* culture # 0962 (CMS-UNCW silica gel collection).

#### *Molecular vouchers*

Specimen NSW #15, 1396 bp *rbcL* accession # AY350779; identical *rbcL* sequences from specimens NSW #8, NSW #10, LHI #3, LHI #4, LHI #7, LHI #8, LHI #10, LHI #11; specimen from Western Cape, South Africa, 1369 bp *rbcL* accession # AY350778; specimen from KwaZulu-Natal, South Africa, 1363 bp *rbcL* accession # AF305798.

*Gelidium maidenii* Lucas, *Proc. Linn. Soc. N.S.W.* 60: 217, pl. 7, fig. 3 (1935). May 1965: 371. Lewis 1984: 10

Figs 81–84, 86–91.

*Type*: NSW 288794, from Lord Howe Island, iii.1898, *J.H. Maiden*.

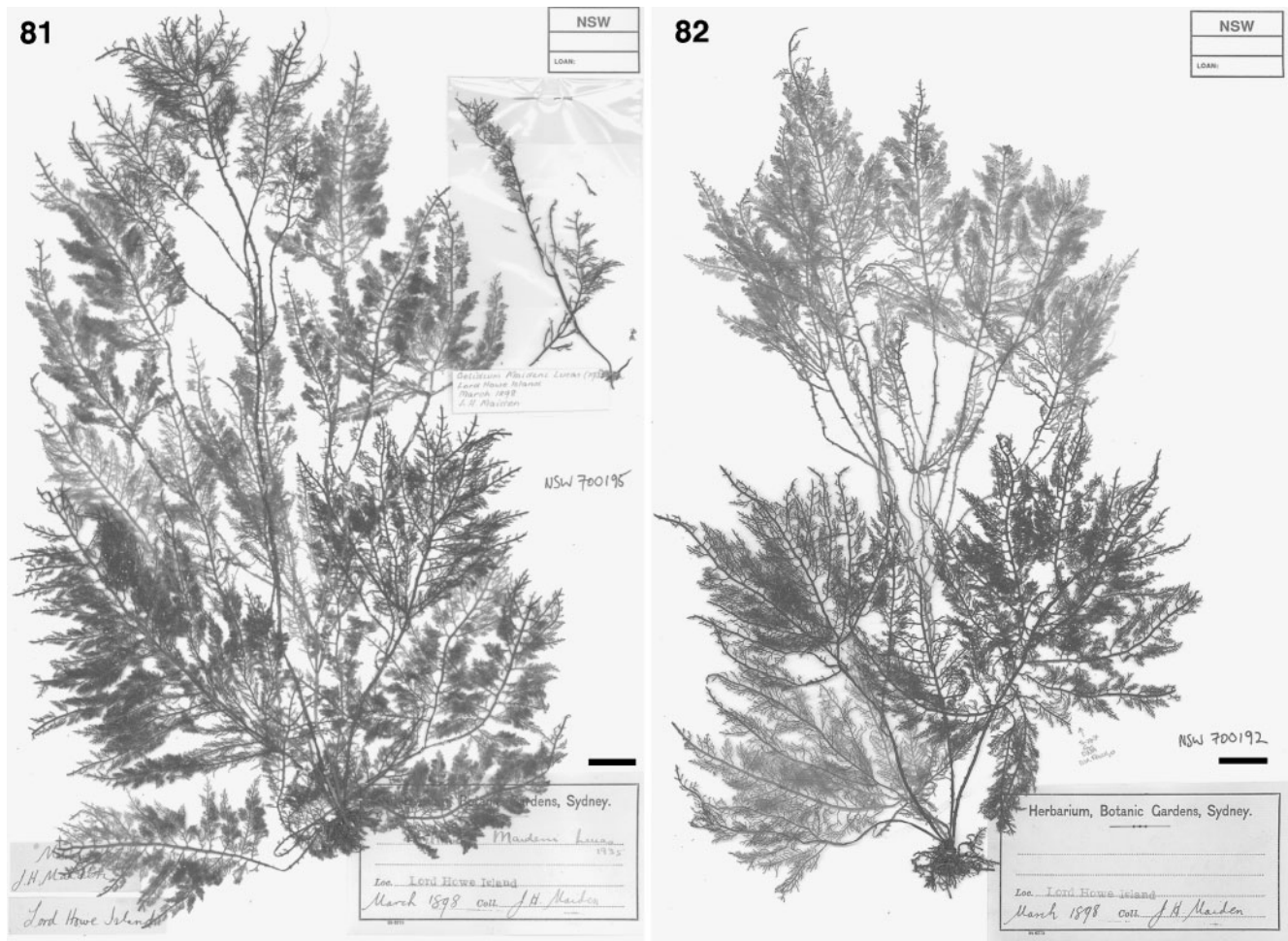
#### *Habitat and morphology*

Plants are presumably strictly subtidal in deep water habitats. Thallus of dark purple to red-brown erect axes (Fig. 81), arising from an entangled, fibrous holdfast of terete, rhizome like branchlets (Fig. 82). Erect axes cartilaginous, compressed, up to 37 cm in height and 1.5 mm in width, the lower half mostly bare (Fig. 83) with vestigial lateral branch bases forming dentate margins (Fig. 84). Upper half of axes distichously pinnate with opposite, alternate to irregularly distichously branched laterals with up to three orders of branching. Lateral branches 3–5 mm distant, mostly determinate, although some seemingly indeterminate, often basally constricted, up to 14 cm long, proximally bare and distally distichously pinnately branched and bearing lateral branchlets up to 2.5 cm long. Apices are rounded/obtuse without a prominent apical cell.

Thallus composed of a medulla of tightly packed longitudinally elongate filamentous cells lacking rhizines (Fig. 88) grading sharply to open meshed out medulla/inner cortex. Rhizines abundant only in the outer medulla/inner cortex (Fig. 87). Cortex relatively thick, of up to seven cells in files, of isodiametric to radially elongate pseudoparenchymatous cells (Figs 87, 88).

Tetrasporangia cruciately to irregularly divided, obovate to 40 µm long and 32 µm wide, borne in slightly inflated sori (Fig. 89) on ultimate lateral branchlets and on distal portions of penultimate branchlets.

Cystocarps are borne on ultimate branchlets (Fig. 90) forming swellings at either branch apices or subterminally.



**Figs 81, 82.** *Gelidium maidenii*. **Fig. 81.** Habit of pressed isotype. NSW 700195. Scale = 2 cm. **Fig. 82.** Habit of pressed isotype showing basal fibrous holdfast. NSW 700192. Scale = 2 cm.

Cystocarps are bilocular (Fig. 91), the carposporangia are produced singularly or in clusters from gonimoblast cells that form a placental tissue layer that surrounds the second-order cell rows in the centre of the cystocarp cavity (Fig. 91). At maturity the pericarp is composed of several dozen layers of cortical cells.

#### *Distribution*

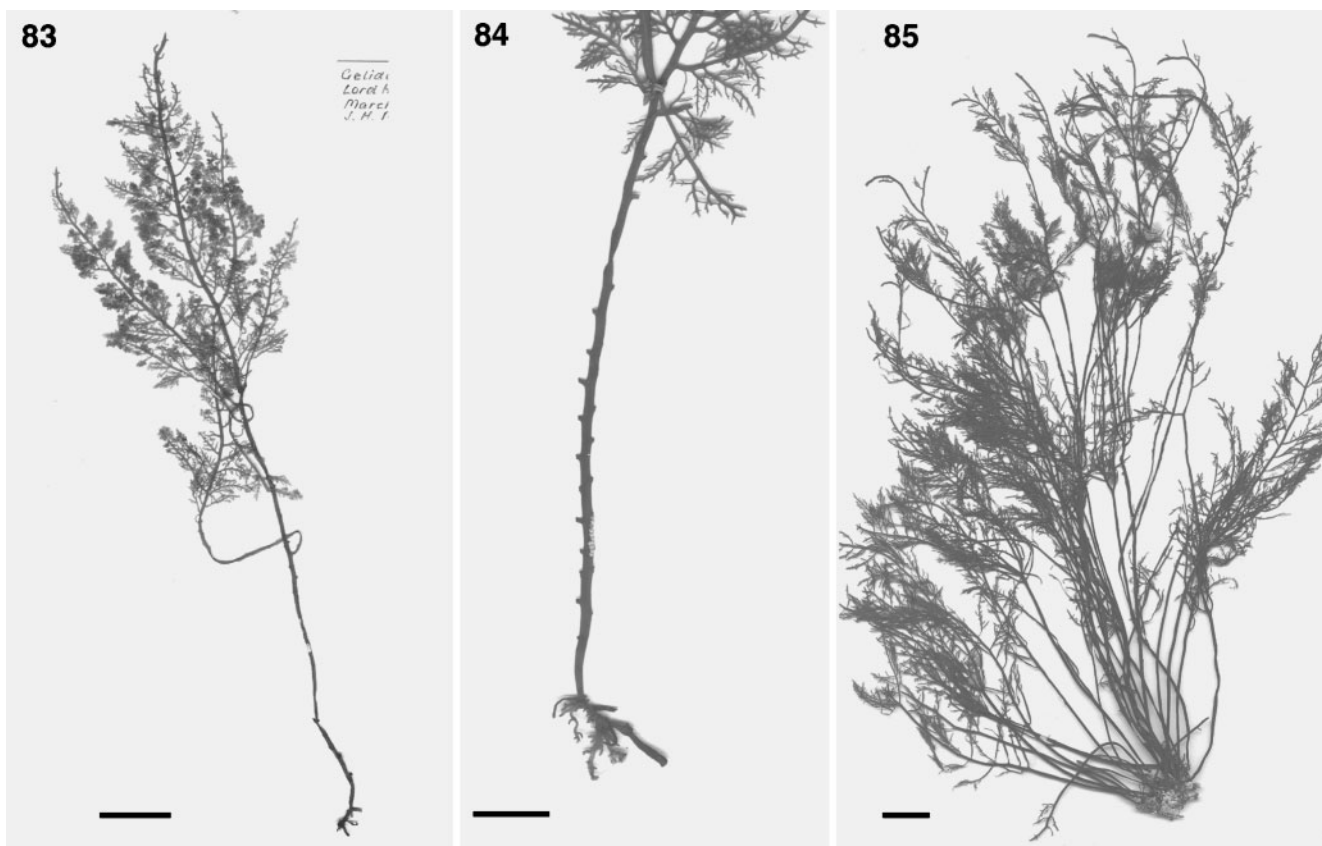
Known only from a single collection of nine specimens, presumably collected in the drift.

#### *Remarks*

*Gelidium maidenii* is very distinctive, consisting of plants that are very large in size, with thick, compressed axes, and adaxially curved distichously arranged laterals arising at 45° angles that impart a trident configuration on ultimate and penultimate branchlets. Only one other species of *Gelidium* appears to share this suite of features, *G. robustum* (N.L. Gardner) Hollenberg

& Abbott (= *G. cartilagineum* var. *robustum*) from California and Baja Mexico (Fig. 85). In addition to these macromorphological similarities, *G. robustum* also has a remarkably similar cross section of main axes in which the rhizines are restricted solely to the outer medulla/inner cortex and the cortex is very thick and made up of files of cells up to seven deep. Lastly, in both species the lower half of the main axes are devoid of lateral determinate branches (Figs 83–85). The main difference appears to be that in *Gelidium maidenii*, the deciduous laterals leave vestigial bases on the lower half of the axes giving them a serrated appearance, while in *G. robustum*, no such vestigial branches are apparent and the lower half of the axes are thus smooth. Additionally, several axes arise from a common conglomerate base in *G. robustum* (Fig. 85), whereas in *G. maidenii* (Figs 83, 84), each plant is actually separate or solitary, even though herbarium specimens (Figs 81, 82) appear as if several axes arise from a common base. A curious phenomenon was noted during examination of the *Gelidium maidenii* specimens in that





**Figs 83–85.** *Gelidium maidenii*. **Fig. 83.** Habit of solitary plant. NSW 700193. Scale = 2 cm. **Fig. 84.** Lower portion of main axis showing remnant bases of deciduous laterals. NSW 700191. Scale = 1 cm. **Fig. 85.** *Gelidium robustum*. Habit of specimen from Baja California. NSW 701899. Scale = 2 cm.

on all but two sheets, up to seven main and percurrent axes/plants seemingly arise from a common fibrous holdfast (Fig. 82), suggesting that they grow in tight clumps. On closer examination, however, it was noted that these main axes have been tied together with a waxed string or fibre of some description (Fig. 86) by a person or persons unknown. In essence, therefore, each plant presumably consists of one main axis arising from a fibrous holdfast (Figs 83, 84), not several as is seemingly the case when observing some pressed specimens (Figs 81, 82).

