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Phylogenetic relationships of *Gelidiella* (Gelidiales, Rhodophyta) from Madagascar with a description of *Gelidiella incrassata* sp. nov.

Ga Hun BOO[a]*, Line Le GALL*[b]*, Florence ROUSSEAU*[b]*, Bruno de REVIERS*[b]*,*
Eric COPPEJANS[c]*, Robert ANDERSON*[d] *& Sung Min BOO*[a]*

[a]*Department of Biology, Chungnam National University, Daejeon 305-764, Korea*

[b]*Muséum National d'Histoire Naturelle, Institut de Systématique, Évolution,*
Biodiversité, UMR 7205 CNRS-EPHE-MNHN-UPMC, Équipe Exploration,
Espèces, Évolution, case postale N° 39, 57 rue Cuvier, 75231 Cedex 05 Paris, France

[c]*Biology Department, Ghent University, Krijgslaan 281 (S8), 9000, Ghent, Belgium*

[d]*Department of Biological Sciences and Marine Research Institute,*
University of Cape Town, Rondebosch, South Africa/Seaweed Unit,
Department of Agriculture, Forestry and Fisheries, Pvt Bag X2,
Roggebaai 8012, South Africa

Abstract – We evaluated the relationships among species in the genus *Gelidiella* using 47 *rbc*L and 29 COI sequences, including those from 18 specimens collected in Madagascar. Molecular analiysis revealed the presence of three major lineages among Magalasy *Gelidiella* which were assigned, based on morpho-anatomical observation, to *Gelidiella acerosa*, *G. ligulata* and a so far not described species for which we here proposed the name *G. incrassata*. Both molecular and morphological data demonstrated the presence of three species in Madagascar: the *G. acerosa* complex, *G. ligulata,* and *G. incrassata* sp. nov., described here. *Gelidiella incrassata* was collected on small gravel from the intertidal down to a depth of 14 m on the southeast coast of Madagascar. It is distinguished by its large size (up to 7 cm), opposite to alternate ramuli, thick-walled cortical and medullary cells, and stalked tetrasporangial stichidia with irregular arrangement of tetrasporangia. Phylogenetic analyses of *rbc*L and COI sequences revealed the sister relationship between *G. incrassata* and *G. fanii* from southeast Asia and Hawaii. *Gelidiella acerosa* comprised three genetic groups in Madagascar, each being genetically distinct (pairwise distances, 4.9-8.3% for COI and 1.2-2.3% for *rbc*L). Further sampling of *G. acerosa* is needed before taxonomic revisions can be proposed. The distribution of *G. ligulata* is expanded to include the southwest Indian Ocean.

COI / *Gelidiella* / *Gelidiella acerosa* complex / *Gelidiella ligulata* / Indian Ocean / *rbc*L / red algae / systematics

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* Corresponding author: smboo@cnu.ac.kr

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INTRODUCTION

The red algal family Gelidiellaceae currently includes 16 species of *Gelidiella* Feldmann & G. Hamel and eight species of *Parviphycus* B. Santelices. The Gelidiellaceae is characterized by unicellular rhizoids emerging from cortical cells and the absence of both rhizines (= thick-walled internal filaments) and female sexual reproductive structures (Feldmann & Hamel, 1934; Fan, 1961; Santelices, 2004; Bottalico *et al*., 2014). *Gelidiella* and *Parviphycus* are widely distributed in tropical and subtropical waters (Feldmann & Hamel, 1936; Womersley & Guiry, 1994; Shimada & Masuda, 1999; Lin & Freshwater, 2008; Bottalico *et al*., 2014). Although *Gelidiella acerosa* (Forsskål) Feldmann & Hamel, one of the most common species of red algae reported in tropical waters, has been studied to assess its commercial value and to increase its biomass production (Ganesan *et al*., 2008, 2009), molecular studies of species in the Gelidiellaceae remain limited.

The genus *Gelidiella* was established by Feldmann & Hamel (1934) to replace *Echinocaulon* Kützing (1843), an illegitimate name previously applied to a genus in the angiosperm family Polygonaceae. Originally, the diagnostic characters of *Gelidiella* were the absence of rhizines in the cortex and medulla and the regular arrangement of tetrasporangia on ultimate ramuli (Feldmann & Hamel, 1934, 1936). However, two types of tetrasporangial arrangement were described: the "*acerosa*-type" tetrasporangia produced in a compact and random pattern in fertile axes and the "*pannosa*-type" tetrasporangia produced in transverse rows in stichidia (Feldmann & Hamel, 1934, 1936; Ganzon-Fortes, 1994; Womersley & Guiry, 1994; Kraft & Abbott, 1998; Santelices, 2002). Two division patterns in axial cells were also observed in *Gelidiella*: a decussate pattern resulting in the subapical and subsequent cells in the axial filament dividing at right angles to each other, and a lateral pattern resulting from the axial cells cutting off two to four periaxial cells, which cut off further cells laterally (Rico *et al*., 2002; Santelices, 2002). Therefore, Santelices (2004) established the new genus *Parviphycus*, characterized by "*pannosa*-type" tetrasporangia and near distichous patterns of subapical cell division, and transferred three species of *Gelidiella*, including *G. adnata* E.Y. Dawson, into *Parviphycus*, with *P. adnata* (E.Y. Dawson) B. Santelices as the generitype. Subsequently, *G. setacea* (Feldmann) Feldmann & Hamel and *G. trinitatensis* W.R. Taylor were transferred into *Parviphycus* (Afonso-Carrillo *et al*., 2007; Wynne, 2010).

Fan (1961) considered the absence of a gametophyte generation to be a diagnostic character of *Gelidiella* and therefore the Gelidiellaceae. However, Rao (1974) observed the reduction of eight chromosomes in tetraspore-mother cells to four in tetraspores in *G. acerosa*. In the same species, Kapraun *et al*. (1974) demonstrated an alternation of diploid nuclear DNA amounts in tetrasporophytes with haploid amounts in tetrasporelings. Although cystocarps have not been found in *Gelidiella*, male reproductive structures were observed in *G. acerosa* (Santelices & Flores, 2004) and *G. ramellosa* (Kützing) Feldmann & Hamel (Huisman *et al*., 2009). The genus *Gelidiella* is thus characterized by a decussate pattern of subapical cell division, unicellular rhizoids and irregular arrangement of tetrasporangia in the stichidia (Santelices, 2004; Millar & Freshwater, 2005; Lin & Freshwater, 2008).

