

Rediscovery of *Gelidiella ramellosa* (Kützting) Feldmann *et* Hamel (Gelidiales, Rhodophyta) from near the type locality in Western Australia

John M. HUISMAN^{a*}, Julia C. PHILLIPS^b & D. Wilson FRESHWATER^c

^a School of Biological Sciences and Biotechnology, Murdoch University, Murdoch, W.A. 6150, Australia and Western Australian Herbarium, Department of Environment and Conservation, George St., Kensington, W.A. 6151, Australia

^b CSIRO Marine & Atmospheric Research, Private Bag No. 5, Wembley, W.A. 6913, Australia

^c Center for Marine Science, University of North Carolina at Wilmington, 5600 Marvin Moss Lane, Wilmington, NC 28409. U.S.A.

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Abstract – The poorly known red alga *Gelidiella ramellosa* (Kützting) Feldmann *et* Hamel is described from specimens collected near the type locality in Western Australia. Plants occur as turfs to 1-2 cm in height, with prostrate stolons attached by clusters of rhizoids to rock. Erect axes are irregularly pinnately branched and terete to slightly compressed. Structurally, the medulla is pseudoparenchymatous with no discernable central axis, and rhizines are absent. Spermatangia occur in surface sori. Tetrasporangia are borne in irregular whorls in terete, basally constricted stichidia that are lateral on erect axes. LSU nrDNA and *rbcL* sequence analyses clearly place *G. ramellosa* in a clade containing species of *Gelidiella* and *Parviphycus*, but are equivocal regarding its relationship with either genus.

Gelidiella / Gelidiales / *Parviphycus* / Rhodophyta / *RbcL* / nrDNA LSU / Western Australia

Résumé – Redécouverte du *Gelidiella ramellosa* (Kützting) Feldmann *et* Hamel (Gelidiales, Rhodophyta) près de la localité-type en Australie Occidentale. L'algue rouge peu connue, *Gelidiella ramellosa* (Kützting) Feldmann *et* Hamel, est décrite à partir de spécimens récoltés près de la localité-type en Australie Occidentale. Les plantes de 1-2 cm de hauteur présentent des stolons prostrés, fixés aux rochers grâce à des faisceaux de rhizoïdes. Les axes sont dressés, cylindriques et légèrement effilés ou légèrement comprimés, et ramifiés de façon irrégulièrement pennée. D'un point de vue structurel la moelle est pseudoparenchymateuse sans axe central reconnaissable. Les rhizines sont absentes. Les spermatanges forment des sores superficiels. Les tétrasporanges forment des verticilles irréguliers sur des stichidia cylindriques, légèrement effilés, rétrécis à la base et portés latéralement par des axes dressés. Les séquences des LSU nrDNA et *rbcL* placent *G. ramellosa* dans un clade contenant des espèces de *Gelidiella* et *Parviphycus* sans pour autant élucider de façon définitive ses relations phylogénétiques avec l'un ou l'autre genre.

Australie Occidentale / *Gelidiella* / Gelidiales / *Parviphycus* / Rhodophyta / *RbcL* / nrDNA LSU

* Correspondence and reprints: J.Huisman@murdoch.edu.au
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INTRODUCTION

Gelidiella ramellosa (Kützing) Feldmann *et* Hamel is a small red algal turf species known with certainty only from the type material (Womersley & Guiry, 1994: 122), a collection made from southwestern Australia over 165 years ago. Since that time the species has not been recorded from the type locality or anywhere else in Australia, but has been attributed to Tunisia (Feldmann, 1931; Feldmann & Hamel, 1936; Boudouresque, 1967: 152, figs 1-7; Maggs & Guiry, 1987: 429) and Japan (Yoshida *et al.*, 1990: 290). Womersley & Guiry (1994) doubted the veracity of these records, as most descriptions do not agree entirely with the type material. Recently, Perrone & Delle Foglie (2006) mentioned a collection from the Cheradi Islands attributed to *G. ramellosa* by Lapenna & Perrone (1999) that “seems quite distinct from the Australian specimens”.

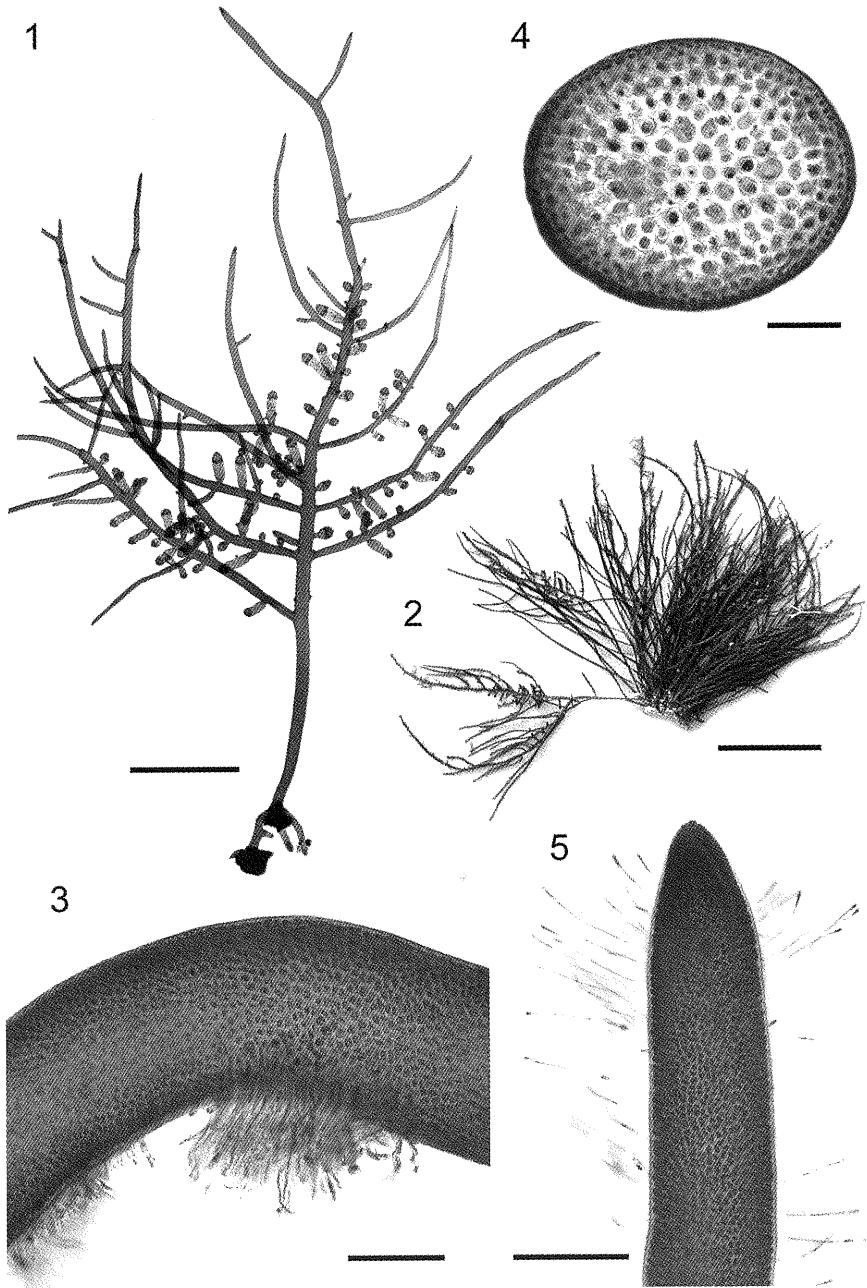
Given the apparent rarity of this species, and its questionable occurrence in other regions, it was therefore of great interest when specimens were collected by one of us (JP) from a limestone reef habitat near Perth, Western Australia, in 2005. A subsequent collection was made in 2007 from the same location. These specimens are tetrasporangial and spermatangial and are wholly compatible with the type collection. Unfortunately the exact provenance of the type specimens is unknown, but it is known that their collector, Johan August Ludwig Preiss (1811-1883), collected from south-western Australia, including localities near Perth. The new specimens therefore represent authentic new material of this apparently rare species from the probable vicinity of the type locality.