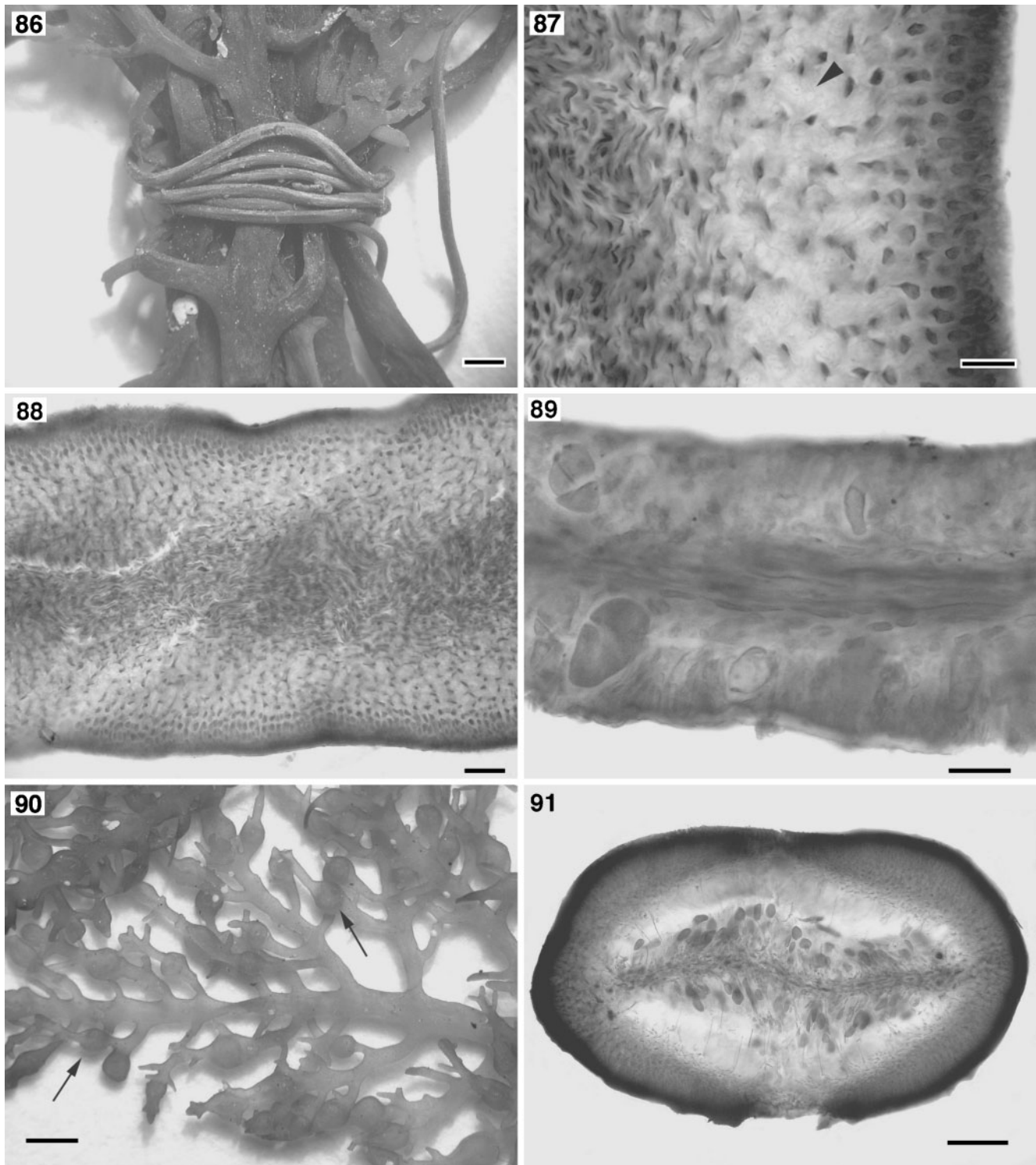
In the protologue, Lucas (1935) made no mention of reproductive structures or fertile branchlets and thus the generic placement of this taxon has until now been unconfirmed. Of the nine sheets in the collection, we could identify one cystocarpic plant and the others are mostly tetrasporic. The bilocular nature of the cystocarps confirms the placement of this species in the genus *Gelidium*. Attempts to extract and sequence *rbcL* from these 106-year-old specimens have been unsuccessful and thus we cannot comment on the phylogenetic position of this species within the genus, nor its sister taxa at the molecular level.

Allender and Kraft (1983: 74) reported *G. maidenii* from vertical intertidal walls on the island, but the voucher specimens on which this statement is based may represent *G. allanii*.

Some 28 years of collecting has failed to rediscover this species and it is tempting to surmise that there may well have been an error in labelling and curation and that this species has never occurred on Lord Howe Island. There remains the possibility that the species grows only in deep water on a reef somewhere distant from the island itself that we have not yet discovered. *Ecklonia radiata* (C. Agardh) J. Agardh has been found growing in deep water around Lord Howe Island and reports of *Macrocystis pyrifera* (Turner) C. Agardh by deep-sea fishermen have also been noted (Lucas 1935: 213).

#### *Specimens examined*

***Gelidium maidenii*** Lucas: Lord Howe Island, exact locality unknown, *J.H.Maiden*, iii.1898, NSW 288794 (holotype), NSW 288795, NSW 700191–700196 (isotypes). ***Gelidium robustum*** (Gardner) Hollenberg & Abbott: Mexico, Baja California, 7 miles north of Descanso, *N.C.Cooper* 818, 3.iii.1947, NSW 701899.



**Figs 86–91.** *Gelidium maidenii*. **Fig. 86.** Cord used to tie several plants together in a bouquet. NSW 288795. Scale = 1 mm. **Fig. 87.** Section showing rhizines (arrowhead) in outer medulla/inner cortex. NSW Slide 21-79. Scale = 25  $\mu$ m. **Fig. 88.** Transverse section of main axis showing tightly packed medulla. NSW Slide 21-80. Scale = 50  $\mu$ m. **Fig. 89.** Transverse section through tetrasporangial sorus. NSW Slide 21-79. Scale = 25  $\mu$ m. **Fig. 90.** Cystocarps (arrows) borne on ultimate branchlets. NSW 288795. Scale = 1 mm. **Fig. 91.** Transverse section through cystocarp. NSW Slide 21-81. Scale = 50  $\mu$ m.

Genus *Pterocladia* J. Agardh, *Species Genera et Ordines Algarum Vol.2* part1: xi (1851); part 2: 482 (1852)

This genus has had some 28 species credited to it since its description some 150 years ago. Owing to the many taxonomic and nomenclatural changes that have taken place in the last two decades, a majority of the former *Pterocladia* species have been placed in other genera or in synonymy with other species. The type species *P. lucida* and the west and south Australian endemic *P. rectangularis* are the only two species considered to belong to it (Womersley and Guiry 1994; Santelices 1999), although a few remain to be critically examined. The genus is characterised by its having carpogonia that develop on and are directed towards only one thallus surface; nutritive filaments that develop across the width of the fertile area but on only one side of the thallus, and a carposporophyte that develops to cover the floor of the cystocarp cavity (Hommersand and Fredericq 1996). The distinctiveness of *Pterocladia* within the Gelidiales has been supported by analyses of both nuclear- and chloroplast-encoded gene sequences (e.g. Freshwater *et al.* 1995; Freshwater and Bailey 1998).

*Pterocladia lucida* (R. Brown ex Turner) J. Agardh, *Species Genera et Ordines Algarum Vol.2* part 2: 483 (1851). Allender and Kraft 1983: 74. Gepp and Gepp 1906: 253 in part. Lewis 1984: 10. Lucas 1909: 23; 1935: 218. Lucas and Perrin 1947: 144, fig. 19. May 1965: 371. Millar 1990: 313, fig. 8E. Millar 1999: 500

Figs 92–96.

*Basionym:* *Fucus lucidus* Turner, *Fuci sive Plantarum* 4: pl. 238 (1819).

*Type:* in BM, from ‘S coast of N. Holl.’ by R. Brown.

#### *Habitat and morphology*

Plants grow mostly subtidally although in some instances they can be found in the lower intertidal or surf zone. Thalli (Figs 92, 93) are dark red to brown-red, cartilaginous, consisting of tufts of erect axes, up to 40 cm high, from a fibrous stoloniferous base. Axes linear, flattened, 3–4 mm in width, centrally thickened distally, with a midrib proximally, and up to four orders of alternate distichous branching (Fig. 92). Branches often tapered at the base, apices often broad with truncate to obtuse tips (Fig. 93).

Thallus composed of a 3–5-cell-layered cortex of generally globose cells that increase in size towards the medulla (Fig. 94). Medullary cells are elongated with relatively wide lumens and narrow cell walls. Rhizines numerous throughout the medulla and extend into the inner cortex, but may be more abundant towards the outer medulla (Fig. 94).

Tetrasporangial sori have a narrow sterile margin (Fig. 95) and are borne on flattened elliptical stichidia. Tetrasporangia

(to 40 µm long and 28 µm diameter) are often arranged in capreolate rows (Fig. 95), but do not always develop synchronously, and therefore the regular pattern may be lost in older portions of sori. Unilocular cystocarps of the *Pterocladia*-type (Fig. 96) develop subterminally on the distal portions of ultimate branchlets.

#### *Distribution*

Western, southern and eastern Australia; Lord Howe Island; Norfolk Island, and New Zealand. NSW mainland distribution is from Coffs Harbour south to the border.

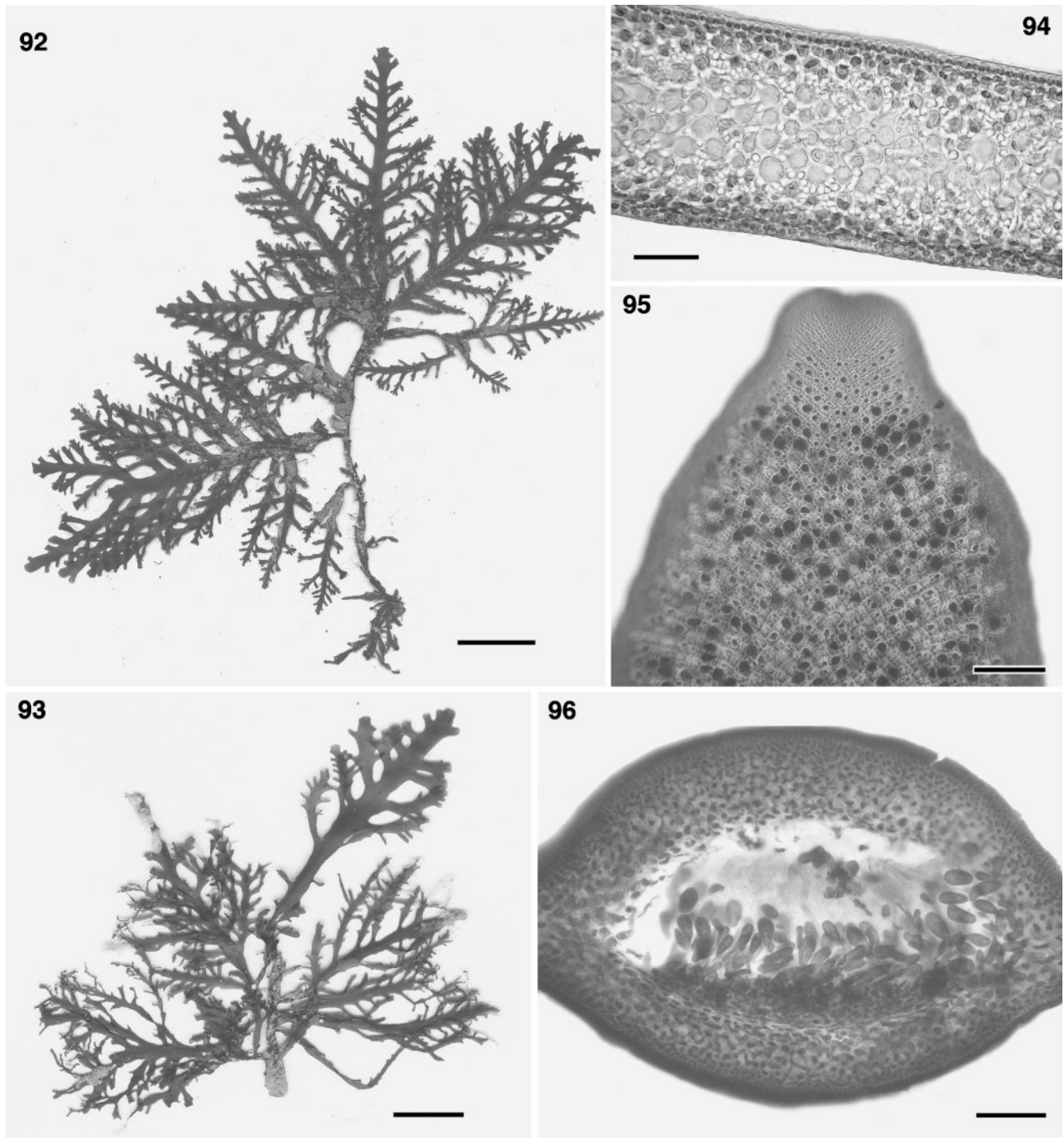
#### *Remarks*

First collected on Lord Howe Island in 1898 by J.H. Maiden, this is one of the more common Gelidiales species there, the morphology of the plants of which varies considerably, with some becoming very fine and almost like *Pterocladia capillacea*. Mainland *Pterocladia lucida* is generally from deep water and the plants are very large, robust and broadly flattened (Fig. 92). Turner’s (1819) protologue describes and illustrates plants that are finer than the deep-water specimens from southern NSW, but *rbcL* sequence analyses of Australian specimens exhibiting a wide range of morphologies suggest that they all represent a single species. The *rbcL* sequences of a fine form specimen from Lord Howe Island and a robust-form specimen from South Australia varied at only four sites (Fig. 113). Likewise, multiple Western Australia *P. lucida* specimens demonstrating a wide range of morphological variation were found to have identical *rbcL* sequences (data not shown). Australian and New Zealand specimens are resolved within a strongly supported monophyletic clade that is one of the four major lineages resolved in all molecular analyses of the Gelidiales (Fig. 113; Bailey and Freshwater 1997; Freshwater and Bailey 1998).

