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ORIGINAL PAPER

# Marine macroalgal biodiversity of northern Madagascar: morpho-genetic systematics and implications of anthropic impacts for conservation

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## Abstract

A floristic survey of the marine algal biodiversity of Antsiranana Bay, northern Madagascar, was conducted during November 2018. This represents the first inventory encompassing the three major macroalgal classes (Phaeophyceae, Florideophyceae and Ulvophyceae) for the little-known Malagasy marine flora. Combining morphological and DNA-based approaches, we report from our collection a total of 110 species from northern Madagascar, including 30 species of Phaeophyceae, 50 Florideophyceae and 30 Ulvophyceae. Barcoding of the chloroplast-encoded *rbc*L gene was used for the three algal classes, in addition to *tuf*A for the Ulvophyceae. This study significantly increases our knowledge of the Malagasy marine biodiversity while augmenting the *rbc*L and *tuf*A algal reference libraries for DNA barcoding. These efforts resulted in a total of 72 new species records for Madagascar. Combining our own data with the literature, we also provide an updated catalogue of 442 taxa of marine benthic macroalgae from Madagascar, comprising 85 Phaeophyceae, 1 Compsopogonophyceae, 240 Florideophyceae and 116 Ulvophyceae. This diversity holds 29 (ca. 6.5%) endemic species to Madagascar. Our results are discussed in the context of increasing threats to biodiversity on Madagascar's coastal reefs from both anthropic and anthropogenic activities including sewage effluent runoffs and unsustainable agricultural practices such as massive deforestation, leading to ecosystem shifts to algal dominance on reefs, which are recommended to be addressed through integrated land-sea management in a Reef-to-Ridge conservation approach.

**Keywords** Seaweed · DNA-barcoding · Conservation · Florideophyceae · Phaeophyceae · Flora · Ulvophyceae

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## Introduction

Located in the western Indian Ocean, ca. 400 km off the coast of East Africa, Madagascar is the fourth largest island in the world with a coastline of 5603 km. The island stretches approximately 1500 km from North to South, spanning more than 13 degrees of latitude between 11°57′06.8"S and 25°36′23.7"S, and is characterized by a notable diversity of marine and coastal habitats under increasing threats from coastal development and overfishing (Harris 2011). Relentless deforestation spanning several decades took a heavy toll on the island's terrestrial and marine biodiversity, including coral reefs through sedimentation (Maina et al. 2012, 2013; Morelli et al. 2020). Madagascar is home to over 13,780 plant species, 2108 animal species with a rate of endemism between 37% and 100% (CBD 2020). The marine diversity was estimated to encompass over 5000 species, comprising approximately 200 species of marine algae (Goodman and Benstead 2003, 2005). Surprisingly, these authors noted that the marine algal diversity was reasonably well known at the time (Goodman and Benstead 2005). AlgaeBase, on the other hand, provides a much greater number of 377 species, for the three main classes, i.e., 67 Phaeophyceae, 208 Florideophyceae and 102 Ulvophyceae (Guiry and Guiry 2020; accessed on December 24th 2020). Due to its geographical position and large territory, Madagascar is characterized by a variety of climates, dominated by tropical features (Donque 1972). Marine seaweeds from Madagascar present tropical to subtropical affinities (Bolton et al. 2007; De Clerck et al. 2008; Mattio et al. 2015; Steen et al. 2015).

However, the marine flora of Madagascar still remains poorly documented and present estimates most likely represent only a small fraction of the actual algal diversity. Surveys of the potential economic seaweed species of Madagascar were carried out by Mollion (1998, 2017, 2020), which also included inventories of the main macrophytes. Several new species and genera of algae from Madagascar were described in scattered publications over the years (Andriamampandry 1988; Marcot-Coqueugniot et al. 1988; West et al. 2006; Wynne 1982). The first molecular-based seaweeds inventories in Madagascar resulted from the Atimo Vatae expedition to South Madagascar in 2010, and focused on specific groups, e.g., *Codium*, Dictyotales, Fucales, Gelidiales (Boo et al. 2018, 2015; Le Gall et al. 2015; Manghisi et al. 2015; Mattio et al. 2015; Steen et al. 2015; Verbruggen and Costa 2015).

The last decade saw a rapid increase in the production of molecular data for algae in all groups (Bringloe et al. 2020; Leliaert et al. 2012; Rousseau et al. 2017). These molecular data, freely accessible on GenBank, potentially represent today a taxonomic-framework for molecular-based seaweeds biodiversity inventories and the identification of cryptic species (Hind et al. 2019; Koh and Kim 2018; Vieira et al. 2014). The concept of barcoding consists of identifying seaweeds taxa based on DNA sequences from a single or multiple genes. An attempt to develop a universal marker for seaweeds, the mitochondrially encoded cytochrome c oxidase I gene (*cox*1) (Hall et al. 2010; Poong et al. 2014; Robba et al. 2006), has proven unsuccessful across taxa (only 32 Ulvophyceae; Table 1). Overall the chloroplast ribulose-bisphosphate carboxylase gene (*rbc*L) stands as the most sequenced marker for the brown (with 4801 sequences; Table 1) and red (16,942 sequences; Table 1) seaweeds based on the number of sequences available on GenBank (Table 1), and *tuf*A for the green seaweeds (4514 sequences; Table 1) followed closely by *rbc*L (4203 sequences) (Table 1). The *rbc*L marker was recommended by several authors across taxa (Hall et al. 2010; Poong et al. 2014; Robba et al. 2006) and the mitochondrial elongation factor Tu (*tuf*A) was recommended as a standard marker for the routine barcoding of green marine macroalgae (Saunders 2010).