These new collections have allowed us to make a detailed examination of the habit, morphology, tetrasporangia, previously unknown spermatangia, and molecular relationships of *G. ramellosa*.

MATERIALS AND METHODS

Specimens were collected by SCUBA and either frozen (2005) or preserved in 5% formalin/sea water (2007) for morphological examination. Portions of the 2007 collections were dried in silica gel desiccant for DNA extraction. For microscopical examination, plants were sectioned by hand and stained in 1% aniline blue, then mounted in 50% Karo (CPC International, Westchester, IL, USA) corn syrup. Herbarium specimens and slide preparations are held in PERTH. Specimens and slide preparations were examined with a Nikon SMZ800 stereo microscope and Nikon Eclipse 80i compound microscope and photographed using a Nikon DSFi1 digital camera (Nikon, Tokyo, Japan). Photographic plates were prepared using Adobe Photoshop CS2.

Total genomic DNA was extracted from a silica gel dried specimen following the procedure of Hughey *et al.* (2001). Amplifications of the plastid-encoded *rbcL* and partial nuclear-encoded large-subunit rRNA genes (LSU) were performed using Hot Star Taq DNA polymerase (Qiagen, Valencia, CA, USA) and the reaction mixture and thermocycling protocol described in Freshwater *et al.* (2005). Big Dye (Applied Biosystems, Foster City, CA, USA) sequencing reactions were set up following the manufacturer's protocol and run on an ABI 3130xl Genetic Analyzer. Amplification and sequencing primers were the same as those published in Freshwater & Rueness (1994) and Freshwater & Bailey (1998). Sequence reaction results were edited and compiled using Sequencher (Gene Codes Corp., Ann Arbor, MI, USA).



Figs 1-5. *Gelidiella ramellosa*, vegetative features (all PERTH 07895399 except where indicated). **1.** Detail of a portion of a tetrasporangial plant, showing irregularly pinnate branching. **2.** Pressed herbarium specimen showing clumped habit (PERTH 07857616). **3.** Detail of prostrate axis showing unicellular, clustered attachment rhizoids. **4.** Section of thallus showing medulla without obvious axial and periaxial cells and lacking rhizines. **5.** Apex of branch with prominent apical cell and surface hairs. Scales: 1 = 1 mm; 2 = 5 mm; 3, 5 = 100 μ m; 4 = 50 μ m.

Table 1. Collection information/source and GenBank accession numbers for species included in molecular analyses. Newly generated sequences are indicated in bold

Species	Collection information/source	Accession #	
		<i>rbcL</i>	LSU
<i>Aphanta pachyrrhiza</i>	KwaZulu-Natal, South Africa (Tronchin & Freshwater, 2007)	EF190244	EF190257-
<i>Gelidiella acerosa</i>	Oahu, Hawaiian Islands (Freshwater <i>et al.</i> , 1995)	L22475	AF039551
<i>Gelidiella acerosa</i>	Lord Howe Island (Millar & Freshwater, 2005)	AY352424	AY359963
<i>Gelidiella acerosa</i>	Cahuita, Costa Rica (Thomas & Freshwater, 2001)	AF305812	AF296519
<i>Gelidiella acerosa</i>	Matemwe, Zanzibar, Tanzania. F. Leliaert & E. Coppejans, 14.vii.01	EU146837	FJ215875
<i>Gelidiella "acerosa"</i>	9-mile reef, Sodwana Bay, KwaZulu-Natal, South Africa. D.W. Freshwater, 12.ii.01	FJ215878	FJ215876
<i>Gelidiella fanii</i>	Lungkeng, Kenting National Park, S. Taiwan. S.M. Lin, 17.x.02	EU146838	–
<i>Gelidiella ligulata</i>	Miyake Island, Japan (Shimada & Masuda, 1999)	AB017678	–
<i>Gelidiella ramellosa</i>	Cook Lump, near Perth, Western Australia. J. Phillips, 10.i.07	FJ215879	FJ215877
<i>Gelidium corneum</i>	Asturias, Spain (Freshwater <i>et al.</i> 1995 [as <i>G. sesquipedale</i>])	L22071	AF039539
<i>Parviphycus antipae</i>	Lord Howe Island (Millar & Freshwater, 2005)	AY352425	–
<i>Parviphycus sp.</i>	Siaton, Maloh, Negros Oriental, Philippines. J. West culture #3433	AF309386	AF308798
<i>Parviphycus tenuissimus</i>	Lectotype, Biarritz, France (Santelices & Rico, 2002)	AF309385	AF308799
<i>Parviphycus tenuissimus</i>	Gran Canaria, Canary Islands (Rico <i>et al.</i> , 2002)	AF320983	AF320984
<i>Pterocladia lucida</i>	Wellington, New Zealand (Freshwater <i>et al.</i> , 1995)	U01048	AF39550
<i>Pterocладиella capillacea</i>	California, USA (Freshwater <i>et al.</i> , 1995)	U01896	AF039549

The five newly generated sequences and ones available from GenBank (Table 1) were aligned using MacClade (v. 4, Maddison & Maddison, 2000). Three different sequence alignment data sets were compiled and analysed in this study: one containing 16 *rbcL* sequences; one consisting of 13 LSU sequences, and a combined *rbcL* + LSU alignment including the 13 taxa for which both sequences are available. Characteristics and models of molecular evolution for these alignments were determined using Modeltest v. 3.06 (Posada & Crandall, 1998) and PAUP* v. 4.b10 (Swofford, 2002). All three data sets were analysed using maximum likelihood (ML), maximum parsimony (MP) and distance methods as implemented in PAUP*. ML searches used the Modeltest derived models of sequence evolution and consisted of 10 random sequence additions (RADs) with tree bisection-reconnection (TBR) branch swapping and MULTREES option. ML bootstrap analyses consisted of either 303 (*rbcL*), 1000 (LSU), or 702 (combined) replications of 7 RADs, TBR and MULTREES. MP analyses consisted of branch-and-bound searches, and parsimony bootstrap values were based on either 675 (*rbcL*) or 1000 (LSU & combined) replications of branch-and-bound searches. Distance analyses consisted of neighbor-joining (NJ) tree building using the Modeltest derived distance correction. Distance bootstrap values were based on 5000 replications of neighbor-joining tree building.