Rarely have female plants of this species been collected and we have only observed one such specimen in the NSW herbarium. Almost all specimens are tetrasporic with only a few being sterile.

#### *Specimens examined*

NEW SOUTH WALES: Coffs Harbour, *A.J.K.Millar & T.Mix*, 16.iv.1980, NSW Ex MELU AM082; Collaroy Beach, *V.May* #1149, 5.v.1944, NSW 703763; Maroubra Bay, *A.H.S.Lucas*, vii.1901, NSW 700295; Aughinish Rocks, southern pinnacle, near Montague Island, *A.J.K.Millar, N.Yee & P.Richards*, 1.iii.2000, NSW 439761; Green Cape, *A.J.K.Millar & P.G.Richards*, 7.ii.1992, NSW A010790; West of Green Cape Lighthouse, Disaster Bay, *A.J.K.Millar, P.G.Richards & N.Yee*, 24.ii.2000, NSW 439070. LORD HOWE ISLAND: *G.Kraft* K9617 & *R.Ricker*, 12.xii.1978, MELU A40027; *F.Perrin & A.H.S.Lucas*, vi.1933 (NSW); Ned’s beach, *A.J.K.Millar & R.Green*, 14.xii.1985, MELU A035722; *A.J.K.Millar & D.W.Freshwater*, 1.x.2002 (NSW 506160, LHI #12, WNC2003009). NORFOLK ISLAND: Swiss Cheese Reef, off Kingston jetty, *A.J.K.Millar & J.Marges*, 21.ix.1996, NSW 402980, NSW 482981.



**Figs 92–96.** *Pterocladia lucida*. **Fig. 92.** Specimen from NSW mainland, deepwater. NSW 439070. Scale = 2 cm. **Fig. 93.** Specimen from Lord Howe Island, shallow. WNC 2003009. Scale = 1 cm. **Fig. 94.** Transverse section of secondary branch. WNC Slide 2003-S027. Scale = 50 µm. **Fig. 95.** Tetrasporangial sorus showing a narrow sterile margin and tetrasporangia initially arranged in capreolate rows. WNC Slide 2003-S029. Scale = 150 µm. **Fig. 96.** Section of mature unilocular cystocarp. NSW Slide 21-82. Scale = 100 µm.

*Molecular vouchers*

Specimen LHI #12, 1350 bp *rbcL* accession # AY352423.

Genus *Pterocliadiella* Santelices & Hommersand, *Phycologia* 36: 117 (1997)

The genus *Pterocliadiella* was erected by Santelices and Hommersand (1997) to accommodate species formerly placed within the genus *Pterocladia* and *Gelidiella*. The defining characters of the new genus and the principal features that distinguish it from *Pterocladia* are its intercalary carpogonia that are directed towards both surfaces of the thallus, nutritive filaments that grow centripetally and form a collar around the central axis, and carposporophytes that are mostly attached to one side of the cystocarp floor with chains of carposporangia on the remaining three sides (Hommersand and Fredericq 1996). Four species were initially transferred to *Pterocliadiella* including the type *P. capillacea*, *P. melanoidea* (Schousboe ex Bornet) Santelices & Hommersand, *P. minima* (Guiry & Womersley) Santelices & Hommersand, and *P. caerulescens* (Kützing) Santelices & Hommersand. Santelices (1997b, 1998), having re-examined several other *Pterocladia* species, transferred *P. bartlettii* (W.R. Taylor) Santelices, *P. bulbosa* (Loomis) Santelices, *P. caespitosa* (Kylin) Santelices and *P. caloglossoides* (Howe) Santelices to *Pterocliadiella*, and Shimada *et al.* (2000b) resurrected and transferred *P. nana* (Okamura) Shimada, Horiguchi & Masuda and *P. tenuis* (Okamura) Shimada, Horiguchi & Masuda, which had been synonymised with *P. capillacea*. Thomas and Freshwater (2001) described the new species, *P. beachiae* Freshwater, bringing to 11 the number of presently recognised *Pterocliadiella* species, although a number of *Pterocladia* species remain to be studied.

*Pterocliadiella caerulescens* (Kützing) Santelices & Hommersand, *Phycologia* 36: 118 (1997)

Figs 97–99.

*Basionym:* *Gelidium caerulescens* Kützing (1868), *Tabulae Phycologicae* 18: 19, t.56c, d (1868).

*Homotypic synonym:* *Pterocladia caerulescens* (Kützing) Santelices, *Phycologia* 15: 165 (1976).

*Type:* L 941,11–91 from Wagap, New Caledonia, *Vieillard* #2103, in 1863. Barcode L 0056117. (Isotype L 941,11–98).

*Habitat and morphology*

Growing on rocks in the shallows and down to 14-m depths, the thalli are dark green to black, consisting of terete to subterete prostrate branches giving rise to ligulate erect branches up to 5 cm in height (Figs 97–99). Prostrate branches attached to the substrate by tapering peg-like holdfast. Erect branches have subterete, attenuate bases and are flattened distally with obtuse to acute apices and generally distinct apical cells. Branching variable and ranges from simple to multiple orders of distichous branching. Marginal

branches of larger specimens are often somewhat geniculate and grow to the height of the main axes resulting in a corymbose-shaped habit (Fig. 98).

Thallus composed of a three- or four-cell-layered cortex surrounding a medulla of elongated thick-walled cells. Rhizines surrounding medullary cells.

All examined NSW specimens were sterile. The type specimen was also examined and found to be cystocarpic.

*Distribution*

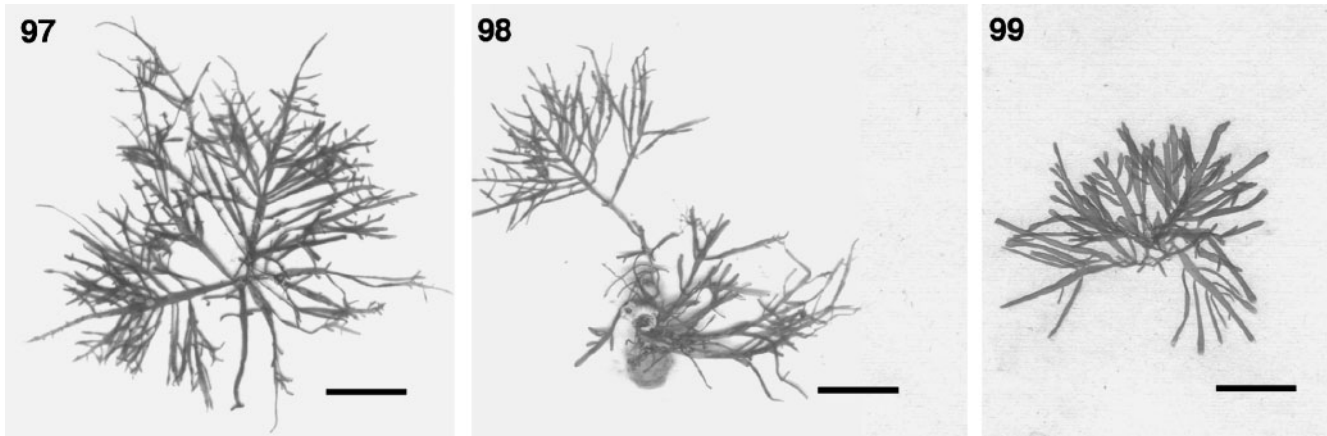
Northern and north-eastern parts of the Indian Ocean; Pacific Ocean; Atlantic, Gulf of Mexico, Caribbean, Bermuda, western South Atlantic. In New South Wales, known only from Lord Howe Island.

*Remarks*

Only five specimens of this species are known from NSW and these are all from Lord Howe Island. Although sterile, in all anatomical details (height, branching, internal structure), we cannot separate the Lord Howe Island specimens from those of the type collection from New Caledonia (Fig. 99). Additionally, the descriptions and illustrations of this distinctive species by Santelices (1977), Price and Scott (1992), and more recently Shimada and Masuda (2000) agree with NSW specimens in all details.

At Lord Howe Island, *P. caerulescens* could easily be misidentified in the field with small specimens of *Gelidium allanii* and/or *Pterocliadiella capillacea*. Ultimately, cystocarpic specimens easily separate the two genera *Gelidium* and *Pterocliadiella*, but we have also noticed small morphological differences as well. *Pterocliadiella caerulescens* is often a dark green to reddish black color, fine in texture and the basal branches tend to grow out and somewhat up so that the overall specimen shape is corymbose. *Pterocliadiella capillacea* on the other hand is more in the reddish range of colours, much more ‘robust’ and definitely pyramidal in overall habit shape. Neither *Pterocliadiella* species has the shallowly zig-zag main axis of *Gelidium allanii*.

Santelices (1976) compared Hawaiian *P. caerulescens* specimens with the type and a ‘cotype’ specimen from New Caledonia, and determined that they represented the same species. *Pterocliadiella caerulescens* has subsequently been reported from many locations in the Indo-Pacific (e.g. Cribb 1983; Hatta and Prud’homme van Reine 1991). Santelices (1976) refers to a Bartlett specimen from Haiti as representing *P. caerulescens* and other reports of this species outside of the Indo-Pacific have been made for the western Gulf of Mexico (Wynne 1993), Bermuda (Schneider and Lane 2005), Venezuela (Rodríguez de Rios 1992) and Brasil (Ugadim 1987). Determining the relationship of the reported non-Indo-Pacific *P. caerulescens* to *P. beachiae*, which is a morphologically similar Caribbean species that is sister to *P. caerulescens* in molecular phylogenies (Fig. 113;



**Figs 97–99.** *Pterocladia caerulescens*. **Fig. 97.** Habit of evenly branched specimen. MELU (unnumbered). Scale = 1 cm. **Fig. 98.** Habit of irregularly branched specimen. MELU (unnumbered). Scale = 1 cm. **Fig. 99.** Habit of lectotype. L941,11–91 (= barcode L0056117). Scale = 1 cm.

Thomas and Freshwater 2001), will require further study. In the protologue, *Pterocladia beachiae* was incorrectly spelt with the masculine ending *beachii*.

#### *Specimens examined*

LORD HOWE ISLAND: Old Gulch, 14 m deep in tufts on the ridge crest on the east side at the mouth of the gulch. *G.Kraft & R.Ricker*, 9.xii.1978 (MELU K9531); Far Rocks, 1–2 m, *G.Kraft*, 13.v.1977 (MELU). NEW CALEDONIA: Wagap, *Vieillard* #2103 in 1863 (L 941,11–91. Barcode L 0056117 and isotype L 941,11–98).

*Pterocladia caloglossoides* (Howe) Santelices, *J. Appl. Phycol.* 10: 244 (1998). Dawson *et al.* 1964: 37, pl. 29, fig. D Figs 100, 101.

*Basionym:* *Gelidium caloglossoides* Howe, *Mem. Torrey Bot. Club* 15: 96, pls 34, fig. 7, pl. 35 (1914).

*Homotypic synonym:* *Pterocladia caloglossoides* (Howe) E.Y. Dawson, *Allan Hancock Pacific Expeditions* 17: 76, pl. 6, fig. 1 (1953).

*Type:* NY, from Isla San Lorenzo, Peru by *R. Cocker* 59 p.p. (*vide* Dawson *et al.* 1964).

#### *Habitat and morphology*

The single specimen collected (Fig. 100), was diminutive, decumbent, creeping over the surface of a small shell (Fig. 101), and 15 mm long. Main axis percurrent, compressed to flattened and attached to the substratum by pads of consolidated rhizoidal cells that issue at every branch juncture. Opposite to multiple divaricate-radiate lateral branches arise from the margins of main axes at the points of holdfast pads. Young lateral branches are initially lanceolate and develop the same habit characteristics as the main axis. Branch apices are acuminate to acute.