**Table 1** Total number of sequences available on GenBank for the 19 most used genetic markers (5.8S, 18S, 28S, 23S, *atp*9, *atp*B, *cox*1, *cox*3, ITS1, ITS2, *nad*1, *nad*4, *psa*A, *psa*B, *psb*C, *rbc*L, *tuf*A and UPA), for the three major macroalgal classes. In bold the highest numbers of *rbc*L and *tuf*A sequences for each class

| | 5.8S | 18S | 28S | 23S | *atp*9 | *atp*B | *cox*1 | *cox*3 | ITS1 | ITS2 | *nad*1 | *nad*4 | *psa*A | *psa*B | *psb*A | *psb*C | *rbc*L | *tuf*A | UPA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phaeophyceae | 2907 | 1468 | 720 | 1213 | 264 | 219 | 3062 | 4342 | 2351 | 2798 | 283 | 195 | 934 | 837 | 1551 | 164 | **4801** | 48 | 9 |
| Florideophyceae | 2506 | 3214 | 3703 | 3388 | 201 | 355 | 13,386 | 2691 | 1489 | 1332 | 193 | 193 | 1192 | 977 | 4378 | 362 | **16,942** | 497 | 1114 |
| Ulvophyceae | 3280 | 3203 | 2103 | 312 | 31 | 164 | 32 | 33 | 1804 | 2170 | 29 | 29 | 141 | 170 | 131 | 124 | 4203 | **4514** | 642 |

Data accessed on July 3rd 2019 on Genbank

In the present study, we chose to focus on *rbc*L with the goal to consolidate a reference library for this particular marker, which is relatively easy to amplify across algal groups while still being variable enough to be diagnostic on the species level. Nevertheless, our decision to focus on *rbc*L by no means diminishes the usage of other markers. The marker *cox*1 has its own merits, for instance by holding greater fidelity than *rbc*L for parsing inter- vs. intra-specific variation, and the usage of multiple markers may also be necessary in some groups to resolve phylogenetic relationships. There are still few exhaustive molecular-assisted surveys of macroalgal flora covering the three main algal groups (e.g., Bringloe et al. 2017, 2019; Saunders and McDevit 2013).

The objective of this work was to generate a DNA-based floristic survey of marine macroalgae in northern Madagascar using two genetic markers (*rbc*L and *tuf*A) backed up wherever possible with morphological identifications. Moroever, we provide a comprehensive and updated catalogue of marine benthic algae from Madagascar. This study also aims to analyses and discuss the limitations of DNA-based floristic surveys with current tools.

## Materials and methods

### Sampling

The study site (Fig. 1) was located in Antsiranana Bay (also known as Diego-Suarez Bay) in northern Madagascar (12.3231° S, 49.2943° E). This locality consists of a sheltered basin of late Paleozoic origin between 20 m and 50 m deep, and is an important geological and paleontological site (Babinot et al. 2009; Papini and Benvenuti 2008). Northern Madagascar features a tropical climate and the sea surface temperature in Antsiranana Bay oscillates between ca. 24 °C and 30 °C yearly.

Algal specimens were collected by snorkeling, between 0 and 5 m depth, from four localities: (1) Baie de Tonnerre, (2) Orangea, (3) Petite passe Orangea, (4) Mer d'Emeraude (Fig. 1) between November 20 and 23 2018. Portions of specimens were preserved in silica gel for molecular analyses shortly after collection, while voucher specimens were prepared using standard herbarium techniques and deposited at the Herbaria of the University of Antsiranana, Madagascar or the Meise Botanic Garden, Belgium (BR; the *Lobophora* collection). Aditionally, *in situ* and *ex situ* photographs were taken of most specimens collected. Each specimen was field-identified to the genus-level based largely on regional field guides by De Clerck et al. (2005a) and Oliveira et al. (2005). In the laboratory, further morphological and anatomical examinations were made to narrow our morphological-based identification to the species-level whenever possible. Further examinations were made by the second author for the Floridophyceae and Ulvophyceae, and by L. Mattio for the Fucales to confirm species-level identifications. Identifications were largely based on comparisons with previously published keys and floras for the Indian Ocean in localities geographically close to Madagascar, such as southeastern Africa (De Clerck et al. (2005a); Oliveira et al. (2005) and Mauritius (Borgesen 1940, 1941, 1942, 1943, 1944, 1945, 1946, 1948, 1949, 1950, 1951, 1952, 1953, 1954a, b, 1957; Coppejans et al. 2004; De Clerck et al. 2004; Schils et al. 2004). Morphology-based identifications served to quality-check DNA-based identifications and alert us to any possible errors or contamination of samples.

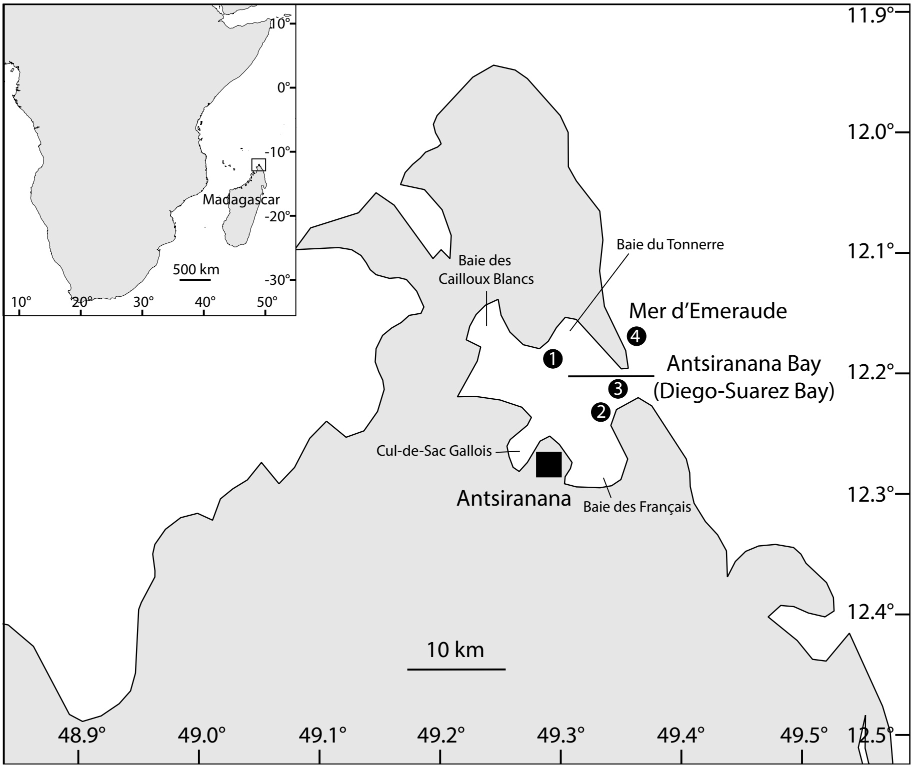


**Fig. 1** Map showing the four seaweed sampling localities in northern Madagascar: (1) *Baie du Tonnerre*, (2) *Orangea*, (3) *Petite passe Orangea*, and (4*) Mer d'Emeraude*