In 2010, the Muséum National d'Histoire Naturelle together with a NGO Pro Natura International organized an expedition, called in Madagascan Atimo Vatae, the Great South, to the southern tip of Madagascar within the framework of "Our Planet Reviewed", to explore coastal biodiversity (http://laplaneterevisitee.org/en/88/context). During this expedition, specimens of *Gelidiella* were collected at sites where only *G. acerosa* was previously reported (Silva *et al.*, 1996). The aim of this study was to assess the diversity among Malagasy collections of *Gelidiella* with an integrated approach that couples thorough morphological and anatomical observations with molecular sequences from both the plastid gene *rbc*L, widely used for the Gelidiellaceae (Freshwater *et al.*, 1995; Shimada & Masuda, 1999, 2000; Rico *et al.*, 2002; Millar & Freshwater, 2005; Lin & Freshwater, 2008; Huisman *et al.*, 2009) and the mitochondrial DNA barcode COI gene, recently used in the Gelidiellaceae (Wiriyadamrikul *et al.*, 2010; Bottalico *et al.*, 2014).

MATERIALS AND METHODS

Sample collection and morphology observation

Information on specimens used in this study is given in Table 1. Specimens collected in Madagascar were pressed onto herbarium sheets and subsamples were dehydrated in silica gel for molecular work. For anatomical observation, plants were sectioned using a freezing microtome (FX-801, Yamato Kohki Industrial Co., Ltd, Japan) and were stained with 1% aqueous aniline blue. Photographs were taken with a DP-71 camera (Olympus, Tokyo, Japan) mounted on a BX-51 microscope (Olympus, Tokyo, Japan). Voucher specimens are housed at the Herbarium of Cryptogamie Botany (PC) in Paris (Thiers, 2014) and voucher genomic DNA samples are deposited in the Department of Biology, Chungnam National University, Daejeon, Korea.

DNA extraction and sequencing

DNA extraction, PCR amplification, and sequencing were performed as described in Boo *et al.* (2013). The primers used for amplifying and sequencing were F7, F645, R753, and RrbcS start for *rbc*L (Freshwater & Rueness, 1994; Lin *et al.*, 2001; Gavio & Fredericq, 2002), and COXI43F and COXI1549R for COI (Geraldino *et al.*, 2006). Maximum likelihood (ML) phylogenies of *rbc*L and COI were reconstructed using RAxML v.7.2.8 (Stamatakis, 2006). Modeltest 3.7 (Posada & Crandall, 1998) determined different models of evolution as the best fit for the two datasets: GTR + G for *rbc*L and K81uf + G + I for COI. Finally, because the tree topologies reconstructed using the different models were similar to those of the GTR model, we employed GTRGAMMA instead of different models for each gene.

Bayesian inference (BI) was performed for individual datasets with MrBayes v.3.2.1 (Ronquist *et al.*, 2012) using the Metropolis-coupled Markov Chain Monte Carlo (MC3) with the GTR + G + I model. For each matrix, two million generations of two independent runs were performed with four chains and sampling trees every 100 generations. The burn-in period was identified graphically by tracking the likelihoods at each generation to determine whether they reached a plateau. The 36,002 trees sampled at the stationary state were used to infer Bayesian posterior probabilities (BPP).

Table 1. Information on *Gelidiella* material used in the present study. Bold letters indicate sequences generated in the present study

Taxa	*Voucher-code*	*Collectors*	*Collection date*	*Collection site*	*Latitude*	*Longitude*	*rbc*L	*COI*
Gelidiella acerosa (Forsskål) Feldmann & G. Hamel	PC0166043	F. Rousseau, R. Anderson, J. Tsarahevitra	28-Apr-2010	Plage Monseigneur, Fort Dauphin, Madagascar	25°02'09'' S	46°59'54'' E	**KM204100**	**KM204082**
Gelidiella acerosa	PC0166111	F. Rousseau, R. Anderson, J. Tsarahevitra	30-Apr-2010	Chez Patrick, Mahanoro, Madagascar	24°58'06'' S	47°06'06'' E	**KM204101**	**KM204083**
Gelidiella acerosa	PC0166446	F. Rousseau, R. Anderson, J. Tsarahevitra	11-May-2010	Cap d'Antsirabe, Libanona, Madagascar	25°02'36'' S	46°59'48'' E	**KM204102**	**KM204084**
Gelidiella acerosa	PC0166584	F. Rousseau, R. Anderson, J. Tsarahevitra	12-May-2010	South of bay, Lokaro, Madagascar	24°57'00'' S	47°06'30'' E	**KM204103**	**KM204085**
Gelidiella acerosa	PC0166851	B. de Reviers, B. Rakotonirina	24-May-2010	Near Soamanitse, Ambatobe, Madagascar	25°27'24'' S	44°57'24'' E	**KM204104**	**KM204086**
Gelidiella acerosa	PC0171320	B. de Reviers, B. Rakotonirina	28-May-2010	Bavarama, Ambatobe, Madagascar	25°27'54'' S	44°57'36'' E	**KM204105**	**KM204087**
Gelidiella acerosa	PC0171384	B. de Reviers, B. Rakotonirina	30-May-2010	Plage, Lavanono, Madagascar	25°25'12'' S	44°56'18'' E	**KM204106**	**KM204088**
Gelidiella acerosa	PC0171444	B. de Reviers, B. Rakotonirina	31-May-2010	East of cape, Cap Malaimpioka, Madagascar	25°21'30'' S	44°50'00'' E	**KM204107**	**KM204089**
Gelidiella acerosa	PC0171483	B. de Reviers, B. Rakotonirina	2-Jun-2010	Andramara, Madagascar	25°28'48'' S	44°58'18'' E	**KM204108**	**KM204090**
Gelidiella acerosa	PC0171484	B. de Reviers, B. Rakotonirina	2-Jun-2010	Andramara, Madagascar	25°28'48'' S	44°58'18'' E	**KM204109**	**KM204091**
Gelidiella acerosa	PC0171609	B. de Reviers	9-Jun-2010	Cap Malaimpioka, Madagascar	25°20'36'' S	44°48'18'' E	**KM204110**	**KM204092**
Gelidiella acerosa	PC0171632	B. de Reviers	9-Jun-2010	Cap Malaimpioka, Madagascar	25°20'36'' S	44°48'18'' E	**KM204111**	**KM204093**
Gelidiella acerosa	PC0142839	L. Le Gall	5-Jun-2010	Sainte Luce, Madagascar	24°45'54'' S	47°12'48'' E	**KM204112**	**KM204094**
Gelidiella acerosa	PC0143028	L. Le Gall	10-Jun-2010	Anse d'Itaperina, Madagascar	25°00'12'' S	47°06'12'' E	**KM204113**	**KM204095**
Gelidiella acerosa				Bonaire, Netherlands Antilles			AF305809	–
Gelidiella acerosa				Cahuita, Limon, Costa Rica			AF305812	–
Gelidiella acerosa				Playa a Sol, Puerto Rico			AF305810	–

Table 1. Information on *Gelidiella* material used in the present study. Bold letters indicate sequences generated in the present study *(continued)*