RESULTS

Gelidiella ramellosa (Kützinger) Feldmann *et* Hamel, 1934: 533.

Basionym: *Acrocarpus ramellosus* Kützinger, 1843: 405; 1849: 762; 1868: 12, pl. 34d-g. Sonder 1848: 174.

Synonym: *Echinocaulon ramellosum* (Kützinger) Feldmann, 1931: 8, figs. 1-3.

Type: From W. Aust (*J.A.L. Preiss*); holotype in L, 941, 11...11 (Barcode: L 0055890). The exact provenance of the type specimens from Western Australia is unknown. Preiss collected from the southwest of Western Australia from 4 December 1838 to 8 January 1842 (Marchant, 1990). Sonder (1848) gives additional habitat information: "Ad conchas et inter caespites *Janiae antenninae* in litore occidentali Novae Hollandiae. Herb Preiss No. 2559", but again no specific locality. Further details and an image of the type sheet are available at the Leiden Herbarium website (<http://145.18.162.53:81/c8?ent=300017&rec=48643&sct=1>). A fragment of the type is also held in UC, No. 93568 (Santelices, 2007).

Specimens examined: Cook Lump (31° 26.914 S, 115° 32.830 E), north of Two Rocks, Western Australia, on high relief limestone reef at 4.2 m depth, 25 Jan. 2005, *J. Phillips 652* (PERTH 07857616, Fig. 2). Same location, 11 Jan. 2007, *J. Phillips & J. Huisman*, (PERTH 07895399) (Figs 1, 3-5, 6-12).

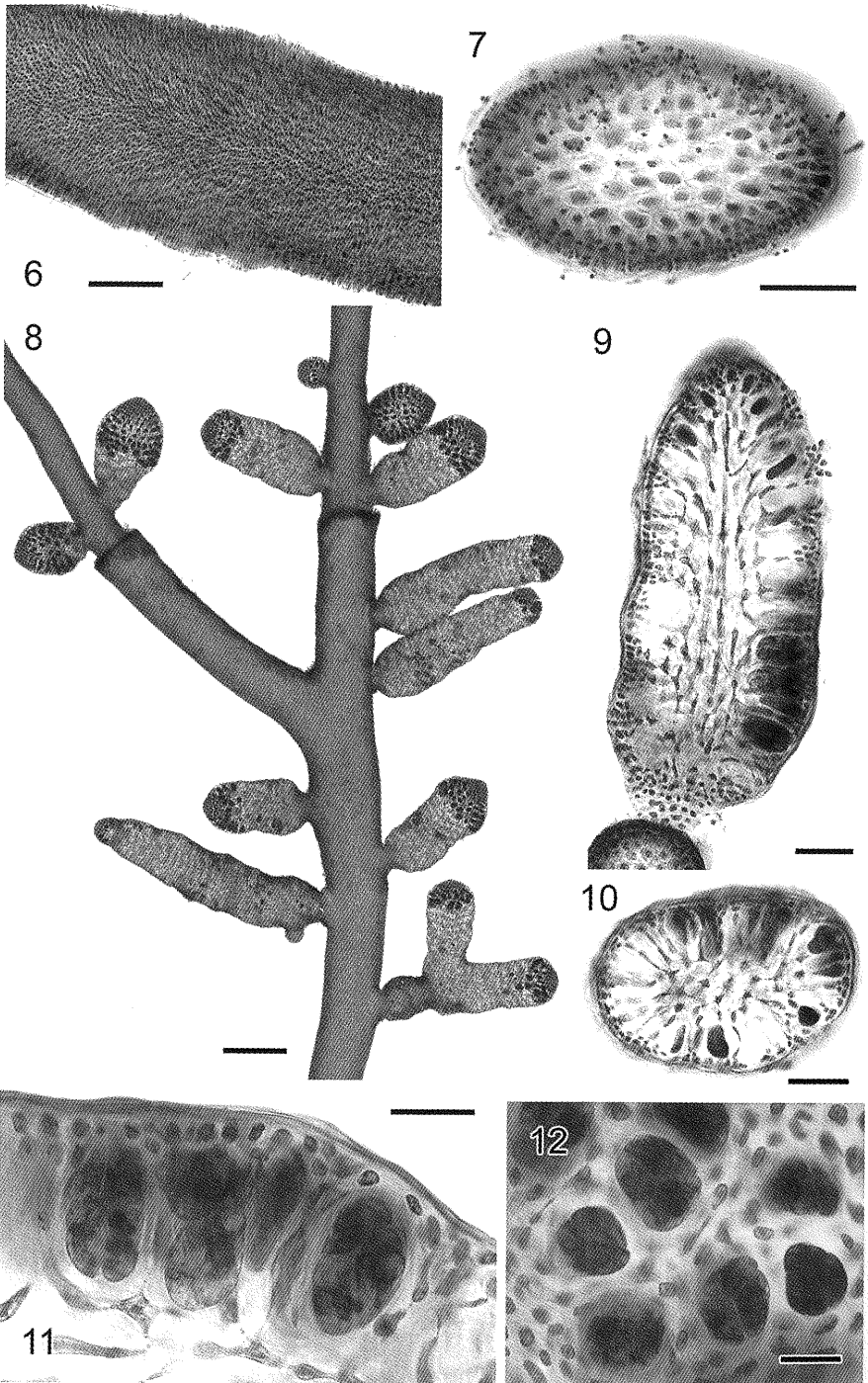
Habit and morphology

Plants grow as a turf to 1-2 cm in height (Fig. 2), with prostrate stolons 110-210 µm in diameter, attached by clusters of discrete rhizoids (Fig. 3) to rock. Erect branches are sparsely irregularly pinnately branched, terete to slightly compressed, 230-300 µm in diameter and tapering to a prominent domed apical cell (Fig. 5). Surface hairs are common, particularly near the apices (Fig. 5). Lateral branches are 110-140 µm broad, tapering to ca 70 µm broad below apices. Following damage, new branches regenerated from the cut surface are often of a smaller diameter than the parent branch (Fig. 8). Structurally, the medulla is pseudoparenchymatous with no discernable central axis, the cells 9-16 µm in diameter, grading into a pigmented cortex (Fig. 4). Cells of the epidermal layer are equidimensional in transverse section and 3-5 µm broad. Rhizines are absent, but under the light microscope some sections of the thallus (particularly near branch bases) appear to be refractive, indicating cell-wall thickening. In surface view, cells are angular, somewhat equidimensional (particularly in prostrate axes) to longitudinally elongate, 9-12 µm long by 3-5 µm wide µm, and aligned in vaguely splayed rows. Plants were often heavily epiphytized by species of *Acrochaetium*, including *A. microscopicum* (Kützinger) Nägeli.