## DNA extraction, PCR amplification and sequencing

Extraction of total genomic DNA was carried out using the protocol from OmniPrep for Plant Tissue (G-Biosciences, St. Louis, MO). Sequences were generated from the chloroplast ribulose-bisphosphate carboxylase gene (*rbcL*) for the three classes (Phaeophyceae, Florideophyceae and Ulvophyceae), in addition to the chloroplast-encoded elongation factor Tu (*tufA*) for the Ulvophyceae. PCR reactions were carried out in 96 well plates in 25 µl reaction volumes containing: 10X PCR buffer, 200 µM of Themo Fisher Scientific dNTPs (N8080261), 10 µM of each primer (Integrated DNA Technologies, IDT, Leuven, Belgium), 10 µg/µl BSA, 10 ng (1 µl) of genomic DNA, and 1U/µl of Thermo Fisher Scientific AmpliTaq DNA polymerase with Buffer I (N8080152) using a thermocycling profile with specific parameters for each marker (Table S1) with specific primers for each markers defined in Table S2. Sequencing reactions and runs were performed by Macrogen Europe (Amsterdam, Netherlands).

### Sequences alignment and phylogenetic reconstruction

Homologies of newly-generated nucleotide sequences with sequences on GenBank sequence database (Benson et al. 2012) were identified through the National Center for Biotechnology Information (NCBI) Basic Local Alignment Search Tool (BLAST) searches (Johnson et al. 2008). Based on these BLASTs results for *rbc*L and *tuf*A but also on morphological identification (i.e., sequences labeled the species name corresponding to the morphological identification), a set of sequences was downloaded from GenBank. Nucleotide sequences from GenBank and from this study were compiled by class (Phaeophyceae, Florideophyceae and Ulvophyceae) and aligned using MUSCLE v.3.5 (Edgar 2004) with default parameters implemented in the eBioX software package v.1.5.1 (http://www.ebioinformatics.org/ebiox/). Maximum Likelihood phylogenetic trees were reconstructed from each marker (*rbc*L and *tuf*A) separately for each class using a best fit substitution model and a SPR branch swapping algorithm in PhyML v.3.0 (Guindon et al. 2010). Macroalgal species identifications were based on the BLAST and phylogenetic results, the *rbc*L and *tuf*A phylogenetic trees and morphological analyses. Based on the BLAST method, if the percentage of identical sites of a sequence calculated between intraspecific individuals of a given species were higher than interspecific individuals, then the sequence was considered as conspecific with this species. Phylogenetic trees allowed confirming the placement of a sequence among the sequences of the species identified based on the BLAST method.

### Compilation of a revised catalogue of marine algae from Madagascar

A revised and taxonomically updated listing of marine algae from Madagascar was compiled from scattered published past records in the literature as well as the present study, and presented in the form of a table combining both taxonomic identification backed up by molecular data, as well as based on morphological examination only. For the purpose of this study, we refer to the flora of Madagascar with the word qualifier "Malagasy" as advocated by Voarintsoa et al. (2019).

## Results

### Macroalgal inventory

A total of 110 distinct algal species were identified from the northern Madagascar collections from this study (Table 2, Figs. S4–S8). A total of 89 species were identified based on molecular data including 87 confirmed with morphological observations. An additional 21 species were identified based on morphological observations only. These encompassed 62 genera (12 Phaeophyceae; 33 Florideophyceae; 17 Ulvophyceae), 36 families (5 Phaeophyceae; 19 Florideophyceae; 12 Ulvophyceae) and 20 orders (5 Phaeophyceae; 11 Florideophyceae; 4 Ulvophyceae) and represented 72 new records for the Malagasy marine flora. The combined catalogue of marine algae known to date from both past published records and the present study (Table 2) comprise a total of 442 taxa

**Table 2** Catalogue of marine algae from Madagascar based on molecular and morphological identifications and compiled from published past records and the present study

| | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|
| | *Phaeophyceae* | | | | | |
| | Dictyotales | | | | | |
| | Dictyotaceae | | | | | |
| | *Canistrocarpus* De Paula & De Clerck | | | | | |
| * | | *Canistrocarpus cervicornis* (Kützing) De Paula & De Clerck | P17 | | G | a, b, c |
| | *Chlanidophora* J.Agardh | | | | | |
| | | *Chlanidophora madagascariensis* Farghaly | | E | M | B |
| | *Dictyopteris* J.V.Lamouroux | | | | | |
| | | *Dictyopteris acrostichoides* (J.Agardh) Bornet | | | M | b |
| | | *Dictyopteris delicatula* J.V.Lamouroux | | | M | b |
| | | *Dictyopteris divaricata* (Okamura) Okamura | | | M | b |
| | | *Dictyopteris plagiogramma* (Montagne) Vickers | | | M | b |
| * | | *Dictyopteris* sp. | P13 | | G | a |
| | *Dictyota* J.V.Lamouroux | | | | | |
| | | *Dictyota anastomosans* Steen et al | | | G | c |
| * | | *Dictyota bartayresiana* J.V.Lamouroux | P14 | | G | a, b |
| * | | *Dictyota ceylanica* Kützing | P16 | | G | a, c |
| | | *Dictyota ciliolata* Sonder ex Kützing | | | M | b |
| | | *Dictyota dichotoma* (Hudson) J.V.Lamouroux | | | M | b |
| | | *Dictyota humifusa* Hörnig, Schnetter & Coppejans | | | G | b, c |
| | | *Dictyota liturata* J.Agardh | | | G | c |
| | | *Dictyota major* W.R.Taylor | | | M | b |
| * | | *Dictyota rigida* De Clerck et Coppejans | P15 | | G | a, c |
| | | *Dictyota stolonifera* E.Y. Dawson | | | G | c |
| | *Lobophora* J.Agardh | | | | | |
| * | | *Lobophora antsirananaensis* C.W.Vieira & F.A.Rasoamanendrika | P5 | E | G | a |
| * | | *Lobophora evanii* C.W.Vieira & F.A.Rasoamanendrika | P3 | E | G | a |
| * | | *Lobophora garyi* C.W.Vieira & F.A.Rasoamanendrika | P4 | E | G | a |
| * | | *Lobophora henae* C.W.Vieira & F.A.Rasoamanendrika | P2 | E | G | a |