Taxa	*Voucher-code*	*Collectors*	*Collection date*	*Collection site*	*Latitude*	*Longitude*	*rbc*L	*COI*
Gelidiella acerosa				Matemwe, Zanzibar, Tanzania			EU146837	–
Gelidiella acerosa				Sail Rock, Kenting National Park, Taiwan			EU146834	–
Gelidiella acerosa				Little Yeliu, Taiwan			EU146833	–
Gelidiella acerosa				Wan Li Dong, Kenting National Park, Taiwan			EU146832	–
Gelidiella acerosa				Bulusan, Luzon, Philippines			EU146835	–
Gelidiella acerosa				Noumea, New Caledonia			EU146836	–
Gelidiella acerosa				Oahu, Hawaii			L22457	–
Gelidiella acerosa				Ned's Beach, Lord Howe Island, Australia			AY352424	–
Gelidiella acerosa	G5003			Mactan, Cebu, Philippines			HM629846	HM629886
Gelidiella acerosa	G5027			Alona Beach, Panglao Island, Philippines			–	HM102420
Gelidiella fanii S.-M. Lin	G5016			Arago Beach, Cebu, Philippines			HM026530	HM026510
Gelidiella fanii	G5132			Sesoko Island, Okinawa, Japan			HM026536	HM026516
Gelidiella fanii	G5137			Koh Jarakae, Chonburi, Thailand			HM026535	HM026515
Gelidiella fanii	G5239			Muluk Bay, Lombok, Indonesia			HM026541	HM026521
Gelidiella fanii				Lungkeng, Kenting National Park, Taiwan			EU146838	–
Gelidiella fanii	ARS02617			Ka'a'awa Beach Park, Oahu, Hawaii			–	HQ423118
Gelidiella incrassata	PC0166029	F. Rousseau, R. Anderson, J. Tsarahevitra	28-Apr-2010	Plage Monseigneur, Fort Dauphin, Madagascar	25°02'09'' S	46°59'54'' E	**KM204114**	**KM204096**
Gelidiella incrassata	PC0171776	E. Coppejans	15-May-2010	Baie des Galions, Madagascar	25°08'48'' S	46°45'00'' E	**KM204115**	**KM204097**
Gelidiella incrassata	PC0143039	L. Le Gall	10-Jun-2010	Anse d'Itaperina, Madagascar	25°00'12'' S	47°06'12'' E	**KM204116**	**KM204098**
Gelidiella incrassata (*Geldiella* sp., Huisman *et al.*, 2009)				9-mile Reef, Sodwana Bay, KZN, South Africa			FJ215878	–

Table 1. Information on *Gelidiella* material used in the present study. Bold letters indicate sequences generated in the present study *(continued)*

Taxa	*Voucher-code*	*Collectors*	*Collection date*	*Collection site*	*Latitude*	*Longitude*	*rbc*L	*COI*
Gelidiella ligulata E.Y. Dawson	PC0166624	F. Rousseau, R. Anderson, J. Tsarahevitra	13-May-2010	Flacourt, Madagascar	25°01’42’’ S	47°00’06’’ E	**KM204117**	**KM204099**
Gelidiella ligulata	SAP063883			Miyake Island, Japan			AB017678	–
Gelidiella ramellosa (Kützing) Feldmann & Hamel				Cook Lump, Perth, Australia			FJ215879	–
Gelidiella sp.	WestJ3433			Maloh, Siaton, Negros Oriental, Philippines			AF309386	–
Parviphycus albertanoae A. Bottalico, G.H. Boo, C. Russo, S.M. Boo & C. Perrone	BACO1192			Cozze, Mola di Bari, Bari, Italy			KC993805	KC993799
Parviphycus antipai (Celan) B. Santelices				Far Rocks, Lagoon, Lord Howe Island, Australia			AY352425	–
Parviphycus felicinii Perrone & Delle Foglie	BASG1032			San Giorgio, Bari, Italy			KC993806	–
Parviphycus felicinii	BASG1031			San Giorgio, Bari, Italy			–	KC993800
Parviphycus pannosus (Feldmann) G. Furnari				Gran Canaria, Canary Islands, Spain			AF320983	–
Parviphycus pannosus				*France*			*AF309385*	–
Outgroup								
Aphanta pachyrrhiza Tronchin & Freshwater				9-mile Reef, Sodwana Bay, KZN, South Africa			EF190245	–
Gelidium corneum (Hudson) J.V. Lamouroux	G2483			Morocco			HM629821	HM629861
Pterocladiella capillacea (Gmelin) Santelices & Hommersand	G2114			Wando, Korea			GU731207	–
Pterocladiella capillacea	P1251			Cheonbu, Ulreungdo, Korea			–	HM629885

RESULTS

Molecular phylogenies

The *rbc*L alignment (1,358 bp) included 47 taxa, of which 18 were newly generated sequences from Madagascar specimens. Variable sites occurred at 178 positions (13.1%), and 150 positions (11.0%) were parsimoniously informative. Phylogenetic trees constructed with ML and BI had similar topologies. The ML tree is shown in Figure 1.

The COI alignment (1,312 bp) included 29 sequences, of which 18 were generated from the same Madagascar specimens from which we generated the *rbc*L sequences (Fig. 2). This alignment included previously published sequences of *Gelidiella* and two outgroup taxa from GenBank. Variable sites occurred at 335 positions (25.5%), and 255 positions (19.4%) were parsimoniously informative.

In the *rbc*L analysis, the sequences from 18 specimens of *Gelidiella* from Madagascar and 21 sequences of *Gelidiella* from GenBank were resolved in a fully supported lineage, with the exception of *G. ramellosa* (FJ215879) which did not allied to the remaining *Gelidiella* but was resolved with *Parviphycus* albeit with moderate support (56% for ML and 0.57 for BPP). The remaining *Gelidiella* specimens were in a lineage comprising the *G. acerosa* complex, *G. fanii*, *G. ligulata* and *G. incrassata*. The *rbc*L sequence of *G. ligulata* from Madagascar differed by 0.3% (4 bp) from the Japanese specimen, and this species was the sister to the remaining above mentioned *Gelidiella*. *Gelidiella incrassata* was resolved as sister to *G. fanii* from southeast Asia and Hawaii (92% for ML and 1.0 for BPP). These species differed by 1.9-2.2% (24-28 bp) in *rbc*L and 8.8-9.4% (50-123 bp) in COI.

Both *rbc*L and COI phylogenies allow us to assign our 18 specimens from Madagascar to the *G. acerosa* complex (which contains three groups (I-III) among Malagasy specimens), *G. incrassata* and *G. ligulata* (Figs 1, 2).