Thallus composed of a three- or four-cell-layered cortex surrounding a one- or two-cell-thick medulla of larger thick-walled cells. Rhizines surround medullary cells.

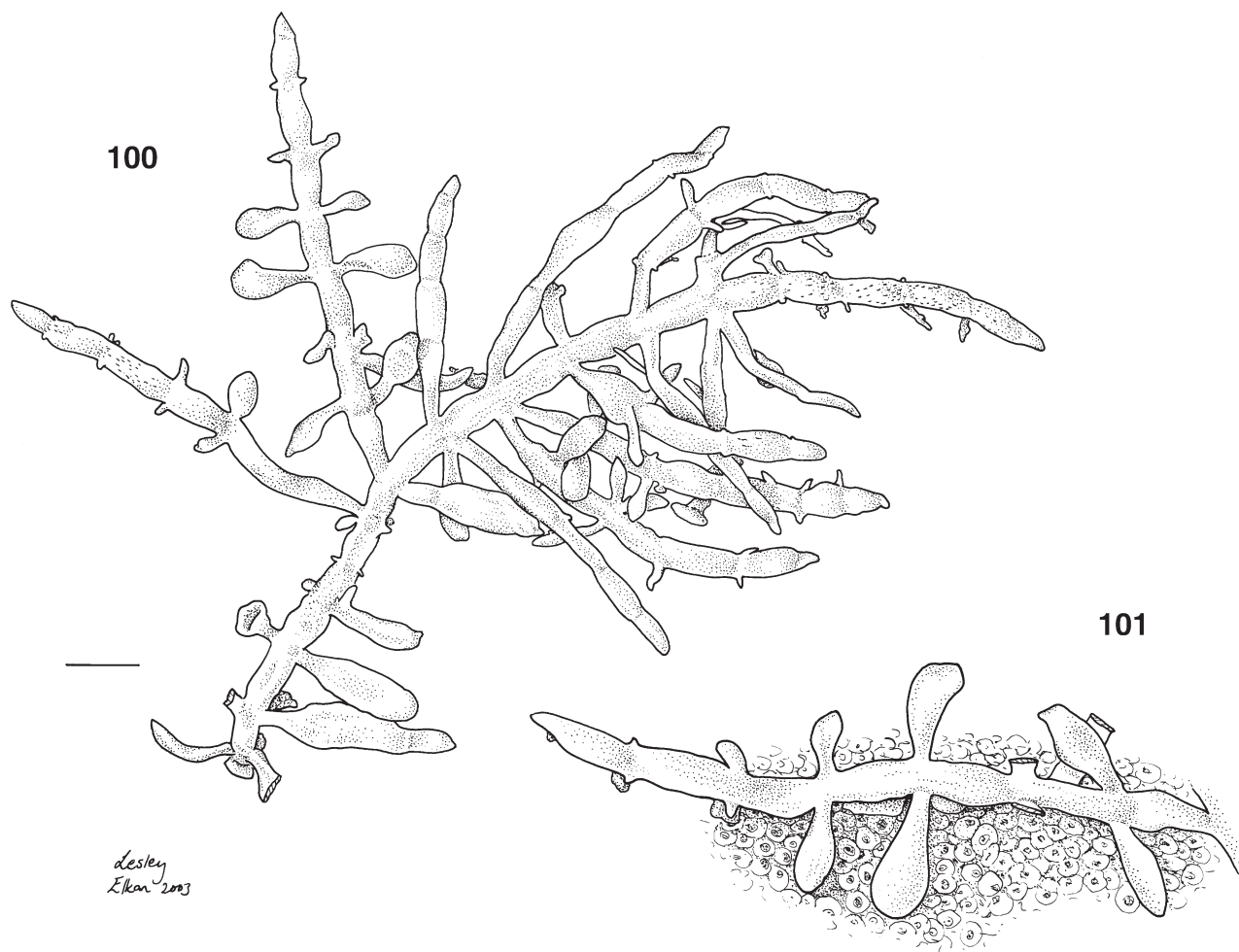
Tetrasporangial, spermatangial and cystocarpic plants not observed.

#### *Distribution*

This species has been reported from north-eastern and south-western parts of the Indian Ocean (Silva *et al.* 1996), and throughout the Pacific Ocean (Santelices 1977; Renfrew *et al.* 1989; Xia and Wong 1999; Shimada and Masuda 2000). In New South Wales, it is known only from La Parouse, Botany Bay, Sydney metropolitan region.

#### *Remarks*

*Gelidium caloglossoides* Howe (= *Pterocladia caloglossoides*) was described by Howe (1914) based on dredged specimens that were growing on shells at 2.5 fathoms depth near the island of San Lorenzo, Peru. Explicitly expressed in Howe's description was that the thallus of *G. caloglossoides* was repent and complanate throughout with only tetrasporangia bearing branches being free and ascending. Smith (1944) and later Dawson (1953) expanded the concept of the species to include specimens with erect lateral branches, and this expanded concept has been followed and widened by subsequent authors (e.g. Santelices 1977; Renfrew *et al.* 1989; Xia and Wong 1999; Shimada and Masuda 2000). Determining whether the many specimens identified as *G. caloglossoides*, *Pterocladia caloglossoides*, or *Pterocladia caloglossoides* actually represent the same species as that originally described by Howe will require further study and may be difficult because the type specimen is reported to be lost (Renfrew *et al.* 1989).



**Figs 100, 101.** *Pterocladia caloglossoides*. **Fig. 100.** Habit of specimens from La Parouse. NSW 707405. Scale = 1 mm. **Fig. 101.** Axes creeping across shell substrate. NSW 707405. Scale = 1 mm.

Only a single small specimen from Bare Island, La Parouse, Botany Bay was collected in this study. This specimen fits the original description of the species in being complanate throughout and having compressed to flattened axes with opposite to divaricate–radiate marginal branching at the same point of the axes as holdfast pads (Figs 100, 101). This habit distinguishes *P. caloglossoides* from all other small NSW Gelidiales species. Both *rbcl* (Fig. 113) and 28S rRNA gene (not shown) sequence analyses resolve the Botany Bay *P. caloglossoides* specimen within the strongly supported *Pterocladia* clade. Lord Howe Island specimens of *P. caloglossoides* cited by Millar and Kraft (1993) actually represent *Gelidium isabelae* (G.Kraft & A.J.K.Millar, 17.xii.1986, MELU K11040).

#### Specimens examined

Botany Bay, La Parouse, D.W.Freshwater & A.J.K.Millar, 17.vii.2002 (NSW 707405, NSW#1).

#### Molecular vouchers

Specimen NSW #1, 1396 bp *rbcl* accession # AY352422, 1137 bp 28S rDNA accession # AY359962.

***Pterocladia capillacea*** (S.G. Gmelin) Santelices & Hommersand, *Phycologia* 36: 118 (1997). De Toni 1924: 165. Gepp and Gepp 1906: 251. Lewis 1984: 10. Lucas 1909: 23; 1935: 218. May 1947: 276; 1981: 342, 343. May *et al.* 1978: 97. Millar 1990: 312, figs 8C–D

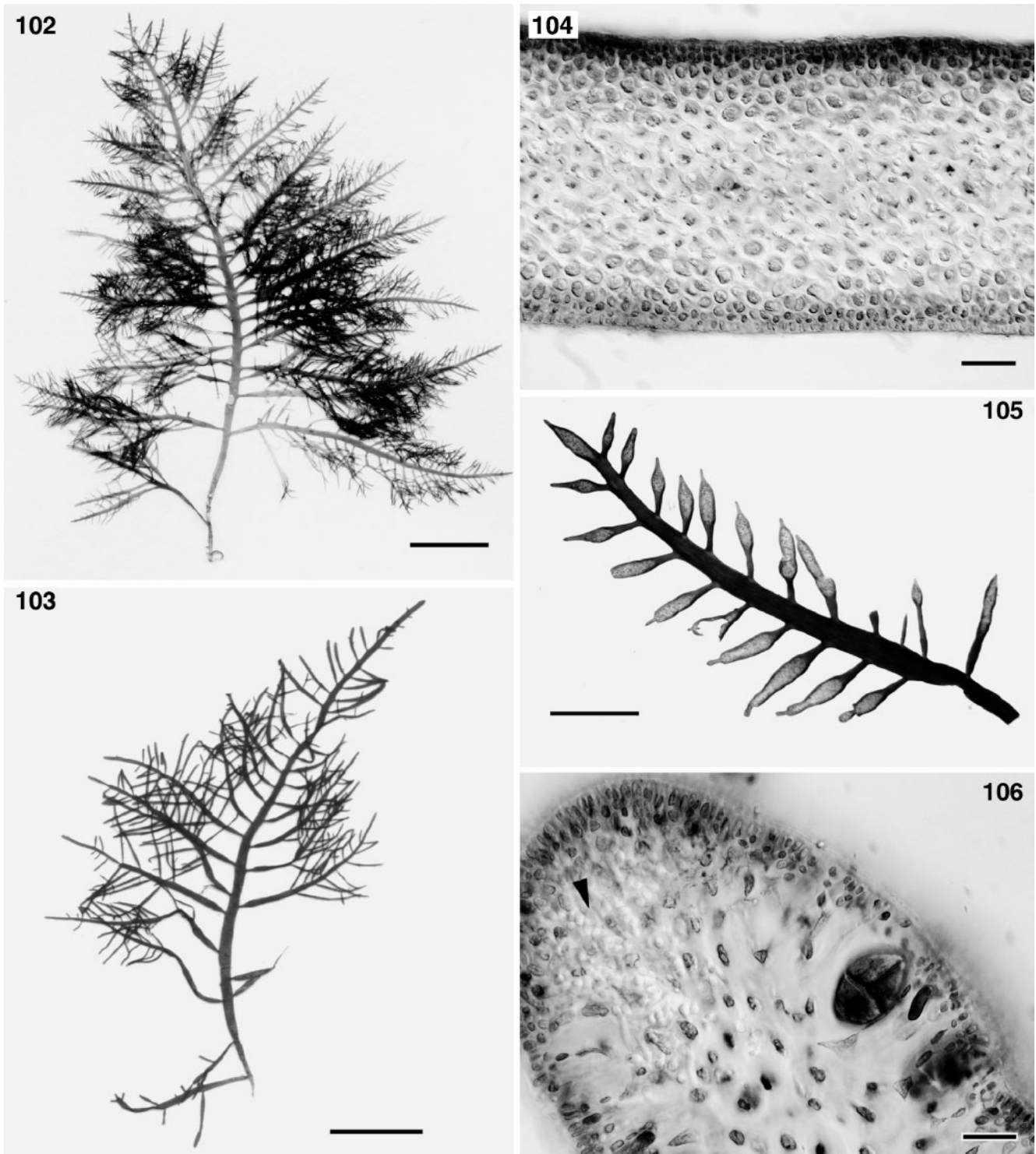
Figs 102–106.

*Basionym:* *Fucus capillaceus* S.G. Gmelin, *Historia Fucorum*: 146, pl. 15, fig. 1 (1768).

*Homotypic synonym:* *Pterocladia capillacea* (S.G. Gmelin) Bornet in Bornet and Thuret (1876), *Notes algologiques...* Fasc. 1: 57 (1876).

*Misapplied name:* *Pterocladia pinnata sensu* May, *Contr. N.S.W. Natn. Herb.* 3: 371 (1965).

*Type:* from the Mediterranean, but according to Womersley and Guiry (1994) it has been lost and has been



**Figs 102–106.** *Pterocliadiella capillacea*. **Fig. 102.** Habit of specimen from Lord Howe Island showing pyramidal outline and narrowly lanceolate ultimate branches. WNC 2003007. Scale = 1 cm. **Fig. 103.** Habit of mainland specimen showing short clavate ultimate branches. NSW 439766. Scale = 1 cm. **Fig. 104.** Transverse section of erect branch. WNC Slide 2003-S022. Scale = 50  $\mu\text{m}$ . **Fig. 105.** Elongated elliptical tetrasporangial sori produced on narrow lanceolate ultimate branches. WNC Slide 2003-S025. Scale = 3 mm. **Fig. 106.** Transverse section of tetrasporangial sorus showing sterile margin with large concentration of rhizines (arrowhead) and a decussately divided mature tetrasporangium. WNC Slide 2003-S023. Scale = 25  $\mu\text{m}$ .



lectotypified by Gmelin's (1768) illustration (1768: pl. 15, fig. 1).