**Table 2** (continued)

| | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|
| * | | *Lobophora isselii* (Piccone et Grunow) C.W.Vieira, De Clerck & Payri | P6 | | G | a |
| * | | *Lobophora kimiae* C.W.Vieira & F.A.Rasoamanendrika | P1 | | G | a |
| * | | *Lobophora madagascariensis* C.W.Vieira & F.A.Rasoamanendrika | P7 | | G | a |
| * | | *Lobophora obscura* (Dickie) C.W.Vieira, De Clerck & Payri | P8 | | G | a, c |
| * | | *Lobophora* sp. 117 | P9 | E | G | a |
| | *Padina* Adanson | | | | | |
| | | *Padina antillarum* (Kützing) Piccone | | | G | c |
| | | *Padina boergesenii* Allender & Kraft | | | G | c |
| * | | *Padina boryana* Thivy | P12 | | G | a, b |
| | | *Padina gymnospora* (Kützing) Sonder | | | G | b, c |
| | | *Padina melemele* I.A.Abbott & Magruder | | | G | c |
| | | *Padina pavonica* (Linnaeus) Thivy | | | M | b |
| * | | *Padina somalensis* Hauck | P10 | | G | a |
| * | | *Padina* sp. | P11 | | G | a |
| | *Rugulopteryx* De Clerck & Coppejans | | | | | |
| | | *Rugulopteryx suhrii* (Kützing) De Clerck & Coppejans | | | G | c |
| | *Spatoglossum* Kützing | | | | | |
| | | *Spatoglossum asperum* J.Agardh | | | M | b |
| | | *Spatoglossum schroederi* (C.Agardh) Kützing | | | M | b |
| | *Stypopodium* Kützing | | | | | |
| | | *Stypopodium zonale* (J.V.Lamouroux) Papenfuss | | | M | b |
| | | *Stypopodium multipartitum* (Suhr) P.C.Silva | | | G | c |
| | *Stoechospermum* Kützing | | | | | |
| | | *Stoechospermum polypodioides* (J.V.Lamouroux) J.Agardh | | | G | b, c |
| | *Zonaria* C.Agardh | | | | | |
| | | *Zonaria subarticulata* (J.V.Lamouroux) Papenfuss | | | G | b, c |

**Table 2** (continued)

| | | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|---|
| | Ectocarpales | | | | | | | |
| | | Chordariaceae | | | | | | |
| | | | *Levringia* Kylin | | | | | |
| | | | | *Levringia decaryi* Feldmann | | E | M | b, ab |
| | | Ectocarpaceae | | | | | | |
| | | | *Ectocarpus* Lyngbye | | | | | |
| | | | | *Ectocarpus heterocarpus* P.Crouan & H.Crouan | | | M | b |
| | | Scytosiphonaceae | | | | | | |
| | | | *Colpomenia* (Endlicher) Derbès et Solier | | | | | |
| * | | | | *Colpomenia sinuosa* (Mertens ex Roth) Derbès et Solier | P22 | | G | a, b |
| | | | *Hydroclathrus* Bory | | | | | |
| | | | | *Hydroclathrus clathratus* (C.Agardh) M.Howe | | | M | b |
| * | | | | *Hydroclathrus tenuis* C.K.Tseng et Lu Baroen | P20 | | G | a |
| * | | | | *Hydroclathrus* sp. | P21 | | G | a |
| | Fucales | | | | | | | |
| | | Fucaceae | | | | | | |
| | | | *Fucus* Linnaeus | | | | | |
| | | | | *Fucus geniculatus* S.G.Gmelin | | | M | b |
| | | Sargassaceae | | | | | | |
| | | | *Polycladia* Montagne | | | | | |
| * | | | | *Polycladia myrica* (S.G.Gmelin) Draima, Ballesteros, F.Rousseau & T.Thibaut | P28 | | G | a, b |
| | | | *Sargassum* C.Agardh† | | | | | |
| | | | | *Sargassum aquifolium* (Turner) C.Agardh | | | G | d |
| | | | | *Sargassum baccularia* (Mertens) C.Agardh | | | M | b |
| * | | | | *Sargassum* cf. *obovatum* Harvey | P25 | | G | a |
| * | | | | *Sargassum* cf. *robillardii* (Grunow) Mattio et al | P27 | | G | a |

**Table 2** (continued)

| | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|
| * | | *Sargassum* cf. *swartzii* C. Agardh | P26 | | G | a |
| | | *Sargassum cinctum* var. *thiebautii* Grunow | | E | M | b |
| * | | *Sargassum cymosum* C. Agardh var. *scabriusculum* Grunow | P24 | | G | a |
| | | *Sargassum densifolium* Zanardini | | | M | b |
| | | *Sargassum elegans* Suhr | | | G | e |
| | | *Sargassum gracile* var. *pseudogracile* Grunow | | | M | b |
| * | | *Sargassum ilicifolium* (Turner) C. Agardh | P23 | | G | a, b |
| | | *Sargassum ilicifolium* var. *acaraeocarpum* Grunow | | | G | e |
| | | *Sargassum incisifolium* (Turner) C.Agardh | | | G | f, e |
| | | *Sargassum latifolium* (Turner) C.Agardh | | | G | e |
| | | *Sargassum latifolium* var. *seychellense* Grunow | | | M | b |
| | | *Sargassum obovatum* Harvey | | | G | e |
| | | *Sargassum parvifolium* (Turner) C.Agardh | | | M | b |
| | | *Sargassum polycystum* C.Agardh | | | G | b, e |
| | | *Sargassum portierianum* Zanardini | | | G | e |
| | | *Sargassum pulchellum* var. *gracilensis* Grunow | | E | M | b |
| | | *Sargassum robillardii* (Grunow) Mattio et al | | | G | e |
| | | *Sargassum swartzii* C.Agardh | | | G | e |
| | *Sirophysalis* Kützing | | | | | |
| | | *Sirophysalis trinodis* (Forsskal) Kützing | | | M | b |
| | *Turbinaria* J.V.Lamouroux | | | | | |
| | | *Turbinaria conoides* (J.Agardh) Kützing | | | M | b |
| | | *Turbinaria decurrens* Bory | | | M | b |
| | | *Turbinaria murrayana* E.S.Barton | | | M | b |
| * | | *Turbinaria ornata* (Turner) J. Agardh | P29 | | G | a, b |
| | | *Turbinaria trialata* var. *capensis* Kützing | | | M | b |
| | | *Turbinaria turbinata* (Linnaeus) Kuntze | | | M | b |