Gelidiella acerosa specimens from Madagascar were segregated into three genetic groups (Groups I, II, III) in both *rbc*L and COI phylogenies. Group I contained 11 specimens with identical sequences and was sister to a lineage of specimens from Puerto Rico, Costa Rica and Netherlands Antilles (95% for ML and 1.0 for BPP) in the *rbc*L tree and to a specimen from the Philippines in the COI tree. Two specimens from Madagascar (PC0171384 and PC0171444), having identical *rbc*L sequences with a specimen from Tanzania (EU146837), formed a distinct group (Group II). Specimen PC0171320 clustered with a specimen from Australia (0.3% pairwise divergence, 4 bp difference) in the *rbc*L analysis (Group III), and was sister to a specimen from the Philippines in the *rbc*L and COI analysis (Figs 1, 2). Among three groups, pairwise distances were 4.9-8.3% for COI and 1.2-2.3% for *rbc*L.

Morphological characteristics

Plants of *Gelidiella incrassata* (Figs 3, 4) are tufted, up to 7 cm high, and are attached to the substratum by small clumps of independent unicellular rhizoids (Fig. 5). Ramuli are filiform or dichotomously branched, opposite to alternate. Outer cortical cells in surface view are diagonally arranged (Fig. 6). In cross section, main axes are cylindrical (Figs 7, 8) and inner cortical cells are elongated to rounded, refractive, and thick-walled (Fig. 9). Medullary cells in cross section are rounded with thick, refractive walls (arrow, Fig. 10).

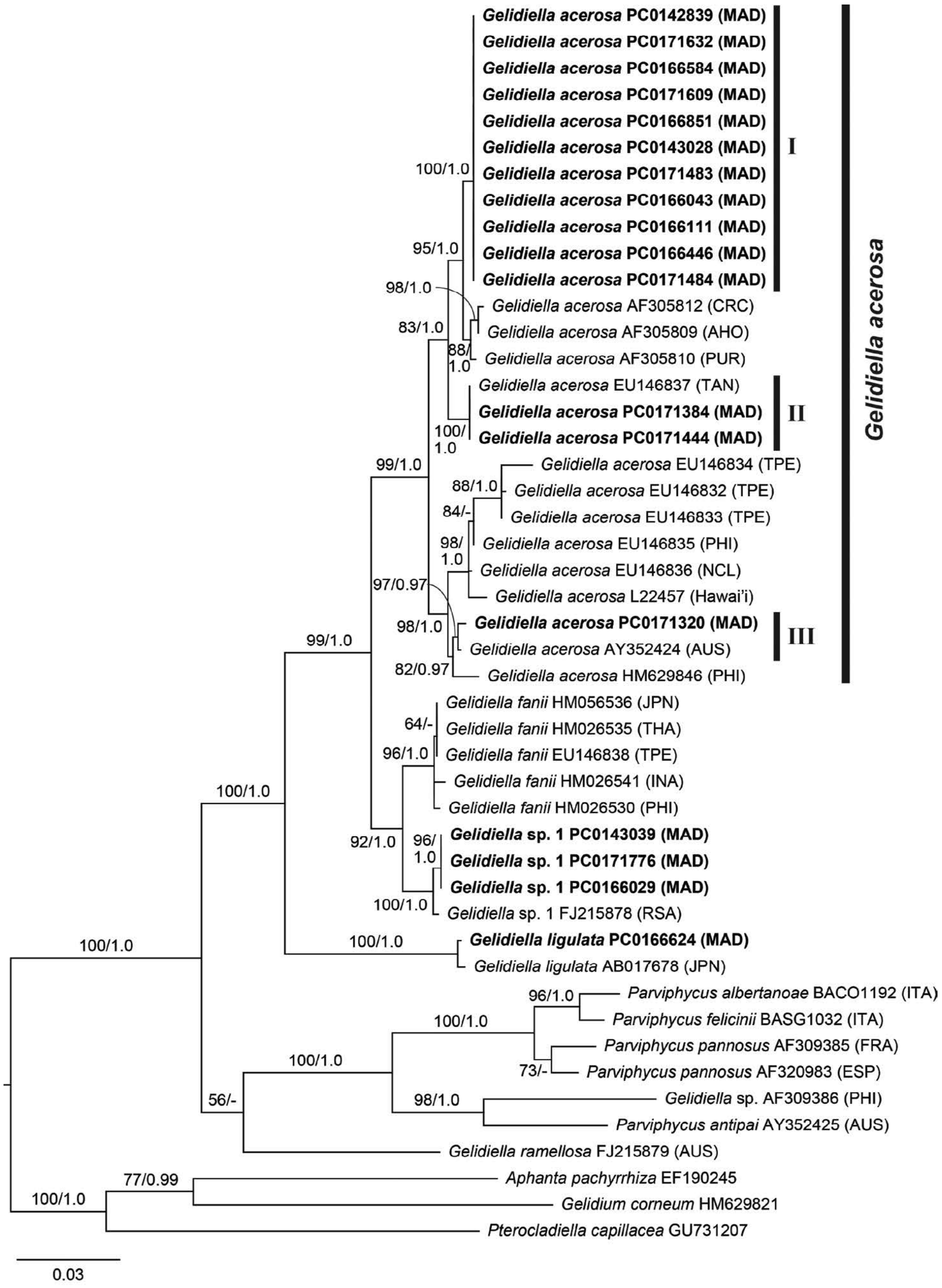


Fig. 1. Maximum likelihood tree of *rbc*L sequences from *Gelidiella* using the GTRGAMMA evolution model. Statistically supported bootstrap values ≥ 50% and Bayesian posterior probabilities ≥ 0.95 are shown. Dash mark (–) represents node without statistical support. Abbreviations: AHO, Netherlands Antilles; AUS, Australia; CRC, Costa Rica; ESP, Spain; FRA, France; INA, Indonesia; ITA, Italy; JPN, Japan; MAD, Madagascar; NCL, New Caledonia; PHI, Philippines; PUR, Puerto Rico; RSA, South Africa; TAN, Tanzania; THA, Thailand; TPE, Taiwan.