#### *Habitat and morphology*

Plants form thick, spongy, mats or carpets in the lower intertidal. Thallus dark red to yellow red, cartilaginous, consisting of tufts of erect branches, up to 15 cm high, sometimes arising from an entangled fibrous holdfast. Prostrate branches attached to the substratum by tapering, peg-like holdfast of consolidated rhizoidal cells. Erect branches with linear, flattened main axes, up to 1.5 mm in width, and three to four or more orders of opposite to alternate distichous branching. The length of branches becomes progressively shorter towards the apex giving the thallus a generally pyramidal outline (Fig. 102). Branches tapering towards the base and those from the main axes often basally constricted (Fig. 103). Ultimate branches either short and clavate with obtuse apices, or longer and narrowly lanceolate with acute apices.

Thallus composed of a four- or five-cell-layer cortex surrounding a medulla of elongated, thick-walled cells (Fig. 104). Outermost cortical cells rectangular to elliptical in transverse section; other cortical cells irregularly globose, increasing in size towards the medulla. Rhizines numerous throughout the medulla, generally more abundant towards the thallus margins (Fig. 106), and sometimes extending into the inner cortex.

Tetrasporangia irregularly arranged in sori on ultimate branches (Fig. 105) with a narrow sterile margin (Fig. 106). Unilocular cystocarps of the *Pterocladia*-type develop on ultimate branches.

#### *Distribution*

Widespread throughout the Atlantic, Indian and Pacific Oceans. In NSW it grows along the entire coastline, including Lord Howe Island. Also from Norfolk Island.

#### *Remarks*

Two slightly different forms varying in the morphology of ultimate branches were encountered in this study. Specimens from the NSW mainland had relatively short, clavate ultimate branches with obtuse apices (Fig. 103), while specimens from Lord Howe Island had relatively long, narrowly lanceolate ultimate branches with acute apices (Fig. 102). Nucleotide sequences of *rbcL* generated from Lord Howe Island and NSW mainland specimens representing these two forms were identical and varied little from sequences of South Australian, New Zealand, and Italian specimens (Fig. 113). Previous *rbcL* analyses including *P. capillacea* sequences from a variety of geographic locations have demonstrated that this is a widespread species (Freshwater *et al.* 1995).

On the NSW mainland, *P. capillacea* forms thick, spongy, almost monoclonal mats or carpets in the lower intertidal. It

is the most common and perhaps largest species in biomass of the Gelidiales in New South Wales.

#### *Specimens examined*

NEW SOUTH WALES mainland: Lennox Head, *A.J.K. Millar & P.G. Richards*, 21.vi.1992, NSW 292643; Gordon Bay, Clovelly, *A.J.K. Millar & D.W. Freshwater*, 17.vii.2002, NSW 705651; Montague Island, North West Trench, *A.J.K. Millar; J. Huisman & N. Yee*, 11.x.1999, NSW 433981; Aughinish Rocks, *A.J.K. Millar; N. Yee & P.G. Richards*, 1.iii.2000, NSW 439764-439766; LORD HOWE ISLAND, Old Gulch, *A.J.K. Millar & D.W. Freshwater*, 2.x.2002 (NSW LHI #9, WNC2003007-2003008); Sylphs Hole, *G. & C. Kraft & C. O'Brien*, 28.ix.1976, MELU GK9855; NORFOLK ISLAND, *J.H. Maiden & J.L. Boorman*, xi.1902, NSW 415016.

#### *Molecular vouchers*

Specimen NSW #3, 1396 bp *rbcL* accession # AY352421; identical *rbcL* sequence from specimen LHI #9.

#### Genus *Ptilophora* Kützing, *Bot. Zeit.* 5: 25 (1847)

One of the larger genera in the Gelidiales, many species of *Ptilophora* had been previously assigned to the genus *Beckerella* Kylin because their thalli lacked surface proliferations. Norris (1987) proposed the inclusion of *Beckerella* in *Ptilophora* after discovering surface proliferations in the type species, *B. pinnatifida*. Additional support for this merger was provided by the more extensive morphological and molecular study of Tronchin *et al.* (2003). *Ptilophora* is well characterised by the presence of a four-layered vegetative construction, which is found in no other Gelidiales taxa.

*Ptilophora pectinata* (A. & E.S. Gepp) Norris, *Bot. Mar.* 30: 252 (excluding fig. 8) (1987). Millar 1990: 311, figs 8A–B. Akatsuka 1987: fig. 9. De Toni 1924: 165. May 1949: 197. May 1965: 371

Figs 107–112.

*Basionym*: *Pterocladia lucida* f. *pectinata* A. & E.S. Gepp, *J. Bot. Lond.* 44: 254 (1906).

*Homotypic synonyms*: *Beckerella pectinata* (A. & E.S. Gepp) Fan & Papenfuss in Fan, *Univ. Calif. Publ. Bot.* 32: 322, pl. 44 (1961).

*Gelidium lucasii* May, *Proc. Linn. Soc. N.S.W.* 69: 226, figs 1–6 (1944).

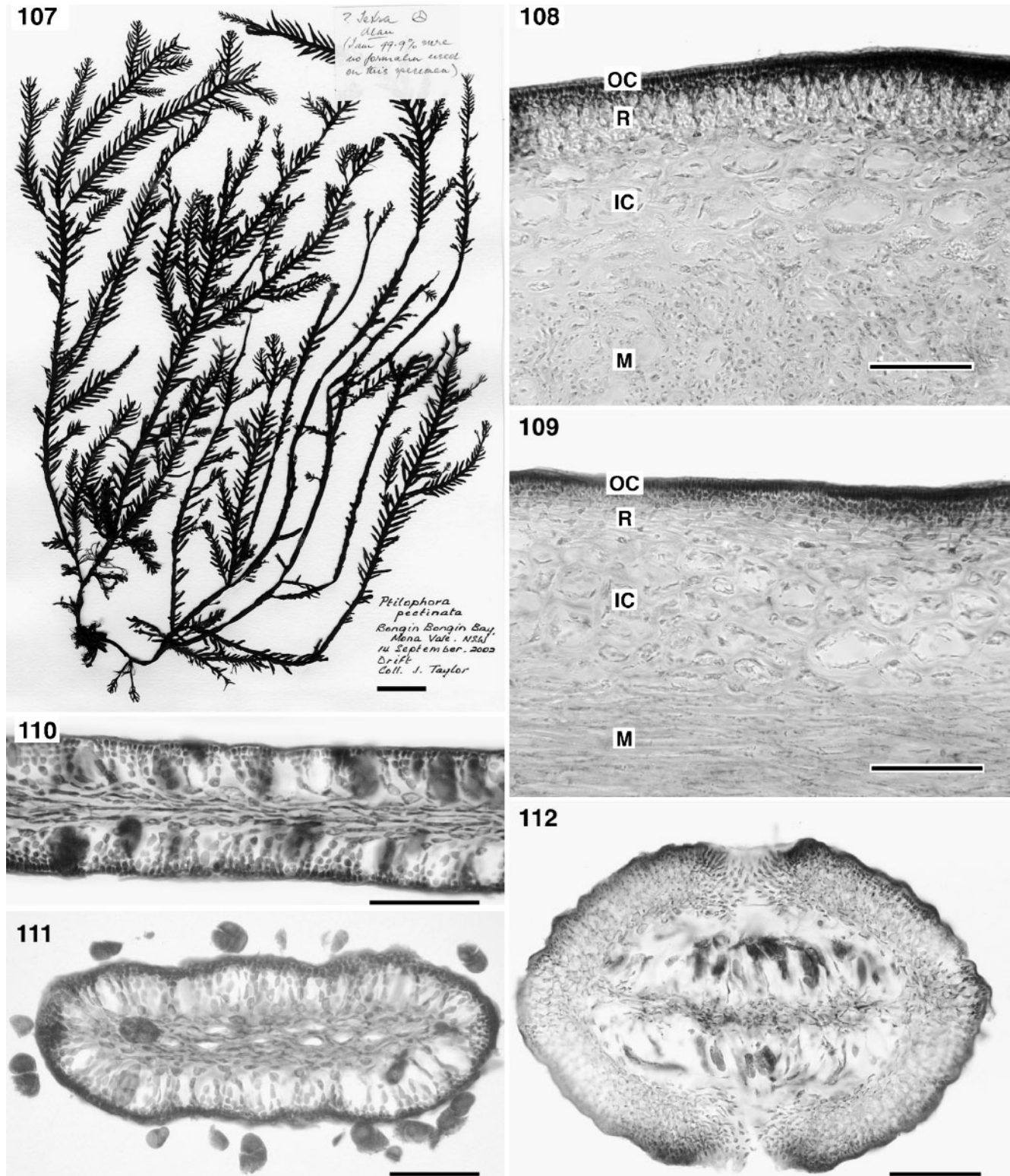
*Pterocladia pectinata* (A. & E.S. Gepp) Lucas, *Proc. Linn. Soc. N.S.W.* 56: 408, pl. 23, fig. 2 (1931).

Non *Gelidium pectinatum* Montagne (1846): 108–109, pl. 10, fig. 1, *nom. illeg.*

*Type*: BM 612225, from Maroubra Bay, July 1901, *A.H.S. Lucas* #9. Isotypes in NSW 492115, NSW 492114, NSW 492116–NSW 492118, NSW 288850–NSW 288853.

#### *Habitat and morphology*

Plants are strictly subtidal on rocks and grow to depths of 26 m. Thalli (Fig. 107) to 50 cm high, erect from a single discoid or fibrous holdfast, sparsely issuing flattened rhizoids (to 4 mm long) at base; axes flattened, distichous, pinnately branched (to four orders), to 4 mm wide in upper parts



**Figs 107–112.** *Ptilophora pectinata*. **Fig. 107.** Habit of tetrasporophytic plant from Bongin Bongin Bay, NSW 707387. Scale = 2 cm. **Fig. 108.** Transverse section showing four-layered vegetative construction. Outer cortex (OC); rhizine band (R); inner cortex (IC); medulla (M). WNC Slide 2003-S033. Scale = 100  $\mu$ m. **Fig. 109.** Longitudinal section showing four-layered vegetative construction. Outer cortex (OC); rhizine band (R); inner cortex (IC); medulla (M). WNC Slide 2003-S034. Scale = 100  $\mu$ m. **Fig. 110.** Longitudinal section of tetrasporangial sorus. NSW Slide 21-84. Scale = 100  $\mu$ m. **Fig. 111.** Transverse section through tetrasporangial sorus. NSW Slide 21-48. Scale = 100  $\mu$ m. **Fig. 112.** Section through mature cystocarp. NSW Slide 21-85. Scale = 100  $\mu$ m.

(to 400 µm thick); lateral branches to 20 cm long, branched in similar manner to main axis (Fig. 107). Thallus composed of four distinct tissue layers (Figs 108, 109) including a three- or four-cell-layered outer cortex of small pigmented cells; a layer of many densely packed rhizine cells transected by files of small cortical cells; an inner cortex of generally large isodiametric cells, and a medulla of elongated thick-walled cells surrounded by rhizines.

Tetrasporangial sori (Fig. 110) are borne in lanceolate, flattened laterals that proliferate from distal parts of ultimate determinate lateral branchlets. The entire branchlet becomes fertile leaving no sterile margin (Fig. 111). Tetrasporangia are ovate to 44 µm long and 36 µm in diameter. Biloculate, biporate cystocarps (Fig. 112) are borne in the same location. Males not observed.

#### Distribution

On the NSW mainland from Byron Bay south to Twofold Bay. Also known from northern New Zealand.

#### Remarks

Based on specimens sent to the Gepps by Lucas, they were of the opinion that the NSW species was nothing more than a variety of *Pterocladia lucida*, a common species from this coast (Gepp and Gepp 1906). Later, Lucas (1931) decided the species was sufficiently different to warrant its own status and thus raised var. *pectinata* to specific rank. On close examination of female material, May (1944) decided that the bilocular cystocarps were indicative of the genus *Gelidium* and not *Pterocladia* where Lucas and the Gepps had initially placed it. Owing to the earlier, albeit illegitimate, name of *Gelidium pectinatum* Montagne, May (1944) re-named the species after Lucas (*Gelidium lucasii*). Kylin (1956) erected the genus *Beckerella* but did not include the Australian species in it, and it was not until some 5 years later that Fan (1961) made the transfer to, and combination of, *Beckerella pectinata*. Most recently, Norris (1987) merged that genus with the earlier described *Ptilophora*, where the species is presently placed and confirmed by Tronchin *et al.* (2003).

May (1944) noted the striking morphological similarity that *P. pectinata* shares with the Japanese *P. subcostata* (as *Gelidium subcostatum*). Okamura's (1907: pl. xlvi) depiction shows a large, broadly compressed, two-edged, distichously pinnate plant that appears to differ mainly in the production of a distinct midrib, a structure that is entirely missing in NSW populations of *P. pectinata*. We can further attest to their specific dissimilarity in that they are markedly different on a molecular level. Analyses of *rbcL* sequences in this study resolve *P. pectinata* as an isolated lineage basal to the other included *Ptilophora* species (Fig. 113). *Ptilophora pectinata* is also resolved as a distinct species with no close sister relationships in more taxon replete analyses of *rbcL* and 28S rRNA gene sequences (Tronchin 2003; Tronchin *et al.* 2004).