**Table 2** (continued)

| | | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|---|
| | Laminariales | | | | | | | |
| | | Lessoniaceae | | | | | | |
| | | | *Ecklonia* Hornemann | | | | | |
| | | | | *Ecklonia radiata* (C.Agardh) J.Agardh | | | M | b |
| | Ralfsiales | | | | | | | |
| | | Neoralfsiaceae | | | | | | |
| | | | *Neoralfsia* P.-E.Lim & H.Kawai | | | | | |
| * | | | | *Neoralfsia expansa* (J.Agardh) P.-E.Lim & H.Kawai ex Cormaci & G.Furnari | P30 | | G | a |
| | | Ralfsiaceae | | | | | | |
| | | | *Ralfsia* Berkeley | | | | | |
| | | | | *Ralfsia verrucosa* (Areschoug) Areschoug | | | M | b |
| | Sphacelariales | | | | | | | |
| | | Sphacelariaceae | | | | | | |
| | | | *Sphacelaria* Lyngbye | | | | | |
| | | | | *Sphacelaria rigidula* Kützing | | | M | b |
| * | | | | *Sphacelaria* sp. 1 | P18 | | G | a |
| * | | | | *Sphacelaria* sp. 2 | P19 | | G | a |
| | Sporochnales | | | | | | | |
| | | Sporochnaceae | | | | | | |
| | | | *Carpomitra* Kützing | | | | | |
| | | | | *Carpomitra madagascariensis* Farghaly | | E | M | b |
| Compsopogonophyceae | | | | | | | | |
| | Erythropeltales | | | | | | | |
| | | Erythropeltales incertae sedis | | | | | | |
| | | | *Madagascaria* J.A.West & N.Kikuchi | | | | | |
| | | | | *Madagascaria erythrocladioides* J.A.West & N.Kikuchi in Zuccarello et al | | | M | aa |

**Table 2** (continued)

| | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|
| | Florideophyceae | | | | | | |
| | Acrochaetiales | | | | | | |
| | Acrochaetiaceae | | | | | | |
| | | *Acrochaetium* Nägeli | | | | | |
| | | | *Acrochaetium crassipes* (Børgesen) Børgesen | | | M | b |
| | | | *Acrochaetium secundatum* (Lyngbye) Nägeli | | | M | b |
| | Bonnemaisoniales | | | | | | |
| | Bonnemaisoniaceae | | | | | | |
| | | *Asparagopsis* (Delile) Trevisan | | | | | |
| * | | | *Asparagopsis taxiformis* (Delile) Trevisan | | | M | a, b |
| | Ceramiales | | | | | | |
| | Callithamniaceae | | | | | | |
| | | *Crouania* J.Agardh | | | | | |
| | | | *Crouania attenuata* (C.Agardh) J.Agardh | | | M | b |
| | | *Spyridia* Harvey | | | | | |
| | | | *Spyridia cupressina* Kützing | | | | b |
| | | | *Spyridia filamentosa* (Wulfen) Harvey | | | M | b |
| | Ceramiaceae | | | | | | |
| | | *Centroceras Kützing* | | | | | |
| | | | *Centroceras clavulatum* (C.Agardh) Montagne | | | M | b |
| | | | *Centroceras gasparrinii* (Meneghini) Kützing | | | G | g |
| | | *Ceramium* Roth | | | | | |
| | | | *Ceramium deslongchampsii* Chauvin ex Duby | | | M | b |
| | | | *Ceramium diaphanum* (Lightfoot) Roth | | | M | b |
| | | *Gayliella* T.O.Cho, L.McIvor & S.M.Boo | | | | | |
| | | | *Gayliella flaccida* (Harvey ex Kützing) T.O.Cho & L.J.McIvor | | | M | b |
| * | | | *Gayliella* sp. 1 | F28 | | G | a |

**Table 2** (continued)

| | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|
| * | | | *Gayliella* sp. 2 | F29 | | G | a |
| | Delesseriaceae | | | | | | |
| | | *Bartoniella* Kylin | | | | | |
| * | | | *Bartoniella crenata* (J.Agardh ex Mazza) Kylin | F27 | | G | a |
| | | *Caloglossa* (Harvey) G.Martens | | | | | |
| | | | *Caloglossa leprieurii* (Montagne) G.Martens | | | M | b |
| | | *Dasya* C.Agardh | | | | | |
| | | | *Dasya elongata* Sonder | | | M | b |
| | | | *Dasya villosa* Harvey | | | M | b |
| | | *Duckerella* M.J.Wynne | | | | | |
| | | | *Duckerella ferlusii* (Hariot) M.J.Wynne | | | M | b, ac, ad |
| | | *Martensia* K.Hering | | | | | |
| | | | *Martensia elegans* Hering | | | M | b |
| | | *Vanvoorstia* Harvey | | | | | |
| * | | | *Vanvoorstia spectabilis* Harvey | | | M | a |
| | Rhodomelaceae | | | | | | |
| | | *Acanthophora* J.V.Lamouroux | | | | | |
| | | | *Acanthophora muscoides* (Linnaeus) Bory | | | M | b |
| * | | | *Acanthophora spicifera* (M.Vahl) Børgesen | F22 | | G | a, b, h |
| | | *Amansia* J.V.Lamouroux | | | | | |
| * | | | *Amansia rhodantha* (Harvey) J.Agardh | F23 | | G | a, b |
| | | | *Amansia dietrichiana* Grunow | | | M | b |
| | | | *Amansia multifida* J.V.Lamouroux | | | M | b |
| * | | | *Amansia* sp. | F24 | | G | a |
| | | *Bostrychia* Montagne | | | | | |
| | | | *Bostrychia moritziana* (Sonder ex Kützing) J.Agardh | | | G | i |