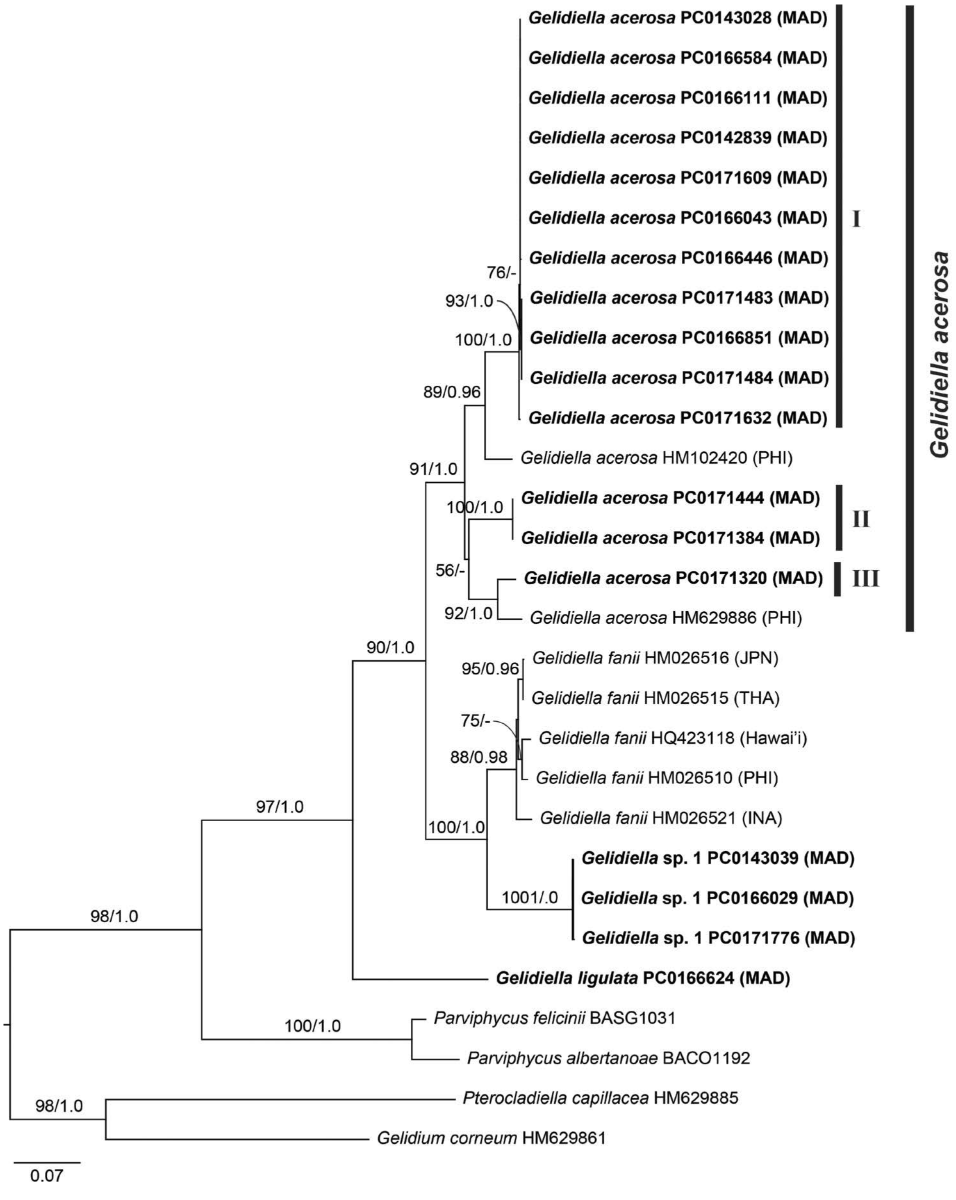
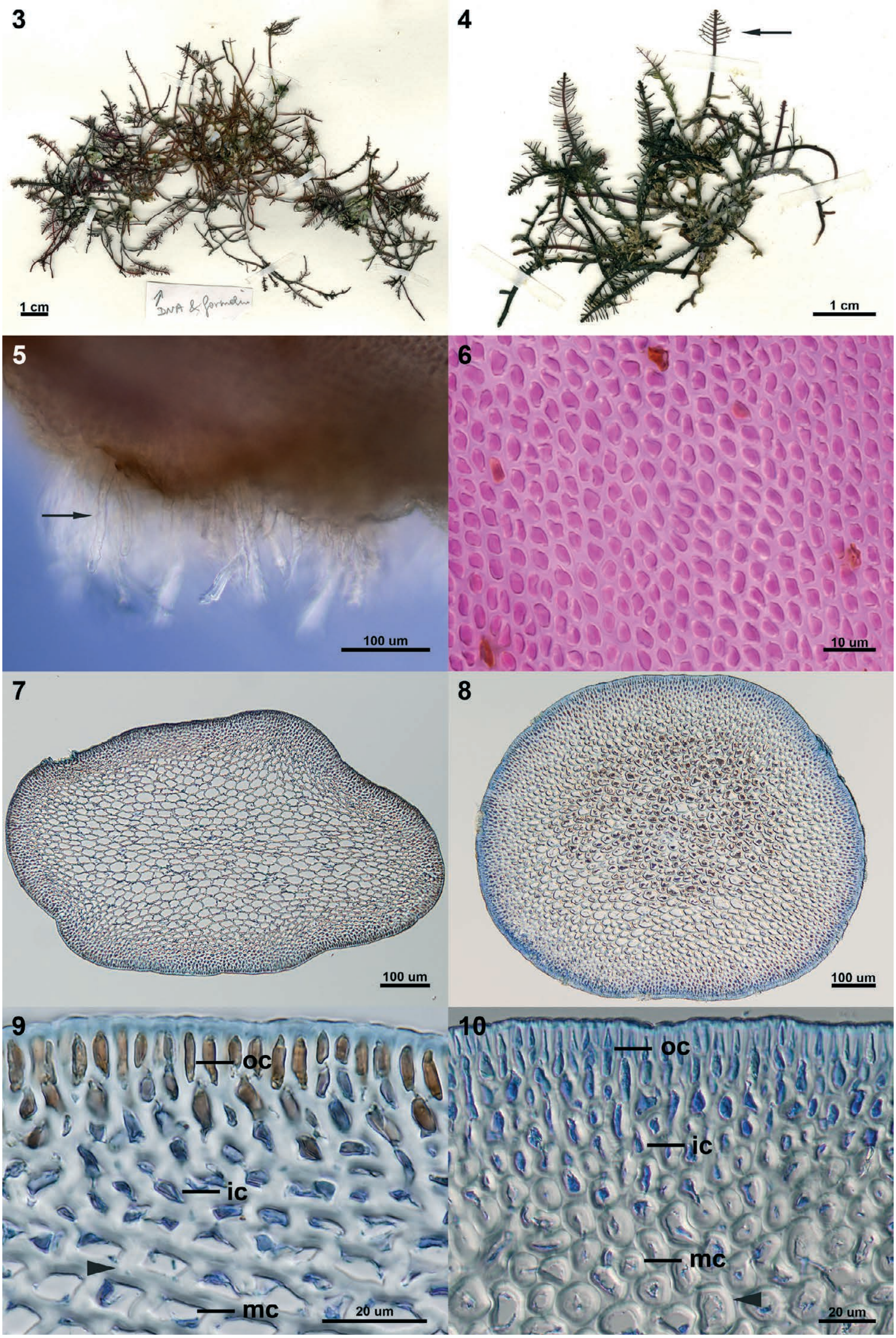


Fig. 2. Maximum likelihood tree of COI sequences from *Gelidiella* using the GTRGAMMA evolution model. Statistically supported bootstrap values ≥ 50% and Bayesian posterior probabilities ≥ 0.95 are shown. Dash mark (–) represents node without statistical support. Abbreviations are same as in Figure 1.