Reproduction

Spermatangia arise in indefinite sori covering most of the surface near the apices of the plants (Fig. 6). The epidermal cells divide to produce 2-4 relatively elongate spermatangial mother cells (2-3 times as long as broad in lateral view), each of these then dividing transversely to produce one small spherical, ellipsoidal or slightly conical spermatangium (2-3 µm in diameter) (Fig. 7).

Tetrasporangia are borne in stichidia that arise laterally on erect axes (Fig. 8). Stichidia are terete, with a basal constriction or shortly stalked, simple or rarely once bifurcate, 400-1000 µm long and 160-250 µm in diameter. The



tetrasporangia are produced acropetally in irregular whorls, with each stichidium distally with 8-15 rows of sporangia, each row with 8-12 sporangia visible (i.e., 16-24 sporangia per whorl). Proximal to the sporangia are numerous empty rows where sporangia have been discharged. These remain empty or occasionally tetrasporangia are regenerated in the cavities. Structurally the stichidia have a more open construction than the vegetative branches (Figs 9, 10). Tetrasporangia are initiated from the inner cortical cells and are pit connected laterally and adaxially to the bearing cell. The bearing and other vegetative filaments lie alongside the sporangia and terminal cells arch over the distal surface. In surface view (best seen after release of sporangia) the vegetative filaments form an irregular honeycomb appearance. Tetrasporangia are ellipsoid to pyriform when young, ellipsoid when mature, 34-50 μm long and 19-30 μm in diameter, and tetrahedrally or irregularly cruciately divided (Figs 11, 12).

Molecular analyses

The first 111 base pairs of the 1467 base pair *rbcL* were excluded from analyses because of missing data for a majority of 16 sequences in the alignment. The remaining sequence included 428 (31.6%) variable and 297 (21.9%) parsimony informative sites and a GTR+I+G model was chosen as the best fit to these data. The same ML tree ($\ln L = -6135.50$) was found in 10 separate searches (Fig. 13) and was identical to the NJ tree and one of the three MP trees. The other MP topologies differed in having *G. ramellosa* sister to the *Gelidiella* clade, and the arrangement of the outgroup species. The partial LSU alignment included 1082 sites covering the middle region of the gene (Freshwater *et al.*, 1999) that has been used in previous Gelidiales analyses (e.g. Rico *et al.*, 2002; Tronchin & Freshwater, 2007). The alignment required the assignment of insertion/deletion mutations (indels) at 17 sites, however there were no indels of more than four contiguous sites, and the assigned gaps were treated as missing data in all analyses. The alignment included 131 (12.1%) variable and 73 (6.7%) parsimony informative sites and a TVM+I model was chosen as the best fit to these data. Ten separate ML searches found the same tree ($\ln L = -2529.57$, Fig. 14), which was identical in topology to one of two MP trees ($L = 186$, $CI = 0.691$). The other MP tree and the NJ tree differed in the arrangement of outgroup species and the positions of *G. ramellosa* and *Parviphycus* sp. were also different in the NJ tree. The combined *rbcL*+LSU alignment included 2438 sites, of which 538 (22.1%) were variable and 352 (16.9%) were parsimony informative. Ten separate ML searches under a GTR+I+G model of sequence evolution all found the same tree ($\ln L = -8218.82$, Fig. 15), which was identical to the single MP tree ($L = 997$, $CI = 0.562$). The NJ tree topology differed only in having *G. ramellosa* sister to a *Gelidiella/Parviphycus* clade.

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Figs 6-12. *Gelidiella ramellosa*, reproductive features (all PERTH 07895399). 6. Surface view of spermatangial sorus. 7. Transverse section of spermatangial sorus, showing spermatangia arising from all surfaces. 8. Portion of tetrasporangial plant showing lateral stichidia with sporangia arranged in mostly irregular rows. 9. Longitudinal section of tetrasporangial stichidium, showing sporangia maturing progressively from apex to base. 10. Transverse section of tetrasporangial stichidium. 11. Closer view of tetrasporangia, showing irregularly cruciate (left sporangium) and tetrahedral (right sporangium) arrangement of spores. 12. Surface view of tetrasporangia, showing mostly tetrahedral arrangement of spores. Scales: 6, 7, 9, 10 = 50 μm ; 8 = 100 μm ; 11, 12 = 25 μm .