**Table 2** (continued)

| | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|
| | | *Bostrychia radicosa* (Itono) J.A.West, G.C.Zuccarello & M.H.Hommersand | | | G | j |
| | *Chondria* C.Agardh | | | | | |
| | | *Chondria capensis* (Harvey) Askenasy | | | M | b |
| | | *Chondria dasyphylla* (Woodward) C.Agardh | | | M | b |
| | *Chondrophycus* (J.Tokida et Y.Saito) Garbary & J.T.Harper | | | | | |
| * | | *Chondrophycus* sp. | F21 | | G | a |
| | *Digenea* C.Agardh | | | | | |
| * | | *Digenea simplex* (Wulfen) C.Agardh | F26 | | G | a, b |
| | *Endosiphonia* Zanardini | | | | | |
| | | *Endosiphonia horrida* (C.Agardh) P.C.Silva | | | M | b |
| | *Herposiphonia* Zanardini | | | | | |
| | | *Herposiphonia secunda* (C.Agardh) Ambronn | | | M | b |
| | | *Herposiphonia secunda* f. *tenella* (C.Agardh) M.J.Wynne | | | M | b |
| | *Laurencia* J.V.Lamouroux | | | | | |
| | | *Laurencia brongniartii* J.Agardh | | | M | b |
| * | | *Laurencia* cf. *dendroidea* J.Agardh | F19 | | G | a |
| | | *Laurencia distichophylla* J.Agardh | | | M | b |
| * | | *Laurencia* cf. *filiformis* (C.Agardh) Montagne | F20 | | G | a |
| | | *Laurencia obtusa* (Hudson) J.V.Lamouroux | | | M | b |
| | | *Laurencia obtusa* var. *divaricata* Yamada | | | M | b |
| | | *Laurencia tenera* C.K.Tseng | | | M | b |
| * | | *Laurencia* sp. | | | M | a |
| | *Leveillea* Decaisne | | | | | |
| | | *Leveillea jungermannioides* (Hering & G.Martens) Harvey | | | M | b |
| | *Neurymenia* J.Agardh | | | | | |
| * | | *Neurymenia fraxinifolia* (Mertens ex Turner) J. Agardh | F25 | | G | a, b |

**Table 2** (continued)

| | | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|---|
| | | | *Ohelopapa* F.Rousseau, Martin-Lescanne, Payri & L.Le Gall | | | | | |
| | | | | *Ohelopapa flexilis* (Setchell) F.Rousseau, Martin-Lescanne, Payri & L.Le Gall | | | M | b |
| | | | *Osmundaria* J.V.Lamouroux | | | | | |
| | | | | *Osmundaria fimbriata* (J.V.Lamouroux) R.E.Norris | | | M | b |
| | | | *Palisada* K.W. Nam | | | | | |
| * | | | | *Palisada parvipapillata* (C.K. Tseng) K.W. Nam | | | M | a |
| * | | | | *Palisada perforata* (Bory) K.W. Nam | | | M | a, b |
| | | | *Tolypiocladia* F.Schmitz | | | | | |
| | | | | *Tolypiocladia calodictyon* (Harvey ex Kützing) P.C.Silva | | | M | b |
| | | | | *Tolypiocladia glomerulata* (C.Agardh) F.Schmitz | | | M | b |
| | | | *Vidalia* J.V.Lamouroux ex J.Agardh | | | | | |
| | | | | *Vidalia melvillii* (J.Agardh) F.Schmitz | | | M | b |
| | | Wrangeliaceae | | | | | | |
| | | | *Griffithsia* C.Agardh | | | | | |
| * | | | | *Griffithsia* sp. | | | M | a |
| | | | *Wrangelia* C.Agardh | | | | | |
| | | | | *Wrangelia bicuspidata* Børgesen | | | M | b |
| | Corallinales | | | | | | | |
| | | Corallinaceae | | | | | | |
| | | | *Amphiroa* J.V.Lamouroux | | | | | |
| | | | | *Amphiroa anceps* (Lamarck) Decaisne | | | M | b |
| | | | | *Amphiroa bowerbankii* Harvey | | | M | b |
| | | | | *Amphiroa ephedraea* (Lamarck) Decaisne | | | M | b |
| | | | | *Amphiroa foliacea* J.V.Lamouroux | | | M | b |
| * | | | | *Amphiroa fragilissima* (Linnaeus) J.V.Lamouroux | F30 | | G | b |
| | | | | *Amphiroa gracilis* Harvey | | | M | b |

**Table 2** (continued)

| | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|
| | | *Amphiroa tribulus* (J.Ellis & Solander) J.V.Lamouroux | | | M | b |
| | | *Amphiroa ungulata* Montagne & Millardet | | | M | b |
| * | | *Amphiroa* sp. | | | M | a |
| | *Arthrocardia* Decaisne | | | | | |
| | | *Arthrocardia palmata* (J.Ellis & Solander) Areschoug | | | M | b |
| | | *Arthrocardia wardii* (Harvey) Areschoug | | | M | b |
| | *Haliptilon* (Decaisne) Lindley | | | | | |
| | | *Haliptilon polydactylum* (Montagne & Millardet) Garbary & H.W.Johansen | | | M | b |
| | *Jania* J.V.Lamouroux | | | | | |
| | | *Jania cultrata* (Harvey) J.H.Kim, Guiry & H.-G.Choi | | | M | b |
| | | *Jania longifurca* Zanardini | | | M | b |
| | | *Jania pacifica* Areschoug | | | M | b |
| | | *Jania pedunculata var. adhaerens* (J.V.Lamouroux) A.S.Harvey, Woelkerling & Reviers | | | M | b |
| | | *Jania prolifera* (J.V.Lamouroux) J.H.Kim, Guiry & H.-G.Choi | | | M | b |
| | | *Jania pumila* J.V.Lamouroux | | | M | b |
| | | *Jania rosea* (Lamarck) Decaisne | | | M | b |
| | | *Jania rubens* (Linnaeus) J.V.Lamouroux | | | M | b |
| | *Lithophyllum* Philippi | | | | | |
| | | *Lithophyllum acrocamptum* Heydrich | | | G | k, l |
| | | *Lithophyllum kaiseri* (Heydrich) Heydrich | | | M | b |
| | | *Lithophyllum kotschyanum* Unger | | | M | b |
| | | *Lithophyllum pygmaeum* (Heydrich) Heydrich | | | M | b |
| | | *Lithophyllum subplicatum* (Foslie) Basso, Caragnano, Le Gall & Rodondi | | | M | b |
| | *Mastophora* Decaisne | | | | | |
| | | *Mastophora variegata* Pichon | | | M | b |