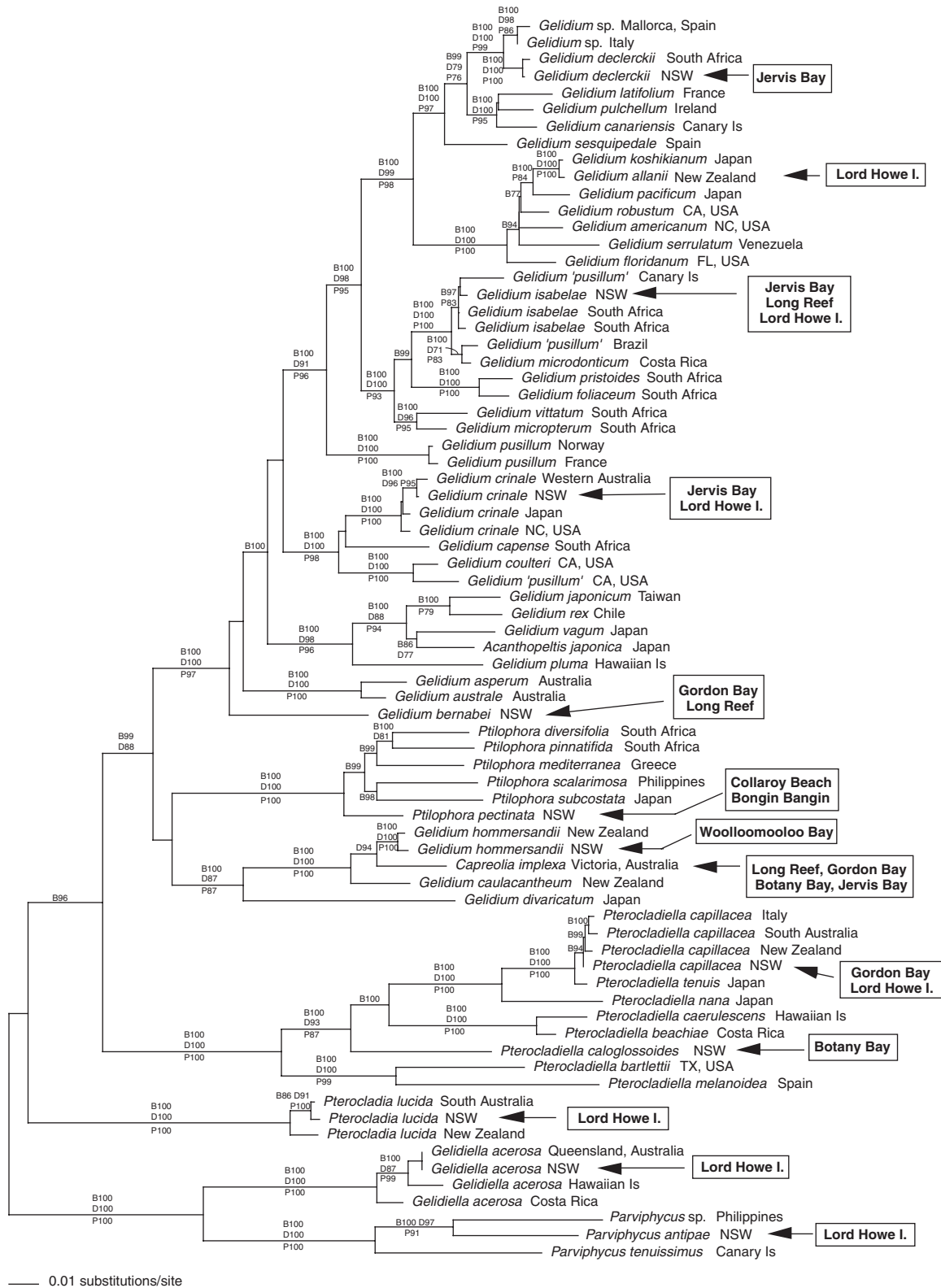
Norris (1987) recorded *P. pectinata* from South Africa on the basis that he thought *Gelidium helenae* Dickinson may be conspecific, and thus related all records of the South African species to *P. pectinata*. In his South African monograph of the Gelidiales representatives, Norris (1992) describes plants with an 'interrupted' midrib, main axes that are not particularly broad, and illustrates pinnules that are uniform in breadth along their lengths. The specimen he illustrates for *P. pectinata* (Norris 1987, fig. 8) from South Africa represents *P. helenae* as we interpret it. New South Wales specimens lack a prominent midrib, are always broadly flattened, and the pinnules are much broader at their base. Akatsuka (1987) illustrates the holotype of *P. helenae*, which is a lot finer than *P. pectinata*, with pinnules that are also much narrower. Specimens collected by Mary Pockock from Richards Bay, South Africa that we have examined are the nearest in general morphology to NSW specimens. There is no morphological variation in NSW specimens and this is the main reason why the variable South African specimens appear to represent a different species. We do not accept the conspecificity of the two species, especially as recent molecular analyses show the two to be very different (Tronchin 2003; Tronchin *et al.* 2004), and that *P. helenae* is most closely related to *P. leliaertii* Tronchin & De Clerck, a new species described in Tronchin *et al.* (2004).

Chapman (1969) records *Pterocladia lucida* var. *sublittoralis* from New Zealand based on a manuscript name and specimens from Lindauer's Exsiccatae No. 315. Later, Adams (1994) suggested this represents *Ptilophora pectinata* as that species is known to occur in the North Island. While we can confirm the presence of *P. pectinata* from New Zealand based on two specimens filed in NSW, our examination of Lindauer's Exsiccatae No. 315 housed in NSW indicates these are not representative of either *Ptilophora pectinata* or even a *Ptilophora* species. Although the plants are sterile, cross sections reveal a simple medulla and thickened, compact cortex, with rhizines spread randomly throughout the interior, very unlike the characteristic four-layered sections typical for *Ptilophora* species as reported by Tronchin *et al.* (2003). We are unsure of the generic placement of these specimens and suggest that they most likely represent an undescribed species. Cystocarp morphology and molecular analyses will be necessary before any further determination can be made.

*Gelidium pectinatum* Montagne, *nom. illeg.* was the intended basionym for *G. corneum* (Hudson) Lamouroux var. *pectinatum* Ardissonne & Strafforello. This is a Mediterranean species, now referred to as *G. corneum*, and has nothing in common with the present taxon.

#### Specimens examined

NEW SOUTH WALES: Byron Bay, drift, *G. Halligan* NSW 289887 v.1916 (NSW); Minnie Waters, SW side of headland, *A.J.K. Millar* &



**Fig. 113.** Maximum-likelihood tree (LnLi = -14569.87857) resulting from analyses of 74 Gelidiales *rbcL* sequences including 13 species found in New South Wales. Clade probability values from Bayesian analyses (B) and bootstrap proportion values from distance (D) and parsimony (P) analyses are shown for branches when greater than 70.

*K.Christian*, 3.vi.1998, NSW 420694, NSW 420695; Coffs Harbour, Hoggart AM471 21.i.1982 (MELU); Coffs Harbour, drift on harbour beach next to jetty, *G.Kraft, D.Hardin & A.J.K.Millar*, 5.vii.1995, NSW 700297; Maroubra Bay, near Bondi, *A.H.S.Lucas*, vii.1901, NSW 288850–NSW 288853 (types); Bongin Bangin Bay, Mona Vale, *J.Taylor*, 14.ix.2002, NSW 707387; Twofold Bay, Henre Bolte Wreck, *J.Huisman, N.Yee & J.Eu*, 13.x.1999, NSW 433867, NSW 433837, NSW 433839. NEW ZEALAND: East Cape, no date, NSW 492831, NSW 713563.

#### Molecular vouchers

Specimen NSW #11b, 1386 bp *rbcL* accession # AY344043; NSW 707387, 1382 bp *rbcL* accession # AY344044, 1043 bp 28S rDNA accession # AY345881.

#### Molecular analyses

Results from phylogenetic analyses of *rbcL* sequences for Gelidiales species, including 13 species found in NSW, are shown in Fig. 113. Only one sample was included in the final analyses when multiple samples of a species varied at two or fewer sites, but all the NSW locations where specimens were collected in this study are indicated. The depicted topology is the maximum-likelihood tree, but it also represents the general tree topologies recovered in maximum-parsimony, distance and Bayesian analyses. All major clades resolved in the maximum-likelihood tree were also present in all other trees, and the relationships of the major clades were consistent between analysis methods except when there was no support with any method for those relationships, e.g. the relationship of the clade containing *Ptilophora* species and the clade containing *Capreolia*. The relationships of species within clades were also usually consistent in the different analyses, and analysis method had no effect on the resolved relationships of any NSW Gelidiales species. More specific remarks on the results of these phylogenetic analyses are included in the treatments of individual NSW species.

Two different Bayesian analyses were conducted, the first used the overall best-fit model of molecular evolution for the sequence dataset, and the second allowed for codon-position-specific models. Clade probability values for both analyses were nearly identical but when they differed those from the first analysis were generally more conservative and therefore they are the values presented in Fig. 113.

#### Discussion

As a result of this study, there are now 15 species of Gelidiales known from the NSW mainland, Lord Howe and Norfolk Islands (Table 3). The previous 12 species recorded were mostly misidentifications, including *Gelidiella bornettii*, *Gelidium australe*, *G. caulacanthum*, *G. pusillum*, and *Pterocladia caloglossoides*. Without exception, all records of *Gelidium pusillum* and *Gelidium australe* from NSW have been shown to represent different species and at least six species were attributed to these names (*Gelidium allanii*, *G. bernabei*, *G. isabelae*, *G. declerckii*, some

specimens of *G. hommersandii* and *Capreolia implexa*). We suggest that records of *G. pusillum* and *G. australe* outside their type localities may also prove to be incorrect identifications. This work also suggests that records of *Gelidium pusillum* from areas other than its type locality, but especially from the southern Hemisphere, may well prove to be misidentifications of *Gelidium bernabei* and *G. declerckii* as was shown in our South African collections. Three species, *Parviphycus antipae*, *Gelidium crinale*, and *Pterocladia caloglossoides* represent new records for mainland NSW; *Gelidium isabelae* and *Gelidium allanii*, are newly reported for Australia and three are new species, *Gelidium bernabei*, *Gelidium declerckii*, and *Gelidium hommersandii*.

Based on prior reports of Gelidiales species from the NSW mainland and Lord Howe Island (Guiry and Womersley 1993; Millar and Kraft 1993), three species occurred only on the mainland coast, four species occurred only on Lord Howe Island (the fifth reported species was a misidentification), and four species were found from both (Table 3). Our research has now shown that six species are found only along the NSW mainland, four species only on Lord Howe Island, and five species occur at both (Table 3). All the larger non-turf species found along the NSW mainland coast are also reported to occur in New Zealand (Chapman 1969; Adams 1994); *Pterocladia capillacea*, *Ptilophora pectinata*, *Pterocladia lucida*, *Gelidium allanii*. A better understanding of the connection between the NSW mainland and New Zealand Gelidiales floras will require a more thorough study of the intertidal turf species in New Zealand.

The NSW Gelidiales flora was found to include representatives of both widespread species (e.g. *Gelidium crinale*, *Pterocladia capillacea*) and those with a regionally restricted distribution (e.g. *G. bernabei*, *G. hommersandii* and *G. maidenii*). The NSW species included in the *rbcL* sequence analyses are resolved within different clades in the overall Gelidiales tree indicating that there is no primary biogeographic affinity among them (Fig. 113). Some biogeographic relationships are apparent among smaller groups of species. For example, *Capreolia implexa*, *Gelidium caulacanthum*, and *G. hommersandii*, species with an Australia–New Zealand distribution, are resolved together in a strongly supported clade (Fig. 113).

Gelidiales species have a reputation for being difficult to identify and even assign to genera. We have found that a combination of sequence analyses and detailed morphological comparisons is necessary in order to identify Gelidiales species with any degree of accuracy. The NSW Gelidiales species studied can all be identified using a suite of morphological characters although strictly autapomorphic character states were generally not found. The following key to species is based largely upon vegetative characters because fertile thalli, especially gametophytic ones are sometimes absent. Specimens bearing tetrasporangia are commonly collected and such soral features are used in this key.