3
1 cm
DNA & formalin
4
1 cm
5
100 um
6
10 um
7
100 um
8
100 um
9
oc
ic
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20 um
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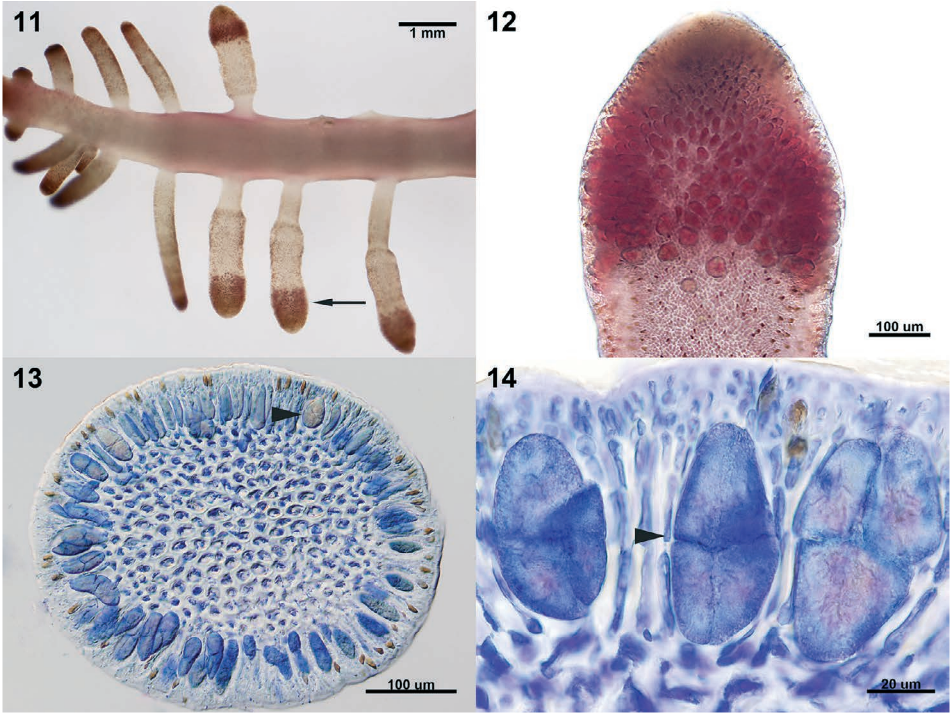
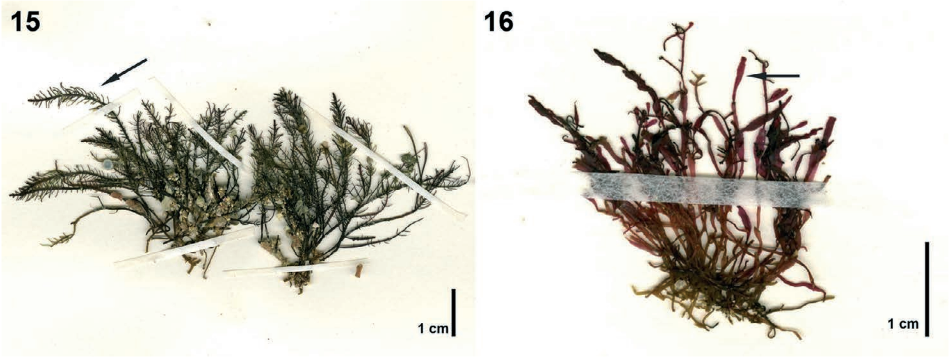


Figs 11-14. *Gelidiella incrassata* sp. nov. : **11.** Plant bearing tetrasporangial stichidia (arrow). **12.** Tetrasporangial stichidium, showing irregularly arranged tetrasporangia. **13.** Transverse section of tetrasporangial stichidium with tetrasporangia (arrowhead). **14.** Cruciately divided tetrasporangium (arrowhead).

Tetrasporangia occur in swollen stichidia on terminal ramuli (Fig. 11). Stichidia are 1.6-2.0 mm long and 350-660 µm in diameter and densely, irregularly covered with tetrasporangia (Fig. 12). Tetrasporangia arise from inner cortical cells, and are cruciately divided (Figs 13, 14) and 50-77 µm long by 15-38 µm in diameter.

Gelidiella acerosa is very similar to *G. incrassata*, with entangled, erect main axes forming tufts, up to 7 cm high (Fig. 15). Branches are regularly pinnate, giving it a feathered appearance. Branch tips terminate in a single apical cell. Short, thick stoloniferous branches are attached to the substratum by rhizoids.

◀ Figs 3-10. *Gelidiella incrassata* sp. nov. : **3.** Image of the type specimen collected in Baie des Galions, Madagascar; 15.v.2010; PC0171776; E. Coppejans. **4.** Herbarium specimen (PC0166029) showing pinnate branchlets (arrow). **5.** Prostrate axis showing a small clump of independent rhizoids (arrow). **6.** Surface view of cortical cells showing their diagonal arrangement. **7.** Transverse section of erect axis. **8.** Transverse section of prostrate axis. **9.** Transverse section of erect axis, showing cortical layers (c), outermost cortical cells (oc), inner cortical cells (ic), and medullary cells (mc). Both cortical and medullary cells are thick-walled (arrowhead). **10.** Transverse section of prostrate axis, showing cortical layers (c), outermost cortical cells (oc), inner cortical cells (ic), and medullary cells (mc) with thick walls (arrowhead).



Figs 15-16. *Gelidiella acerosa* and *G. ligulata*. **15.** Herbarium specimen (PC0171483) of *G. acerosa* showing pinnate branchlets (arrow). **16.** Herbarium specimens (PC0166624) of *G. ligulata* showing flattened blades (arrow).

Gelidiella ligulata is a small species (less than 5 cm) and differs from *G. incrassata* and *G. acerosa* by having compressed main axes and ligulate branches (Fig. 16). This species also lacks terminal ramuli.

A morphological comparison of *Gelidiella incrassata* with *G. acerosa*, *G. ligulata* and other species of *Gelidiella* is given in Table 2.

DISCUSSION

Our analyses of plastid *rbc*L and mitochondrial COI sequences clearly showed the occurrence in Madagascar of *Gelidiella ligulata,* the *G. acerosa* complex containing three genetic groups as well as a new species, *Gelidiella incrassata.* During the Atimo Vatae expedition, *G. incrassata* was collected in three locations in Madagascar: Baie des Galions, Fort Dauphin, and Anse d'Itaperina. The distribution of *G. incrassata* extends to Sodwana Bay, KwaZulu-Natal on the southeast coast of South Africa (FJ215878 in our *rbc*L analysis) (Huisman *et al*., 2009). However, further collections in neighbouring areas are needed to establish the full distribution of this novel species.