**Table 2** (continued)

| | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|
| | *Pneophyllum* Kützing | | | | | |
| | | *Pneophyllum amplexifrons* (Harvey) Y.M.Chamberlain & R.E.Norris | | | M | b, ae |
| | | *Pneophyllum fragile* Kützing | | | M | b |
| Hapalidiaceae | | | | | | |
| | *Lithothamnion* Heydrich | | | | | |
| | | *Lithothamnion proliferum* Foslie | | | M | b |
| Hydrolithaceae | | | | | | |
| | *Hydrolithon* (Foslie) Foslie | | | | | |
| | | *Hydrolithon craspedium* (Foslie) P.C.Silva | | | M | b |
| | | *Hydrolithon cymodoceae* (Foslie) Penrose | | | M | b |
| | | *Hydrolithon farinosum* (J.V.Lamouroux) Penrose & Y.M.Chamberlain | | | M | b |
| Lithophyllaceae | | | | | | |
| | *Titanoderma* Nägeli | | | | | |
| | | *Titanoderma rasile* (Foslie) Woelkerling, Y.M.Chamberlain & P.C.Silva | | | M | b |
| Mastophoraceae | | | | | | |
| | *Lithoporella* (Foslie) Foslie | | | | | |
| | | *Lithoporella melobesioides* (Foslie) Foslie | | | M | b |
| Porolithaceae | | | | | | |
| | *Porolithon* Foslie | | | | | |
| | | *Porolithon onkodes* (Heydrich) Foslie | | | M | b |
| Spongitaceae | | | | | | |
| | *Neogoniolithon* Setchell & L.R.Mason | | | | | |
| | | *Neogoniolithon brassica-florida* (Harvey) Setchell & L.R.Mason | | | M | b |
| | | *Neogoniolithon oblimans* (Heydrich) P.C.Silva | | | M | b |
| Gelidiales | | | | | | |

**Table 2** (continued)

| | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|
| | Gelidiaceae | | | | | | |
| | | *Gelidium* J.V.Lamouroux | | | | | |
| | | | *Gelidium amansii* (J.V.Lamouroux) J.V.Lamouroux | | | M | b, af |
| | | | *Gelidium capense* (S.G.Gmelin) P.C.Silva | | | M | b |
| | | | *Gelidium crinale* (Hare ex Turner) Gaillon | | | M | b |
| | | | *Gelidium serra* (S.G.Gmelin) E.Taskin & M.J.Wynne | | | M | b |
| | | *Ptilophora* Kützing | | | | | |
| | | | *Ptilophora aureolusa* G.H.Bo, L.Le Gall, I.K.Hwang, K.A.Miller & S.M.Boo | | E | G | o |
| | | | *Ptilophora hildebrandtii* (Hauck) R.E.Norris | | | G | o, b |
| | | | *Ptilophora malagasya* G.H.Boo, L.Le Gall, I.K.Hwang, K.A.Miller & S.M.Boo | | E | G | o |
| | | | *Ptilophora pterocladioides* Andriamampandry | | E | G | p, b, o |
| | | | *Ptilophora spongiophila* G.H.Boo, L.Le Gall, I.K.Hwang, K.A.Miller & S.M.Boo | | E | G | o |
| | Gelidiellaceae | | | | | | |
| | | *Gelidiella* Feldmann & G.Hamel | | | | | |
| * | | | *Gelidiella acerosa* (Forsskål) Feldmann & G. Hamel | F10 | | G | a, b, m |
| | | | *Gelidiella incrassata* G.H.Boo & L.Le Gall | | E | G | m |
| | | | *Gelidiella ligulata* E.Y.Dawson | | | G | m |
| | Orthogonacladiaceae | | | | | | |
| | | *Orthogonacladia* G.H.Boo & Le Gall | | | | | |
| | | | *Orthogonacladia madagascariense* (Andriamampandry) G.H.Boo & Le Gall | | E | G | n |
| | Pterocladiaceae | | | | | | |
| | | *Pterocladiella* B.Santelices & Hommersand | | | | | |
| | | | *Pterocladiella australafricanensis* E.M.Tronchin & D.W.Freshwater | | | G | n |

**Table 2** (continued)

| | | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|---|
| | | | | *Pterocladiella bartlettii* (W.R.Taylor) Santelices | | | G | n |
| | | | | *Pterocladiella caerulescens* (Kützing) Santelices & Hommersand | | | G | n |
| | | | | *Pterocladiella capillacea* (S.G.Gmelin) Santelices & Hommersand | | | M | b |
| | | | | *Pterocladiella feldmannii* G.H.Boo, L.Le Gall, I.K.Hwang & S.M.Boo | | E | G | n |
| | | | | *Pterocladiella hamelii* G.H.Boo, L.Le Gall, I.K.Hwang & S.M.Boo | | E | G | n |
| | Gigartinales | | | | | | | |
| | | Acrotylaceae | | | | | | |
| | | | *Acrotylus* J.Agardh | | | | | |
| | | | | *Acrotylus australis* J.Agardh | | | M | b |
| | | | *Ranavalona* Kraft | | | | | |
| | | | | *Ranavalona duckerae* Kraft | | E | M | b, ag |
| | | Caulacanthaceae | | | | | | |
| | | | *Catenella* Greville | | | | | |
| | | | | *Catenella caespitosa* (Withering) L.M.Irvine | | | M | b |
| | | Cystocloniaceae | | | | | | |
| | | | *Hypnea* J.V.Lamouroux | | | | | |
| | | | | *Hypnea charoides* J.V.Lamouroux | | | M | b |
| | | | | *Hypnea esperi* Bory | | | M | b |
| * | | | | *Hypnea musciformis* (Wulfen) J.V.Lamouroux | | | M | b |
| | | | | *Hypnea nidifica* J.Agardh | | | M | b |
| * | | | | *Hypnea* cf. *nidifica* J.Agardh | F3 | | G | a |
| * | | | | *Hypnea* cf. *nidulans* Setchell | | | M | a |
| * | | | | *Hypnea pannosa* J.Agardh | F5 | | G | a, b |
| | | | | *Hypnea rosea* Papenfuss | | | M | b |
| | | | | *Hypnea spicifera* (Suhr) Harvey | | | M | b |
| | | | | *Hypnea spinella* (C.Agardh) Kützing | | | M | b |