**Key to species of Gelidiales from New South Wales (including Lord Howe and Norfolk Islands)**

1. Thallus in cross-section without rhizines (thick-walled refractive filaments with very thin lumens) ..... 2  
Thallus in cross section with rhizines ..... 3
2. Thallus mostly erect with opposite, distichous laterals giving a pyramidal outline ..... *Gelidiella acerosa*  
Thallus mostly decumbent with creeping stolon and minute, erect, mostly simple branches ..... *Parviphycus antipae*
3. Thalli small, turf-like, entangled erect and prostrate axes mostly less than 5 cm high ..... 4  
Thalli large, not turf-like, axes distinctly separate from limited fibrous or discoid holdfast, mostly 5–30 cm high ..... 10
4. Thalli almost entirely prostrate, multiple branches arising from nodes ..... *Pterocladia caloglossoides*  
Thallus consisting of both erect and prostrate axes, branches arising singly and not from nodes ..... 5
5. Distal portions of erect vegetative axes flattened ..... 6  
Distal portions of erect vegetative axes terete or slightly compressed ..... 8
6. Apices of erect axes mostly acute; tips sometimes multifurcate ..... *Gelidium crinale*  
Apices of erect axes obtuse; tips not multifurcate ..... 7
7. Main axes often stipitate; without surface proliferations; decussate lines often visible in surface view ..... *Gelidium isabelae*  
Main axes not stipitate; surface proliferations common; decussate lines not visible in surface view ..... *Gelidium declerckii*
8. Apices acute; axes mostly erect, almost entirely terete, compressed only in tetrasporangia sori ..... *Gelidium hommersandii*  
Apices obtuse; axes mostly prostrate; distal axes compressed ..... 9
9. Tetrasporangial sorus without a sterile margin; tetrasporangia irregularly arranged ..... *Gelidium bernabei*.  
Tetrasporangial sorus with a narrow sterile margin; tetrasporangia arranged in capreolate to straight rows ..... *Capreolia implexa*
10. Axes broadly flattened, sometimes with a central midrib ..... 11  
Axes compressed ..... 12
11. Axes in cross-section with four distinct layers (central filamentous medulla, pseudoparenchymatous outer medulla, rhizine laden fasciculate inner cortex and thin pseudoparenchymatous cortex) ..... *Ptilophora pectinata*  
Axes in cross-section with only a cortex and a medullary layer ..... *Pterocladia lucida*
12. Lower half or proximal portions of main axes of mature thalli often without branches, or with vestigial remnants of lateral branches forming serrations; thalli mostly over 10 cm high ..... 13  
Main axes of mature thalli bearing laterals along entire length; thalli mostly less than 7 cm high ..... 14
13. Thalli large (to 37 cm high); cross-section three layered (densely packed filamentous medulla, open meshed outer medulla and cortex of small files of pseudoparenchymatous cells); rhizines concentrated in outer medulla/inner cortex ..... *Gelidium maidenii*  
Thalli smaller (to 15 cm high); cross-section without clear layers; rhizines concentrated in medulla ..... *Pterocladia capillacea*
14. Main axes mostly percurrent, with laterals arising alternately or irregularly but generally causing a shallow zigzag shape of main axis ..... *Gelidium allanii*  
Main axes not obviously percurrent, not shallowly zig-zag in shape ..... *Pterocladia caerulescens*

**Acknowledgements**

We especially thank Drs Gerald Kraft, Wendy Nelson and Max Hommersand, who supplied many specimens for study. Dr Karla McDermid provided the Latin diagnoses for the three new species and Lesley Elkan kindly drew the botanical illustrations. Fellow diving partners were Dr John Huisman, Chris O'Brien, Peter Richards and David Hardin. This project was funded by an Australian Biological Resources Study (ABRS), a Visiting Research Fellowship to DWF from the Friends of the Gardens (Sydney), and USA National Science Foundation Grant DEB-9726170. We thank Pinetrees Lodge for help on the Lord Howe Island expedition, and Karlene Christian and Jack Marges of Bounty Divers on Norfolk Island. Mr Nick Yee accompanied us on many of the collecting expeditions and assisted with the generation of sequence data at RBGS and his help was greatly appreciated.

**References**

- Abbott IA (1999) 'Marine red algae of the Hawaiian Islands.' (Bishop Museum Press: Honolulu, Hawaii'i)
- Adams NM (1994) 'Seaweeds of New Zealand.' (Canterbury University Press: Christchurch, New Zealand)
- Agardh J (1851) 'Species Genera et Ordines Algarum Vol. 2, part 1.' (Gleerup: Lund.)
- Agardh J (1852) 'Species Genera et Ordines Algarum Vol. 2, part 2.' (Gleerup: Lund.)
- Akatsuka I (1987) Taxonomy and distribution of *Beckerella* (Gelidiales, Rhodophyta). *Aquatic Botany* **28**, 257–274.  
doi: 10.1016/0304-3770(87)90004-0
- Allender BM, Kraft GT (1983) The marine algae of Lord Howe Island (New South Wales): the Dictyotales and Cutleriales (Phaeophyta). *Brunonia* **6**, 73–130.
- Bailey JC, Freshwater DW (1997) Molecular systematics of the Gelidiales: inferences from separate and combined analyses of plastid *rbcL* and nuclear SSU gene sequences. *European Journal of Phycology* **32**, 343–352.
- Børghesen F (1932) A revision of Forsskål's algae mentioned in Flora Aegyptiaco-Arabica and found in his herbarium in the Botanic Museum of the University of Copenhagen. *Danske Botanisk Arkiv* **8**, 1–14.
- Bornet J-BE, Thuret GA (1876) 'Notes algologiques recueil d'observations sur les algues Fasc. 1.' (Masson: Paris)
- Celan M (1938) Notes sur la flore algologique du littoral roumain de la mer Noire. IV. Deux Rhodophycées nouvelles pour la flore de la mer Noire: *Gelidiella antipae* et *Phyllophora brodiaei* (Turn) J. Ag. *Bulletin de la Section Scientifique de l'Académie Roumaine* **19**, 76–79.
- Chapman VJ (1969) 'The marine algae of New Zealand Part III: Rhodophyceae, Issue 1: Bangiophycidae and Florideophycidae (Nemalionales, Bonnemaisoniales, Gelidiales).' (J. Cramer: Germany)
- Cribb AB (1983) 'Marine algae of the southern Great Barrier Reef. Part 1. Rhodophyta.' (Australian Coral Reef Society: Brisbane)

- Cribb AB (1996) 'Seaweeds of Queensland' (Queensland Naturalists Club: Brisbane)
- Dawson EY (1953) Marine red algae of Pacific Mexico. Part I. Bangiales to Corallinaceae subf. Corallinoideae. *Allan Hancock Pacific Expeditions* **17**, 1–239.
- Dawson EY, Acleto C, Foldvik N (1964) 'The seaweeds of Peru.' Beihefte zur Nova Hedwigia 13. (Verlag von J. Cramer, Stuttgart)
- De Toni GB (1924) 'Sylloge Algarum omnium hucusque Cognitarum Vol. 6. Florideae.' (Padua)
- Dixon PS, Irvine LM (1977) 'Seaweeds of the British Isles. Vol. I. Rhodophyta. Part 1, Introduction, Nemaliales, Gigartinales.' (British Museum [Natural History]: London)
- Fan K (1961) Morphological studies of the Gelidiales. *University of California Publications in Botany* **32**, 315–368.
- Feldmann J, Hamel G (1934) Observations sur quelques Géliadiacées. *Revue Générale de Botanique* **46**, 528–550.
- Fredriksen S, Guiry MD, Rueness J (1994) Morphological and biosystematic studies of *Gelidium pusillum* and *G. pulchellum* (Gelidiaceae, Rhodophyta) from Europe. *Phycologia* **33**, 462–470.
- Freshwater DW, Bailey JC (1998) A multigene phylogeny of the Gelidiales including nuclear large-subunit rRNA sequence data. *Journal of Applied Phycology* **10**, 229–236. doi: 10.1023/A:1008075429646
- Freshwater DW, Rueness J (1994) Phylogenetic relationship of some European *Gelidium* (Gelidiales, Rhodophyta) species, based on *rbcL* nucleotide sequence analysis. *Phycologia* **33**, 187–194.
- Freshwater DW, Fredericq S, Hommersand MH (1995) A molecular phylogeny of the Gelidiales (Rhodophyta) based on analysis of plastid *rbcL* nucleotide sequences. *Journal of Phycology* **31**, 616–632.
- Freshwater DW, Fredericq S, Bailey JC (1999) Characteristics and utility of nuclear encoded large-subunit ribosomal gene sequences in phylogenetic studies of red algae. *Phycological Research* **47**, 33–38. doi: 10.1046/j.1440-1835.1999.00148.x
- Gepp A, Gepp ES (1906) Some marine algae from New South Wales. *Journal of Botany* **44**, 249–261.
- Gmelin SG (1768) 'Historia fucorum.' (St. Petersburg)
- Guiry MD, Womersley HBS (1993) *Capreolia implexa* gen. et sp. nov. (Gelidiales, Rhodophyta) in Australia and New Zealand; an intertidal mat-forming alga with an unusual life history. *Phycologia* **32**, 266–277.
- Harvey WH (1846) 'Phycologia britannica.. Vol. 1.' (Reeve and Benham: London, UK)
- Harvey WH (1858) 'Phycologia Australica, Vol. 1.' (Reeve: London, UK)
- Harvey WH (1863) 'Phycologia Australica, Vol. 5.' (Reeve: London, UK)
- Hatta AM, Prud'homme van Reine WF (1991) A taxonomic revision of Indonesian Gelidiales (Rhodophyta). *Blumea* **35**, 347–380.
- Holmgren PK, Holmgren NH, Barnett LC (1990). 'Index Herbariorum. Part. I: The herbaria of the world. 8th edn.' (International Association for Plant Taxonomy, New York Botanical Garden: New York, NY)
- Hommersand MH, Fredericq S (1996) Vegetative and reproductive development of *Pterocliadiella capillacea* (Gelidiales, Rhodophyta) from La Jolla, California. *Nova Hedwigia* **112**, 147–160.
- Howe MA (1914) The marine algae of Peru. *Memoirs of the Torrey Botanical Club* **15**, 1–185.
- Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* **17**, 754–755. doi: 10.1093/bioinformatics/17.8.754
- Hughey JR, Silva PC, Hommersand MH (2001) Solving taxonomic and nomenclatural problems in Pacific Gigartinales (Rhodophyta) using DNA from type material. *Journal of Phycology* **37**, 1091–1109. doi: 10.1046/j.1529-8817.2001.01048.x
- Huisman JM (1993) Supplement to the catalogue of marine plants recorded from Rottnest Island. In 'Proceedings of the fifth international marine biological workshop: the marine flora and fauna of Rottnest Island, Western Australia'. (Eds FE Wells, DI Walker, H Kirkman, R Lethbridge) pp. 11–18. (Western Australian Museum: Perth)
- Huisman JM (1997) Marine benthic algae of the Houtman Abrolhos Island, Western Australia. In 'The marine flora and fauna of the Houtman Abrolhos Islands, Western Australia'. (Ed. FE Wells) pp. 177–237. (Western Australian Museum: Perth)
- Huisman JM (2000) 'Marine plants of Australia.' (University of Western Australia Press: Perth)
- Huisman JM, Walker DI (1990) A catalogue of the marine plants of Rottnest Island, Western Australia, with notes on their distribution and biogeography. *Kingia* **1**, 349–459.
- Jensen A (1993) Present and future needs for algae and algal products. *Hydrobiologia* **260/261**, 15–23. doi: 10.1007/BF00048998
- Kapraun DF (1980) 'An illustrated guide to the benthic marine algae of coastal North Carolina I. Rhodophyta.' (The University of North Carolina Press: Chapel Hill, NC)
- Kapraun DF, Ganzon-Fortes E, Bird KT, Trono G, Breden C (1994) Karyology and agar analysis of the agarophyte *Gelidiella acerosa* (Forsskål) Feldmann et Hamel from the Philippines. *Journal of Applied Phycology* **6**, 545–550.
- Kendrick GA, Huisman JM, Walker DI (1990) Benthic macroalgae of Shark Bay, Western Australia. *Botanica Marina* **33**, 47–54.
- Kraft GT, Abbott IA (1998) *Gelidiella womersleyana* (Gelidiales, Rhodophyta), a diminutive new species from the Hawaiian Islands. *Botanica Marina* **41**, 51–61.
- Kützing FT (1868) 'Tabulae Phycologicae oder Abbildungen der Tange, Vol. 18.' (Nordhausen)
- Kylin H (1938) Verzeichnis einiger Rhodophyceen von Südafrika. *Lunds Universitets Årsskrift, NY Följd, Andra Afdelningen* **34**, 1–26.
- Kylin H (1956) 'Die Gattungen der Rhodophyceen.' (Gleerups: Lund)
- Lewis JA (1984) Checklist and bibliography of benthic marine macroalgae recorded from Northern Australia. I. Rhodophyta. Department of Defence, Materials Research Laboratories, Report MRL-R-912. Melbourne, Vic.
- Lucas AHS (1909) Revised list of the Fucoideae and Florideae of Australia. *Proceedings of the Linnean Society of New South Wales* **34**, 9–60.
- Lucas AHS (1931) Notes on Australian marine algae. VI. *Proceedings of the Linnean Society of New South Wales* **56**, 407–411.
- Lucas AHS (1935) The marine algae of Lord Howe Island. *Proceedings of the Linnean Society of New South Wales* **60**, 194–232.
- Lucas AHS, Perrin F (1947) 'The seaweeds of South Australia. Part 2. The red seaweeds.' (Government Printer: Adelaide, SA)
- Maddison DR, Maddison WP (2000) 'MacClade 4: analysis of phylogeny and character evolution, v. 4.0.' (Sinauer Associates: Sunderland, MA)
- Maggs CA, Guiry MD (1987) *Gelidiella calcicola* sp. nov. (Rhodophyta) from the British Isles and Northern France. *British Phycological Journal* **22**, 417–434.
- May V (1944) Studies on Australian marine algae. I. The corrected name for *Pterocliadia pectinata* (A. & E. S. Gepp) Lucas. *Proceedings of the Linnean Society of New South Wales* **64**, 226–228.