Gelidiella incrassata is distinguished by its pinnate branching, stalked tetrasporangial stichidia and cell wall structure. The distinctive thick refractive cell walls in the inner cortex and medulla of *G. incrassata* are reminiscent of rhizines, a typical cell type present only in the Gelidiaceae and Pterocladiaceae, but absent from the Gelidiellaceae (Feldmann & Hamel, 1934; Fan, 1961; Felicini & Perrone 1994; Perrone *et al*., 2006). Inner cortical cells are thick-walled than outer cortical cells in several species of *Ptilophora* (Tronchin *et al.,* 2003). It is therefore suggested that thick-walls may be plesiomorphic compared to rhizines or vice versa. Further study of the ultrastructure of medullary cell walls in *G. incrassata* would be informative compared to ultrastructure of fibrous rhizines in *Gelidium* and *Pterocladiella* (Boo, unpublished). *Gelidiella incrassata* is similar to *G. acerosa* and *G. fanii* in habit. However, there are no report on the thickened cell walls of *G. acerosa* (e.g., Melo, 1992; Norris, 1992; Lin & Freshwater, 2008), and *G. fanii* is distinguished by curved axes with secondary branchlets (Lin & Freshwater, 2008; Wiriyadamrikul *et al*., 2010).

Table 2. Morphological comparison of *Gelidiella incrassata* with previously described species in the genus *Gelidiella**

Species	*Axes, height*	*Branches*	*Cortical cells*	*Medullary cells*	*Arrangement of tetrasporangia*	*Size of tetrasporangia (µm)*	*Type Locality*
Gelidiella incrassata G.H. Boo & L. Le Gall sp. nov.	Cylindrical to slightly compressed, erect, up to 7 cm	Opposite to alternate, pinnate	Elongated, 3-5 layers, thick-walled	Rounded, very thick-walled	Irregular	15-38 × 50-77	Station TA08, Baie des Galions, Madagascar
Gelidiella acerosa (Forsskål) Feldmann & G. Hamel 1934	Cylindrical, erect, up to 9 cm	Opposite to alternate, Pinnate	Rounded, more than 5 layers	Rounded, smaller than innermost cortical cells	Irregular	17-24 × 34-52	Mokha, Yemen
G. bornetii (Weber-van Bosse) Feldmann & G. Hamel 1934	Flattened, 2-5 mm	Sparsely branched	Quadrate, aligned in rows	–	Irregular	–	Java, Indonesia
G. fanii S.-M. Lin in Lin & Freshwater 2008	Cylindrical to compressed, iridescent under water, with many hairs, 4-7 cm	Unilateral	Ovoid, 3-5 layers	Elongated	Irregular	22-28 × 37-48	South of Lungkeng, Kenting National Park, Taiwan
G. feldmannii Baardseth 1941	Cylindrical below, flattened above, 1-1.5 cm, mat-forming	Irregular	Irregularly arranged	–	Regularly transverse rows	–	Nightingale Island, Tristan da Cunha
G. hancockii E.Y. Dawson 1944	Cylindrical, Up to 0.8 cm	Irregular, congested	Isodiametric	Elongated	Irregular	–	Kino, Sonora, Mexico
G. indica Sreenivasa Rao 1970	Flattened, up to 4.5 cm	Branchlets pinnate in upper part	–	–	Irregular	16-23	Idinthakarai, Tamil Nadu, India
G. ligulata E.Y. Dawson 1953	Ligulate, up to 4 cm	Irregular, branchlets deciduous	Angular	Elongated, with secondary pit connections	Irregular	–	Cabeza Ballena, Baja California, Mexico
G. lubrica (Kützing) Feldmann & G. Hamel 1934	Simple, 3-5 mm	Sparse or unbranched	Irregular, longitudinally arranged	Elongated	Regularly transverse rows	25-30	Naples, France

Table 2. Morphological comparison of *Gelidiella incrassata* with previously described species in the genus *Gelidiella** *(continued)*

Species	*Axes, height*	*Branches*	*Cortical cells*	*Medullary cells*	*Arrangement of tetrasporangia*	*Size of tetrasporangia (µm)*	*Type Locality*
G. machrisiana E.Y. Dawson 1957	Dense turfs, flattened, 1-2.5 cm	Regularly alternate	–	–	–	–	Bahia Ballena, Golfo de Nicoya, Costa Rica
G. mexicana E.Y. Dawson 1944	Small tufts, Cylindrical, up to 0.6 cm	Irregular, polystichous	–	–	–	–	Pond Island, Isla Angel de la Guarda, Gulf of California, Mexico
G. myrioclada (Børgesen) Feldmann & G. Hamel 1934	Terete, up to 2.2 cm	Tripinnate	Irregularly arranged	Ovate, larger than innermost cortical cells	Regularly transverse rows	27-38	Malabar Hill, Bombay, India
G. nigrescens (Feldmann) Feldmann & G. Hamel 1934	Dense low turf, subterete, 1-1.5 cm	–	–	–	–	–	Cherchell, Algeria
G. ramellosa (Kützing) Feldmann & G. Hamel 1934	Terete to slightly compressed, up to 2 cm	Occasionally alternate	Angular to equidimensional	–	Irregular	30-38 × 20-25	Western Australia
G. rigidiuscula (Feldmann) Feldmann & G. Hamel 1934	Up to 5 cm	Secund spinose laterals	–	–	Unknown	–	Ceylon (Sri Lanka)
G. tinerfensis Seoane-Camba 1977	Creeping, 1-2 cm	Irregular, secondarily attached by rhizoids	Angular, irregularly arranged	–	Regularly transverse rows	c. 30 in length	Puerto de la Cruz, Tenerife, Canary Islands, Spain

* *Gelidiella calcicola* Maggs & Guiry is not included here because of its phylogenetic position in *Pterocladiella* (see Millar & Freshwater 2005).

Both *rbc*L and COI phylogenies revealed the sister relationship between *Gelidiella incrassata* and *G. fanii,* a species recently described from Taiwan (Lin & Freshwater, 2008). The characters shared between these two species are cylindrical axes and relatively large size (more than 5 cm), as shown in Fig. 3 in the present study as well as previous studies (Lin & Freshwater, 2008; Wiriyadamrikul *et al*., 2010). *Gelidiella fanii* has been reported from Japan, Taiwan, Thailand, Philippines (Lin & Freshwater, 2008; Wiriyadamrikul *et al*., 2010), and Hawaii (as *G. acerosa* in Sherwood *et al*., 2010) (Fig. 2). The monophyly of *G. incrassata* and *G. fanii* suggests a common ancestor that was broadly distributed in the warm water of the Pacific Ocean.