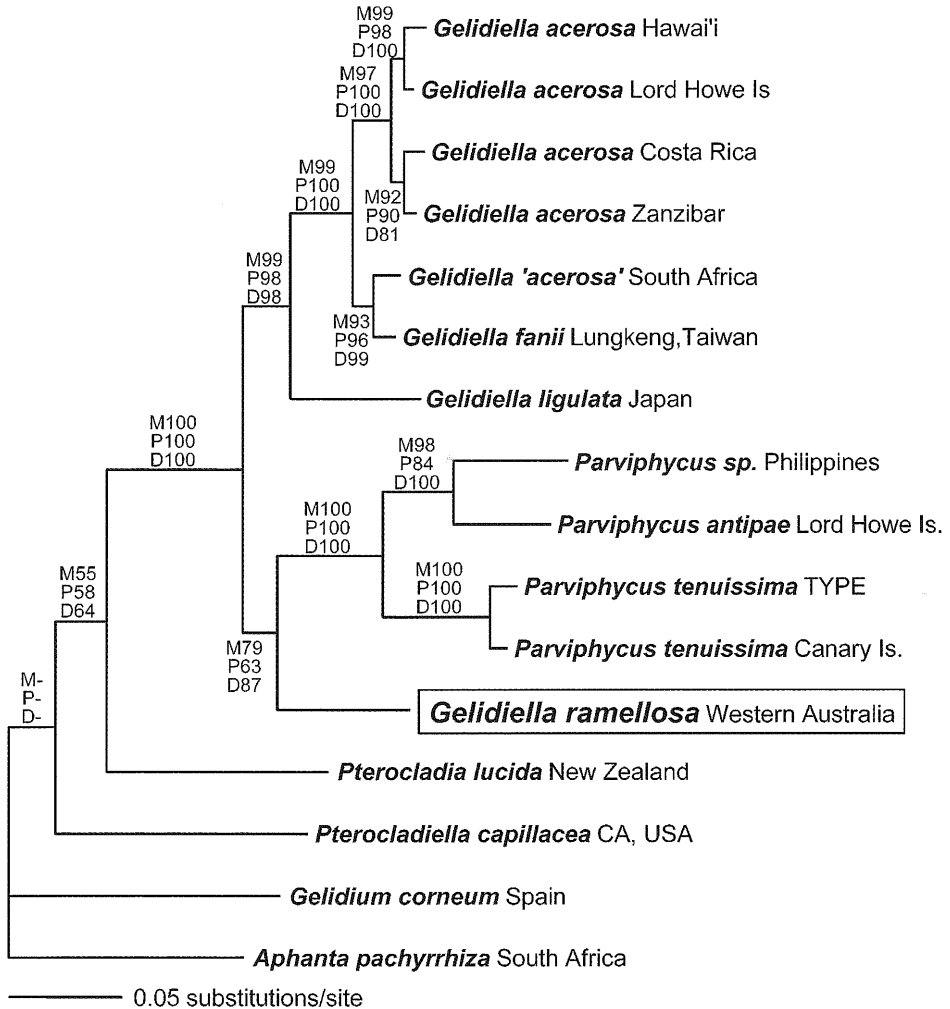


Fig. 13. Maximum-likelihood tree resulting from analysis of *rbcL* sequences for specimens of *Gelidiella*, *Parviphycus* and four gelidialean outgroups. Bootstrap proportion values for maximum-likelihood (M), maximum-parsimony (P), and distance (D) analyses are shown for branches when > 50.

The topological position of *Gelidiella ramellosa* was not consistent in the trees resulting from analyses of the three sequence data sets. It was sister to the clade of *Gelidiella acerosa* (Forsskål) Feldmann *et* Hamel in the LSU and combined analyses but with no bootstrap support. In *rbcL* analyses, *G. ramellosa* was usually resolved sister to the clade of *Parviphycus* species with levels of bootstrap support ranging from high (87%) for NJ to low (63%) for MP.

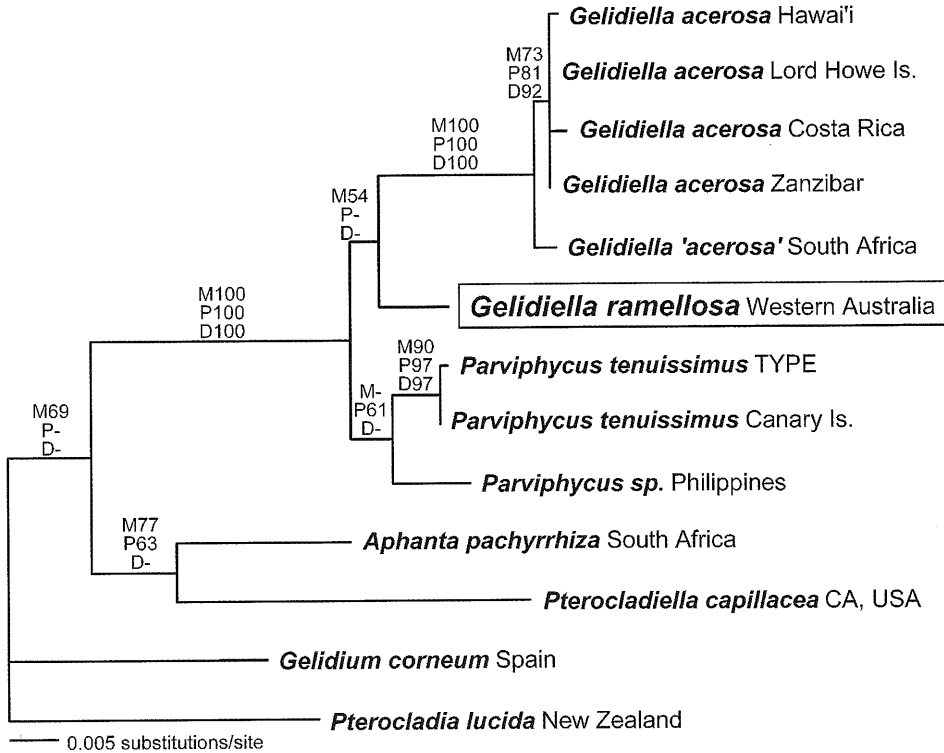


Fig. 14. Partial LSU maximum-likelihood tree resulting from analysis of sequences for specimens of *Gelidiella*, *Parviphycus* and four gelidialean outgroups. Bootstrap proportion values as described in Fig. 13.

DISCUSSION

Gelidiella ramellosa in Australia

The present specimens are almost wholly compatible with the type material of *Gelidella ramellosa* and the subsequent descriptions and illustrations of that material by Kützing (1868) and Womersley & Guiry (1994). Santelices (2007) examined a fragment of the type specimen in UC and reported it to lack rhizines and attached to the substratum by single-celled, externally produced rhizoids. This agrees with our material and is in concordance with the studies of Perrone *et al.* (2006) and Santelices (2007), who showed clustered rhizoids to be characteristic of *Gelidiella* and *Parviphycus* Santelices (see also Lin & Freshwater, 2008). Our material shows some tetrasporangia that appear to be tetrahedrally divided, while others are decussately cruciate as was described by Womersley & Guiry (1994). Given the proximity to the (admittedly vague) type locality, we are certain that our specimens represent authentic *Gelidiella ramellosa* and are the first collection of this species for over 165 years.