- May V (1947) Studies on Australian marine algae. III. *Proceedings of the Linnaean Society of New South Wales* **71**, 273–277.
- May V (1949) Studies on Australian marine algae. V. Observations on and geographical records of various species, particularly those of the *Gelidium* complex. *Proceedings of the Linnaean Society of New South Wales* **74**, 196–202.
- May V (1965) A census and key to the species of Rhodophyceae (red algae) recorded from Australia. *Contributions from the NSW National Herbarium* **3**, 349–429.
- May V, Larkum AWD (1981) A subtidal transect in Jervis Bay, New South Wales. *Australian Journal of Ecology* **6**, 439–457.
- May V, Collins AJ, Collet LC (1978) A comparative study of epiphytic algal communities on two common genera of sea-grasses in eastern Australia. *Australian Journal of Ecology* **3**, 91–104.
- Melo RA (1992) A note on the absence of hyphae (rhizines) in the thallus of *Gelidiella acerosa* Forsskål Feldmann et Hamel (Rhodophyta). In 'Taxonomy of economic seaweeds with reference to some Pacific and western Atlantic species, Volume III'. (Ed. IA Abbott) pp. 173–181. (California Sea Grant College Program: La Jolla, CA)
- Millar AJK (1990) Marine red algae of the Coffs Harbour Region, northern New South Wales. *Australian Systematic Botany* **3**, 293–593.
- Millar AJK (1999) Marine benthic algae of Norfolk Island, South Pacific. *Australian Systematic Botany* **12**, 479–547.
- Millar AJK, Wynne MJ (1992) *Patulophycus eclipses* gen. et sp. nov. (Delesseriaceae, Rhodophyta) from the southwestern Pacific. *Systematic Botany* **17**, 409–416.
- Millar AJK, Kraft GT (1993) Catalogue of marine and freshwater red algae (Rhodophyta) of New South Wales, including Lord Howe Island, south-western Pacific. *Australian Systematic Botany* **6**, 1–90.
- Millar AJK, Kraft GT (2001) Monograph of the green macroalgal genus *Rhipilia* (Udoteaceae, Halimedales), with a description of *R. crassa* sp. nov. from Australia and the Philippines. *Phycologia* **40**, 21–34.
- Montagne C (1846) Ordo I. Phyceae Fries. In 'Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842... Sciences physiques. Botanique. Cryptogamie'. (Ed. MC Durieu de Maisonneuve) (Paris)
- Norris RE (1987) A re-evaluation of *Ptilophora* Kützting and *Beckerella* Kylin (Gelidiales, Rhodophyceae) with a review of South African species. *Botanica Marina* **30**, 243–258.
- Norris RE (1992) The marine red algae of Natal, South Africa: Order Gelidiales (Rhodophyta). *Memoirs of the Botanical Survey of South Africa* **61**, 1–37.
- Okamura K (1907) 'Icones of Japanese Algae. Vol. 1.' (Published by the author: Tokyo, Japan)
- Okamura K (1937) 'Icones of Japanese Algae. Vol. 3.' (Published by the author: Tokyo, Japan)
- Posada D, Crandall KA (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics* **14**, 817–818. doi: 10.1093/bioinformatics/14.9.817
- Price IR, Scott FJ (1992) 'The turf algal flora of the Great Barrier Reef, Part I. Rhodophyta.' (James Cook University of North Queensland: Townsville, Qld)
- Renfrew DE, Gabrielson PW, Scagel RF (1989) The marine algae of British Columbia, northern Washington, and southeast Alaska: division Rhodophyta (red algae), class Rhodophyceae, order Gelidiales. *Canadian Journal of Botany* **67**, 3295–3314.
- Rico JM, Freshwater DW, Norwood KG, Guiry MD (2002) Morphology and systematics of *Gelidiella tenuissima* (Gelidiales, Rhodophyta) from Gran Canaria (Canary Islands, Spain). *Phycologia* **41**, 463–469.
- Rodríguez de Rios N (1992) Estudios taxonomicos en agarofitas de Venezuela II. Notas sobre el genero *Pterocladia* J. Agardh (Rhodophyta, Gelidiales). *Ernstia* **2**, 77–93.
- Santelices B (1976) Taxonomic and nomenclatural notes on some Gelidiales (Rhodophyta). *Phycologia* **15**, 165–173.
- Santelices B (1977) A taxonomic review of Hawaiian Gelidiales (Rhodophyta). *Pacific Sciences* **31**, 61–84.
- Santelices B (1997a) The spermatangial sorus of *Gelidiella acerosa* (Gelidiellaceae, Gelidiales). In 'Taxonomy of economic seaweeds with reference to some Pacific species. Vol. VI'. (Ed. IA Abbott) pp. 77–87. (California Sea Grant College Program: La Jolla, CA)
- Santelices B (1997b) The sexual reproductive development of *Pterocladia bulbosa* (Loomis) comb. nov. (Gelidiales, Rhodophyta). *Cryptogamie. Algologie* **18**, 297–307.
- Santelices B (1998) Taxonomic review of the species of *Pterocladia* (Gelidiales, Rhodophyta). *Journal of Applied Phycology* **10**, 237–252. doi: 10.1023/A:1008095915164
- Santelices B (1999) Taxonomic status of the species originally ascribed to the genus *Pterocladia* (Gelidiales, Rhodophyta). In 'Taxonomy of economic seaweeds with reference to some Pacific species. Vol. VII'. (Ed. IA Abbott) pp. 71–80. (California Sea Grant College Program: La Jolla, CA)
- Santelices B (2002) The taxonomic status of *Gelidiella adnata* (Gelidiales, Rhodophyta). In 'Taxonomy of economic seaweed with reference to some Pacific species. Vol. VIII'. (Eds IA Abbott, K McDermid) pp. 151–166. (California Sea Grant College Program: La Jolla, CA)
- Santelices B (2004) *Parviphycus*, a new genus in the Gelidiellaceae (Gelidiales, Rhodophyta). *Cryptogamie. Algologie* **25**, 313–326.
- Santelices B, Hommersand MH (1997) *Pterocladia*, a new genus in the Gelidiaceae (Gelidiales, Rhodophyta). *Phycologia* **36**, 114–119.
- Santelices B, Rico JM (2002) Nomenclature and typification of *Gelidiella tenuissima* (Gelidiales, Rhodophyta). *Phycologia* **41**, 436–440.
- Schneider CW, Lane CE (2005) Notes on the marine algae of the Bermudas. 7. Additions to the flora including *Chondrocanthus saundersii* sp. nov. (Rhodophyta, Gigartinales) based on *rbcL* sequence analysis. *Phycologia* **44**, 72–83.
- Shimada S, Masuda M (2000) New records of *Gelidiella pannosa*, *Pterocladia caerulescens* and *P. caloglossoides* (Rhodophyta, Gelidiales) from Japan. *Phycological Research* **48**, 95–102. doi: 10.1046/j.1440-1835.2000.00185.x
- Shimada S, Horiguchi T, Masuda M (1999) Phylogenetic affinities of genera *Acanthopeltis* and *Yatabella* (Gelidiales, Rhodophyta) inferred from molecular analyses. *Phycologia* **38**, 528–540.
- Shimada S, Horiguchi T, Masuda M (2000a) Two new species of *Gelidium* (Rhodophyta, Gelidiales), *Gelidium tenuifolium* and *Gelidium koshikianum*, from Japan. *Phycological Research* **48**, 37–46. doi: 10.1046/j.1440-1835.2000.00182.x
- Shimada S, Horiguchi T, Masuda M (2000b) Confirmation of the status of three *Pterocladia* species (Gelidiales, Rhodophyta) described by K. Okamura. *Phycologia* **39**, 10–18.
- Silva PC, Basson PW, Moe RL (1996) 'Catalogue of the benthic marine algae of the Indian Ocean.' (University of California Press: Berkeley, CA)
- Smith GM (1944) 'Marine algae of the Monterey Peninsula, California.' (Stanford University Press: Stanford, CA)
- Sreenivasa Rao P (1974) Some observations on the cytology of *Gelidiella acerosa* (Forsskål) Feldmann et Hamel. *Cytologia* **39**, 391–395.



- Swofford DL (2002) 'PAUP\*. Phylogenetic analysis using parsimony (\*and other methods). Version 4.' (Sinauer Associates: Sunderland, MA)
- Taylor WR (1945) 'Pacific marine algae of the Allan Hancock expeditions to the Galapagos Islands.' (The University of Southern California Press: Los Angeles, CA)
- Thomas DT (2000) A phylogenetic study of *Gelidium crinale* (Gelidiales, Rhodophyta) based on *rbcL* and LSU sequence data. MSc thesis, University of North Carolina at Wilmington.
- Thomas DT, Freshwater DW (2001) Studies of Costa Rican Gelidiales (Rhodophyta): four Caribbean taxa including *Pterocliadiella beachii* sp. nov. *Phycologia* **40**, 340–350.
- Tronchin EM (2003) The systematics, biology and distribution of the Gelidiaceae (Rhodophyta) of South Africa and related taxa. PhD thesis, University of Cape Town.
- Tronchin EM, Freshwater DW, Bolton JJ, Anderson RJ (2002) A reassessment and reclassification of species in the genera *Onikusa* Akatsuka and *Suhria* J. Agardh ex Endlicher (Gelidiales, Rhodophyta) based on molecular and morphological data. *Botanica Marina* **45**, 548–558. doi: 10.1515/BOT.2002.058
- Tronchin EM, Freshwater DW, Bolton JJ (2003) A re-evaluation of the genera *Beckerella* and *Ptilophora* (Gelidiales, Rhodophyta) based on molecular and morphological data. *Phycologia* **42**, 80–89.
- Tronchin EM, De Clerck O, Freshwater DW, Bolton JJ, Anderson RJ (2004) *Ptilophora leliaertii* and *Ptilophora coppejansii*, two new species of Gelidiales (Rhodophyta) from South Africa. *European Journal of Phycology* **39**, 395–410. doi: 10.1080/09670260410001721491
- Trono EC, Ganzon-Fortes ET (1988) 'Philippines seaweeds.' (National Book Store: Manila, Philippines)
- Turner D (1819) 'Fuci sive Plantarum Fucorum Generi a Botanicis Ascriptarum Icones Descriptiones et Historia. Vol. 4.' (London)
- Ugadim Y (1987) Distribuição das espécies de *Gelidium* e *Pterocliadia* (Gelidiaceae-Rhodophyta) no litoral Brasileiro. *Nerítica* **2**, 65–74. doi: 10.1080/09670260410001721491
- Weber-van Bosse A (1921) Liste des algues du Siboga, 2. *Siboga Expeditie* **54b**, 187–310.
- Weber-van Bosse A (1926) Algues de l'expédition danoise aux îles Kei. *Vidensk. Medd. Dansk. Naturh. Foren.* **81**, 57–155.
- Williams LG (1948) Seasonal alternation of marine floras at Cape Lookout, North Carolina. *American Journal of Botany* **35**, 682–695.
- Womersley HBS, Guiry MD (1994) Order Gelidiales. In 'The marine benthic flora of southern Australia: Rhodophyta—Part 111A'. pp. 118–142. (Australian Biological Resources Study: Canberra, ACT)
- Wynne MJ (1993) *Prionitis pterocladina* sp. nov. (Halymeniaceae, Rhodophyta), a newly recognized alga in the western Gulf of Mexico. *Botanica Marina* **36**, 497–502.
- Xia B, Wong Y (1999) Taxonomic studies on *Pterocliadiella* (Gelidiaceae, Gelidiales, Rhodophyta) from China. In 'Taxonomy of economic seaweeds with reference to some Pacific species. Vol. VII'. (Ed. IA Abbott) pp. 81–86. (California Sea Grant College Program, La Jolla, CA)

Manuscript received 12 October 2004, accepted 1 April 2005