Gelidiella acerosa is one of the most common red algal species reported in tropical to subtropical waters of the world (see Guiry & Guiry, 2014). We confirmed previous records in Madagascar and surrounding waters (Norris, 1992; Silva *et al*., 1996). Our study revealed the presence of at least three genetic groups in the southern tip of Madagascar. However, it is difficult to distinguish the three groups on the basis of morphological characters. Genetic groups I and II occur in Madagascar and Tanzania, whereas the third group is distributed from Madagascar to Australia. The genetic divergence in *G. acerosa* ranges from 0.1 to 4.0% for *rbc*L, values that are similar to or higher than levels of genetic divergence reported between different species of *Gelidium* (see Table 2 in Boo *et al*., 2014). Our result is consistent with previous studies reporting genetic discontinuities within *G. acerosa* (Millar & Freshwater, 2005; Lin & Freshwater, 2008). However, because we could not analyze material from the type locality, Al Mokha (Mochhae), Yemen (Forsskål, 1775; Silva *et al*., 1996), we cannot determine which group corresponds to the type of *G. acerosa*. Further analyses of specimens from Africa and East Asia (e.g., Silva *et al*., 1996; Hatta & Prud'homme van Reine, 1991), North and South America (e.g., Wynne, 2011), and the Pacific Islands (e.g., N'Yeurt & Payri, 2010) are needed to determine the range and connectivity of these groups and to assess whether they represent distinct species.

The occurrence of *Gelidiella ligulata* in Madagascar was not expected because this species was originally described from Baja California, Mexico (Dawson, 1953). However, our Madagascar collections fit the original description and illustrations provided by Dawson (1953), and the *rbc*L sequence of the Madagascar specimen was very similar to that of the Japanese specimen (a difference of 4 bp, 0.3% pairwise divergence), identified by Shimada & Masuda (1999) as *G. ligulata*. This result suggests the continuous distribution of this species from Madagascar to the Pacific side of Japan, as well as Baja California, Mexico, or a recent introduction to one or the other of these locations. However, material from the type locality, Cabeza Ballena, near Cabo San Lucas, Baja California, Mexico, must be sequenced to confirm this identification. Further analysis of samples from Brazil and Yemen (Wynne, 2001; Creed *et al*., 2010) will contribute to an accurate delimitation of the range of *G. ligulata*.

Because *G. indica* Rao, a species described from Idinthakarai, India, is similar to *G. ligulata* (Rao, 1970; Shimada & Masuda, 1999), further molecular analyses are needed to assess the relationships between *G. ligulata* and *G. indica*.

Interestingly, *Gelidiella ramellosa* belonged neither to *Gelidiella* nor to *Parviphycus* in our *rbc*L tree, despite increased taxon sampling in our study compared to the previous study by Huisman *et al*. (2009). The tetrasporangial arrangement of *Gelidiella ramellosa* is reported to be "*acerosa*-type" that produced acropetally in irregular whorls (Huisman *et al*., 2009). The generic classification of *G. ramellosa* should be reconsidered after examination of the type material. Our *rbc*L tree provides additional evidence that tetrasporangial arrangement is a key character distinguishing *Gelidiella* and *Parviphycus*: *Gelidiella* has an irregular arrangement of tetrasporangia and *Parviphycus* has tetrasporangia arranged in transverse rows. Accordingly, species of *Gelidiella* with transverse rows of tetrasporangia, including *G. feldmannii* and *G. myrioclada (*Børgesen) Feldmann & G. Hamel, and *G. tinerfensis* Seoane-Camba (Baardseth, 1941; Feldmann & Hamel, 1936; Seoane-Camba, 1977), the latter being suggested by Huisman *et al.* (2009), may belong in *Parviphycus*. Molecular analysis is needed to confirm their generic positions.

In the light of our results which show the occurrence, along the southern coast of Madagascar, of at least three genetic groups in the *Gelidiella acerosa* complex as well as *G. ligulata* and a novel species *G. incrassata*, we strongly recommend pursuing survey of marine algae in this island, which is considered as a hotspots of species diversity of many terrestrial organisms (e.g., Vences *et al.*, 2009).

Systematic Treatment

Gelidiella incrassata G.H. Boo & L. Le Gall **sp. nov.** **Figs 3-14**

Plants tufted, up to 7 cm high; composed of cylindrical prostrate axes, attached to the substratum by small clumps of unicellular rhizoids that are formed from the outermost cortical cells; with erect, rigid, branched or unbranched, straight axes, proximally cylindrical. Erect axes 800-950 µm in diameter; ramuli filiform or dichotomously branched at tip, opposite to alternate. Apices of branches and ramuli conical or attenuate; apical cells apparent from other cells but not very conspicuous. Outer cortical cells in surface view diagonally arranged, radially elongated in cross section; inner cortical cells in cross section rounded, thick-walled. Medullary cells rounded in cross section, very thick-walled. Tetrasporangia in swollen stichidia in the terminal ramuli; stichidia 1.6-2.0 mm long and 350-660 µm wide and densely, irregularly covered with tetrasporangia. Tetrasporangia arising from inner cortical cells, ovate, cruciately divided, 50-77 µm long by 15-38 µm in diameter.

Holotype: A tetrasporic specimen, Station TA08 (25°08′48″ S, 46°45′00″ E), at depth of 0 meter, Baie des Galions, Madagascar; PC0171776 (MAD1757) (collected by E. Coppejans), 15 May 2010 (PC). Isotypes; PC0171776-1, 2, 3, 4 (PC).

Paratypes: Station TM01 (25°02′09″ S, 46°59′54″ E), depth of 0 to 1 meter, Plage Monseigneur, Fort Dauphin, Madagascar; PC0166029 (MAD0062) (collected by F. Rousseau, R. Anderson & J. Tsarahevitra), 28 April 2010 (PC). Station TA51 (25°00′12″ S, 47°06′12″ E), depth of 14-26 meter, intertidal Anse d'Itaperina, Madagascar; PC0143039 (MAD2312) (collected by L. Le Gall), 10 June 2010 (PC).

Etymology: The specific epithet means "very thick", referring to the walls of cortical and medullary cells.

Gelidiella acerosa (Forsskål) Feldmann & G. Hamel **Fig. 15**

Basionym: *Fucus acerosa* Forsskål

Type: P. Forsskål's original specimen, C 874 (illustrated by Børgesen in Dawson 1953, p. 53), "ad Mochhae littoral" (Al Mokha), Yemen, housed in Botanical Museum of Denmark, Copenhagen.

Geographical distribution: Australia, China, Costa Rica, Hawaii, India, Indonesia, Japan, Madagascar, Malaysia, Netherlands Antilles, Oman, Philippines, Puerto Rico, South Africa, Taiwan, Tanzania, Thailand, USA, and many other tropical and subtropical countries (see Silva *et al.*, 1996; Guiry & Guiry, 2014).

Gelidiella ligulata E.Y. Dawson **Fig. 16**

Type: Dawson 6808, HAHF 54721 including vial 2149, intertidal rocky shore, Cabeza Ballena, Baja California, Mexico.

Geographical distribution: Brazil; Baja California, Mexico; Miyaki Island near Tokyo, Japan; southeast Madagascar; Oman.

This is the first report of the occurrence of *Gelidiella ligulata* in Madagascar and even in the whole Indian Ocean.

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