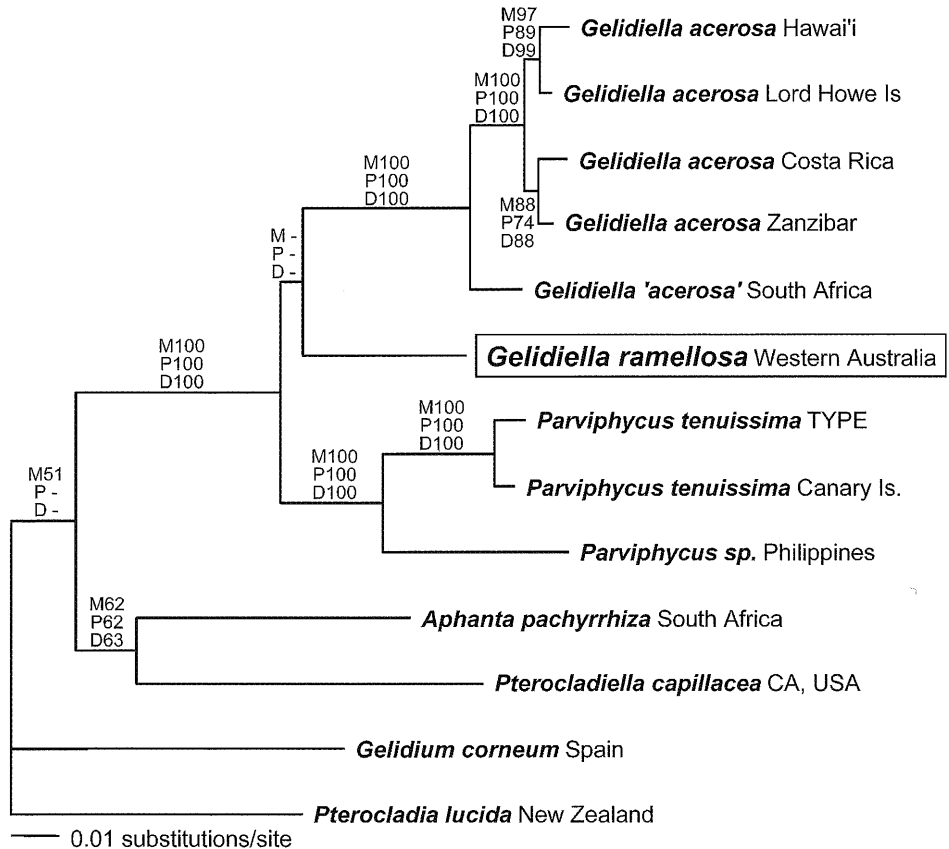


Fig. 15. Combined *rbcl* + partial LSU maximum-likelihood tree resulting from analysis of sequences for specimens of *Gelidiella*, *Parviphycus* and four gelidiales outgroups. Bootstrap proportion values as described in Fig. 13.

Two other species of *Gelidiella* have been reported for southern Australia by Womersley & Guiry (1994), but these have subsequently been transferred to other genera. (*G. minima* Guiry *et* Womersley to *Pterocladia*, *G. antipai* Celan to *Parviphycus*). *Gelidiella ramellosa* is readily distinguished from these species by its lateral tetrasporangial stichidia, which differ markedly from the terminal stichidia of *Pterocladia minima* (Guiry *et* Womersley) Santelices *et* Hommersand and *Parviphycus antipae* (Celan) Santelices (Womersley & Guiry, 1994).

In addition, three taxa of tropical *Gelidiella* have been recorded from Australia, including the type *G. acerosa*, *G. bornetii* (Weber-van Bosse) Feldmann *et* Hamel and *G. pannosa* Feldmann *et* Hamel (Cribb, 1983; Price & Scott, 1992; Huisman, 2000; Huisman & Borowitzka, 2003). Price & Scott (1992) questioned the distinctions between the latter two, referring their collections to *G. pannosa*, a species subsequently considered synonymous with *G. tenuissimus* Feldmann *et* Hamel (= *Parviphycus tenuissimus* (Feldmann *et* Hamel) Santelices) (Santelices &

Rico, 2002). *Gelidiella bornetii* was considered a taxonomic synonym of *G. lubrica* (Kützinger) Feldmann *et* Hamel by Hatta & Prud'homme van Reine (1991). Their taxonomic opinion was later supported by Schneider & Lane (2005), who tentatively attributed vegetative plants from Bermuda to this species. Other authors recognize both *G. bornetii* and *G. lubrica* (Kraft & Abbott, 1998, table 1; Shimada & Masuda, 1999) and, given their widely separate type localities, habitats and overall morphology, this seems justifiable until DNA sequence analyses of specimens from the respective type localities are undertaken. There is, however, some confusion with these species because Weber-van Bosse's protologue of *G. bornetii* (Weber-van Bosse, 1926) does not match the specimen labelled as the Holotype (Millar & Freshwater, 2005). The identity of the Great Barrier Reef specimens attributed to *G. bornetii* by Cribb (1983) is unclear, given these uncertainties.

At the Western Australian collection locality (Cook Lump), *Gelidiella ramellosa* grew in close association with *Gelidium crinale* (Turner) Gaillon, the two species sharing somewhat similar habits. *Gelidium crinale* is readily distinguished by the presence of internal rhizines, but a more immediate distinction can be seen by examining epidermal cells in surface view, which in *Gelidiella ramellosa* are longitudinally elongate whereas those of *Gelidium crinale* are equidimensional. This feature is best observed in the upright axes, as epidermal cells in the prostrate axes of *Gelidiella ramellosa* can also be equidimensional.

"*Gelidiella ramellosa*" from other countries

Maggs & Guiry (1987), Womersley & Guiry (1994) and Kraft & Abbott (1998) questioned the identity of non-type records of *G. ramellosa* from Tunisia and Japan. In their Table II, Maggs & Guiry (1987) reported tetrasporangia of Mediterranean specimens as occurring in chevrons and in rows of 4-6 sporangia when viewed from above. Feldmann (1931), Feldmann & Hamel (1936) and Boudouresque (1967) described plants from Tunisia as being compressed or flat, pinnately branched and the tetrasporangia as tetrahedrally divided. Despite the occurrence of tetrahedrally divided tetrasporangia in the new collections [something not reported by Womersley & Guiry (1994)] and the presence of slightly compressed axes, we agree with Womersley & Guiry in doubting that the Tunisian plants represent true *G. ramellosa*. The type and present specimens are terete to slightly compressed, irregularly sparsely branched, and tetrasporangia occur in irregular whorls of 8-12 sporangia (in surface view). We therefore feel that the Tunisian plants are incorrectly placed in *G. ramellosa* and probably represent a species of *Parviphycus*. At the moment we are unable to suggest an alternative name, but the features described by Feldmann & Hamel (1936) are compatible with the type description of *Gelidiella myrioclada* (Børgesen) Feldmann *et* Hamel (Børgesen, 1934, as *Echinocaulon*), although not necessarily with subsequent descriptions of this species (e.g. Santelices 1977; Abbott, 1999). Børgesen (1934) emphasized that his Indian specimens had tetrasporangia arranged in distinct transverse rows, but this was not the case with specimens from the Hawaiian Islands (Santelices, 1977). Given that this feature is presently accorded generic importance and is used (partly) to distinguish *Parviphycus* from *Gelidiella*, it is likely that the Hawaiian specimens do not represent *G. myrioclada*.

The division pattern of tetrasporangia in *Gelidiella* has been the cause of some uncertainty. Maggs & Guiry (1987) described the pattern in *G. calcicola*

as “perplexing”, as sporangia with two division products were not seen and the division sequence was therefore not successive (as is generally found in cruciately divided sporangia). The tetrasporangia in *G. ramellosa* also do not present a two-celled stage, and we therefore regard the arrangement of spores as tetrahedral.

Santelices (2004), erected the new genus *Parviphycus* for several species previously placed in *Gelidiella*, including *Parviphycus adnatus* (Dawson) Santelices, *P. antipae*, *P. tenuissimus* (Feldmann et Hamel) Santelices and *P. womersleyanus* (Kraft et Abbott) Santelices. The new genus was characterized by several features, including: i) regularly arranged rows of tetrasporangia; ii) axial cells and second order cell filaments obvious in transverse sections; and iii) a distichous pattern of apical division. Millar & Freshwater (2005) suggested that many of the species of *Gelidiella* were poorly known and that further study might result in additional transfers to *Parviphycus*, leaving *Gelidiella* with only the type and perhaps a few other species (Millar & Freshwater, 2005). Their prediction has proved prescient, as subsequently Afonso-Carillo *et al.* (2007) transferred *Gelidiella setacea* (Feldmann) Feldmann et Hamel to *Parviphycus*.

As reported by Womersley & Guiry (1994) and observed in the present material, axial cells and periaxial derivatives are not obvious in *Gelidiella ramellosa* and the sporangia are not in regular rows. Thus it does not show the important features of *Parviphycus* and should be retained in *Gelidiella*.

The relationships of *Gelidiella ramellosa* with other species of *Gelidiella* and *Parviphycus* are uncertain in analyses of chloroplast-encoded *rbcL* and nuclear-encoded LSU sequences. A clade of *Gelidiella* and *Parviphycus* species is fully supported (bootstrap values of 100%) in all trees generated by the different analyses methods. The specimen of *G. ramellosa* is resolved as one of the early diverging lineages within this clade and is variously positioned either sister to the *Gelidiella* or *Parviphycus* clades. Previous studies have shown a high correlation between morphological character states and molecularly defined relationships within the Gelidiales (e.g. Shimada *et al.*, 1999; Tronchin *et al.*, 2003). The equivocal position of *G. ramellosa* in the molecular trees despite its seemingly clear morphological affinity to *Gelidiella* is most likely a product of the small number of sequences for these genera currently available for analysis.

With the removal of several species to *Parviphycus* (*P. adnata*, *P. antipai*, *P. setacea*, *P. tenuissimus* (including *P. pannosa*) and *P. womersleyana*) and *Pterocliadiella* (*P. minima*, *P. sanctarum*, *P. taylorii*, and probably *P. calcicola*, the latter move flagged by Millar & Freshwater, 2005: 222; see also Santelices, 2007), some 17 species of *Gelidiella* are presently recognized. Kraft & Abbott (1998) provided a comprehensive table delineating the species that at the time were included in *Gelidiella*. Of those, *Gelidiella trinitatensis* W.R. Taylor (Taylor, 1960; Littler & Littler, 1997) and the seemingly rare *G. tinerefensis* Seoane-Camba (Seoane-Camba, 1977; Afonso-Carillo & Sanson, 1999: 95) are described as having tetrasporangia arranged in distinct chevrons, which would suggest closer affinities with *Parviphycus*. We refrain from making any new combinations, however, since we have not seen authentic material.

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REFERENCES

- ABBOTT I.A., 1999 — *Marine red algae of the Hawaiian Islands*. Honolulu, Hawai'i, Bishop Museum Press, xv + 477 p.
- AFONSO-CARILLO J. & SANSÓN M., 1999 — *Algas, hongos y fanerógamas marinas de las Islas Canarias*. Universidad de La Laguna, 254 p.
- AFONSO-CARILLO J., SANSÓN M., SANGIL C. & DÍAZ-VILLA T., 2007 — New records of benthic marine algae from the Canary Islands (eastern Atlantic Ocean): morphology, taxonomy and distribution. *Botanica marina* 50: 119-127.
- BØRGESEN F., 1934 — Some Indian Rhodophyceae especially from the shores of the Presidency of Bombay-IV. *Bulletin of miscellaneous information, royal botanic gardens, Kew* 1934: 1-30.
- BOUDOURESQUE C.-F., 1967 — *Gelidiella ramellosa* (Kützing) Feldmann et Hamel et *Antithamnion heterocladum* Funk, Rhodophycées rares ou nouvelles pour la flore française. *Annales de la société des sciences naturelles et d'archéologie de Toulon et du Var* 1967: 152-161.
- CRIBB A.B., 1983 — *Marine algae of the southern Great Barrier Reef. Part 1. Rhodophyta*. Brisbane, Australian Coral Reef Society, 173 p.
- FELDMANN J., 1931 — Remarques sur les genres *Gelidium* Lamour., *Gelidiopsis* Schmitz et *Echinocaulon* (Kütz.) emend. In: *Travaux cryptogamiques dédiés à Louis Mangin*. Paris, pp. 151-166.
- FELDMANN J. & HAMEL G., 1934 — Observations sur quelques Géliadiacées. *Revue générale de botanique* 46: 528-549.
- FELDMANN J. & HAMEL G., 1936 — Floridées de France VII. Géliadiales. *Revue algologique* 9: 85-140.
- FRESHWATER D.W. & BAILEY J.C., 1998 — A multigene phylogeny of the Gelidiales including nuclear large-subunit rRNA sequence data. *Journal of applied phycology* 10: 229-236.
- FRESHWATER D.W. & RUENESS J., 1994 — Phylogenetic relationships of some European *Gelidium* (Gelidiales, Rhodophyta) species, based on *rbcL* nucleotide sequence analysis. *Phycologia* 33: 187-194.
- FRESHWATER D.W., FREDERICQ S. & BAILEY J.C., 1999 — Characteristics and utility of nuclear-encoded large-subunit ribosomal gene sequences in phylogenetic studies of red algae. *Phycological research* 47: 33-38.
- FRESHWATER D.W., BRALY S.K., STUERCKE B., HAMNER R.M. & YORK R.A., 2005 — Phylogenetic analyses of North Carolina Rhodymeniales. I. The genus *Asteromenia*. *Journal of the North Carolina academy of science* 121: 49-55.
- HATTA A.M. & PRUD'HOMME VAN REINE W.F., 1991 — A taxonomic revision of Indonesian Gelidiales (Rhodophyta). *Blumea* 35: 347-380.
- HUGHEY J.R., SILVA P.C. & HOMMERSAND M.H., 2001 — Solving taxonomic and nomenclatorial problems in Pacific Gigartinaceae (Rhodophyta) using DNA from type material. *Journal of phycology* 37: 1091-1109.
- HUISMAN J.M., 2000 — *Marine Plants of Australia*. Nedlands, University of Western Australia Press, ix + 300 p.
- HUISMAN J.M. & BOROWITZKA M.A., 2003 — Marine benthic flora of the Dampier Archipelago, Western Australia. In: Wells F.E., Walker D.I. & Jones D.S. (eds). *The Marine Flora and Fauna of Dampier, Western Australia*. Perth, Western Australian Museum, pp. 291-344.
- KRAFT G.T. & ABBOTT I.A., 1998 — *Gelidiella womersleyana* (Gelidiales, Rhodophyta), a diminutive new species from the Hawaiian Islands. *Botanica marina* 41: 51-61.
- KÜTZING F., 1843 — *Phycologia generalis* oder Anatomie, Physiologie und Systemkunde der Tange... Leipzig, F.A. Brockhaus, xxxii + 458 p.
- KÜTZING F., 1849 — *Species algarum*. Lipsiae [Leipzig], Brockhaus, vi + 922 p.
- KÜTZING F., 1868 — *Tabulae phycologicae*. Vol. 18. Nordhausen, (iii) + 35p, 100 plates.
- LAPENNA G. & PERRONE C., 1999 — Morphological and taxonomical studies of *Gelidiella* spp. (Gelidiales, Rhodophyta) from Apulia (South-East Italy). 2nd European Phycological Congress, Mini-symposium "Taxonomy and phylogeny", Montecatini Terme (Italy) 20-26 Settembre 1999. Book of Abstracts, p. 47.
- LIN S.-M. & FRESHWATER D.W., 2008 — The red algal genus *Gelidiella* (Gelidiales, Rhodophyta) from Taiwan, including *Gelidiella fanii* sp. nov. *Phycologia* 47: 168-176.
- LITTLER D.S. & LITTLER M.M., 1997 — An illustrated flora of the Pelican Cays, Belize. *Bulletin of the biological society of Washington* 9: 1-149.
- MADDISON D.R. & MADDISON W.P., 2000 — MacClade 4: Analysis of Phylogeny and Character Evolution. Version 4.0. Sinauer Associates, Sunderland, Massachusetts, USA.
- MAGGS C.A. & GUIRY M.D., 1987 — *Gelidiella calcicola* sp. nov. (Rhodophyta) from the British Isles and Northern France. *British phycological journal* 22: 417-434.

- MARCHANT N.G., 1990 — The Western Australian collecting localities of J.A.L. Preiss. In: Short P.S. (ed.). *History of systematic botany in Australasia*. South Yarra, Australian Systematic Botany Society Inc., pp. 131-135.
- MILLAR A.J.K. & FRESHWATER D.W., 2005 — Morphology and molecular phylogeny of the marine algal order Gelidiales (Rhodophyta) from New South Wales, including Lord Howe and Norfolk Islands. *Australian systematic botany* 18: 215-263.
- PERRONE C. & DELLE FOGLIE C.I., 2006 — *Parviphycus felicinii* sp. nov. (Gelidiales, Rhodophyta) from south-east Italy. *Cryptogamie, Algologie* 27: 199-209.
- PERRONE C., FELICINI G.P. & BOTTALICO A., 2006 — The prostrate system of the Gelidiales: diagnostic and taxonomic importance. *Botanica marina* 49: 23-33.
- POSADA D. & CRANDALL K.A., 1998 — Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817-818.
- PRICE I.R. & SCOTT F.J., 1992 — *The turf algal flora of the Great Barrier Reef, Part I. Rhodophyta*. Townsville, James Cook University of North Queensland, xii + 266 p.
- RICO J.M., FRESHWATER D.W., NORWOOD K.G. & GUIRY M.D., 2002 — Morphology and systematics of *Gelidiella tenuissima* (Gelidiales, Rhodophyta) from Gran Canaria (Canary Islands, Spain). *Phycologia* 41: 463-469.
- SANTELICES B., 1977 — A taxonomic review of Hawaiian Gelidiales (Rhodophyta). *Pacific science* 31: 61-84.
- SANTELICES B. & RICO J.M., 2002 — Nomenclature and typification of *Gelidiella tenuissima* (Gelidiales, Rhodophyta). *Phycologia* 41: 436-440.
- SANTELICES B., 2004 — *Parviphycus*, a new genus in the Gelidiellaceae (Gelidiales, Rhodophyta). *Cryptogamie, Algologie* 25: 313-326.
- SANTELICES B., 2007 — Testing the usefulness of attachment structures in the taxonomy of small-sized gelidioids. *Phycologia* 46: 293-299.
- SHIMADA S. & MASUDA M., 1999 — First report of *Gelidiella ligulata* (Gelidiales, Rhodophyta) in Japan. *Phycological Research* 47: 97-100.
- SHIMADA S., HORIGUCHI T. & MASUDA M., 1999 — Phylogenetic affinities of genera *Acanthopeltis* and *Yatabella* (Gelidiales, Rhodophyta) inferred from molecular analyses. *Phycologia* 38: 528-540.
- SCHNEIDER C.W. & LANE C.E., 2005 — Notes on the marine algae of the Bermudas. 7. Additions to the flora, including *Chondracanthus saundersii* sp. nov. (Rhodophyta, Gigartinaceae) based on *rbcl* sequence analysis. *Phycologia* 44: 72-83.
- SEOANE-CAMBA J., 1977 — Sur une nouvelle espèce de *Gelidiella* trouvée aux Iles Canaries: *Gelidiella tinerfensis* nov. sp. *Bulletin de la société phycologique de France* 22: 127-134.
- SONDER O.G., 1848 — Algae. In: Lehmann, C. (ed.) *Plantae Preissianae sive enumeratio plantarum quas in Australasia occidentali et meridionali-occidentali annis 1838-1841 collegit Ludovicus Preiss*. Vol. 2, Hamburg, pp. 161-195.
- SWOFFORD D.L., 2002 — PAUP* Phylogenetic analysis using parsimony (*and other methods), version 4. Sinauer Associates, Sunderland, MA, USA.
- TAYLOR W.R., 1960 — *Marine algae of the eastern tropical and subtropical coasts of the Americas*. Ann Arbor, The University of Michigan Press, xi + 870 p.
- TRONCHIN E.M., FRESHWATER D.W. & BOLTON J.J., 2003 — A re-evaluation of the genera *Beckerella* and *Ptilophora* (Gelidiales, Rhodophyta) based on molecular and morphological data. *Phycologia* 42: 80-89.
- TRONCHIN E.M. & FRESHWATER D.W., 2007 — Four Gelidiales (Rhodophyta) new to southern Africa, *Aphanta pachyrrhiza* gen. et sp. nov., *Gelidium profundum* sp. nov., *Pterocliadiella caeruleascens* and *P. psammophila* sp. nov. *Phycologia* 46: 325-348.
- WEBER-VAN BOSSE A., 1926 — Papers from Dr. Th. Mortensen's Pacific expedition 1914-16 XXXIII. Algues de l'expédition danoise aux îles Kei. *Videnskabelige meddelelser fra Dansk Naturhistorisk forening i Kjøbenhavn* 81: 57-155.
- WOMERSLEY H.B.S. & GUIRY M.D., 1994 — Order Gelidiales. In: Womersley H.B.S., *The marine benthic flora of southern Australia: Rhodophyta - Part IIIA*. Canberra, Australian Biological Resources Study, pp. 118-142.
- YOSHIDA T., NAKAJIMA Y. & NAKATA Y., 1990 — Check-list of marine algae of Japan (revised in 1990). *Japanese journal of phycology* 38: 269-320.