**Table 2** (continued)

| | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|
| * | | | *Hypnea* cf. *spinella* (C.Agardh) Kützing | F1 | | G | a |
| | | | *Hypnea valentiae* (Turner) Montagne | | | M | b |
| * | | | *Hypnea* sp. 1 | F2 | | G | a |
| * | | | *Hypnea* sp. 2 | F4 | | G | a |
| | | *Stictosporum* J.Agardh | | | | | |
| | | | *Stictosporum nitophylloides* (Harvey) J.Agardh | | | M | b |
| | Dicranemataceae | | | | | | |
| | | *Tylotus* J.Agardh | | | | | |
| * | | | *Tylotus* sp. | F6 | | G | a |
| | Dumontiaceae | | | | | | |
| | | *Neodilsea* Tokida | | | | | |
| | | | *Neodilsea tenuipes* Yamada & Mikami | | | M | b |
| | Etheliaceae | | | | | | |
| | | *Ethelia* Weber Bosse | | | | | |
| | | | *Ethelia biradiata* (Weber Bosse) Weber Bosse | | | M | b |
| | Furcellariaceae | | | | | | |
| | | *Neurocaulon* Zanardini ex Kützing | | | | | |
| | | | *Neurocaulon thiebautii* (Bornet) Farghaly | | | M | b |
| | Phacelocarpaceae | | | | | | |
| | | *Phacelocarpus* Endlicher & Diesing | | | | | |
| | | | *Phacelocarpus peperocarpos* (Poiret) M.J.Wynne, Ardré & P.C.Silva | | | M | b |
| | | | *Phacelocarpus tortuosus* Endlicher & Diesing | | | M | b |
| * | | | *Phacelocarpus tristichus* J.Agardh | F8 | | G | a, b |
| | Phyllophoraceae | | | | | | |
| | | *Stenogramma* Harvey | | | | | |
| | | | *Stenogramma lamyi* L.Le Gall | | E | G | q |

**Table 2** (continued)

| | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|
| | Rhizophyllidaceae | | | | | | |
| | | *Portieria* Zanardini | | | | | |
| | | | *Portieria harveyi* (J.Agardh) P.C.Silva | | | M | b |
| * | | | *Portieria hornemannii* (Lyngbye) P.C.Silva | F9 | | G | a, b |
| | Solieriaceae | | | | | | |
| | | *Betaphycus* Doty | | | | | |
| | | | *Betaphycus speciosus* (Sonder) Doty ex P.C.Silva | | | M | b |
| | | *Eucheuma* J.Agardh | | | | | |
| * | | | *Eucheuma denticulatum* (N.L.Burman) Collins et Hervey | F7 | | G | a, b |
| | | | *Eucheuma edule* (Kützing) Weber Bosse | | | M | b |
| | | | *Eucheuma horridum* J.Agardh | | | M | b |
| | | | *Eucheuma odontophorum* Børgesen | | | M | b |
| | | | *Eucheuma platycladum* F.Schmitz | | | M | b |
| | | *Kappaphycus* Doty | | | | | |
| | | | *Kappaphycus striatus* (F.Schmitz) Doty ex P.C.Silva | | | M | b |
| | | *Meristotheca* J.Agardh | | | | | |
| | | | *Meristotheca papulosa* (Montagne) J.Agardh | | | M | b |
| | | *Sarconema* Zanardini | | | | | |
| | | | *Sarconema filiforme* (Sonder) Kylin | | | M | b |
| | | *Solieria* J.Agardh | | | | | |
| | | | *Solieria robusta* (Greville) Kylin | | | M | b |
| | | *Wurdemannia* Harvey | | | | | |
| | | | *Wurdemannia miniata* (Sprengel) Feldmann & G. Hamel | | | M | b |
| Gracilariales | | | | | | | |
| | Gracilariaceae | | | | | | |
| | | *Gracilaria* Greville | | | | | |
| * | | | *Gracilaria arcuata* Zanardini | F12 | | G | a |

**Table 2** (continued)

| | | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|---|
| | | | | *Gracilaria beckeri* (J.Agardh) Papenfuss | | | M | b |
| | | | | *Gracilaria canaliculata* Sonder | | | M | b |
| | | | | *Gracilaria corticata* (J.Agardh) J.Agardh | | | M | b |
| | | | | *Gracilaria corticata* var. *ramalinioides* J.Agardh | | | M | b |
| | | | | *Gracilaria debilis* (Forsskål) Børgesen | | | M | b |
| | | | | *Gracilaria hauckii* P.C.Silva | | | M | b |
| * | | | | *Gracilaria lantaensis* Muangmai, Zuccarello, Noiraksa & Lewmanomont | F13 | | G | a |
| * | | | | *Gracilaria salicornia* (C.Agardh) E.Y.Dawson | F14 | | G | a, b |
| * | | | | *Gracilaria* sp. 1 | | | M | a |
| * | | | | *Gracilaria* sp. 2 | | | M | a |
| * | | | | *Gracilaria* sp. 3 | | | M | a |
| * | | | | *Gracilaria* sp. 4 | | | M | a |
| | | | *Hydropuntia* Montagne | | | | | |
| | | | | *Hydropuntia edulis* (S.G.Gmelin) Gurgel & Fredericq | | | M | b |
| | | | | *Hydropuntia millardetii* (Montagne) Gurgel, J.N.Norris & Fredericq | | | M | b |
| | Halymeniales | | | | | | | |
| | | Halymeniaceae | | | | | | |
| | | | *Carpopeltis* F.Schmitz | | | | | |
| | | | | *Carpopeltis maillardii* (Montagne & Millardet) Chiang | | | M | b |
| | | | *Corynomorpha* J.Agardh | | | | | |
| | | | | *Corynomorpha prismatica* (J.Agardh) J.Agardh | | | G | r |
| | | | *Grateloupia* C.Agardh | | | | | |
| | | | | *Grateloupia livida* (Harvey) Yamada | | | M | b |
| | | | | *Grateloupia somalensis* Hauck | | | G | t |
| | | | *Halymenia* C.Agardh | | | | | |
| * | | | | *Halymenia durvillei* Bory | F18 | | G | a |

**Table 2** (continued)

| | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|
| | | | *Polyopes* J.Agardh | | | | |
| | | | *Polyopes affinis* (Harvey) Kawaguchi & Wang | | | M | b |
| | | | *Prionitis* J.Agardh | | | | |
| | | | *Prionitis obtusa* Sonder | | | M | b |
| | | | *Yonagunia* S.Kawaguchi & M.Masuda | | | | |
| | | | *Yonagunia atimo-vatae* Manghisi, M.Morabito, G.H.Boo, S.M.Boo & Le Gall | | E | G | s |
| | | | *Yonagunia formosana* (Okamura) Kawaguchi & Masuda | | | M | b |
| | | | *Yonagunia ligulata* (Harvey ex Kützing) Manghisi, M.Morabito, De Clerck & Le Gall | | | G | s |
| | Hapalidiales | | | | | | |
| | | Hapalidiaceae | | | | | |
| | | | *Melobesia* J.V.Lamouroux | | | | |
| | | | *Melobesia membranacea* (Esper) J.V.Lamouroux | | | M | b |
| | | Mesophyllumaceae | | | | | |
| | | | *Melyvonnea* Athanasiadis & D.L.Ballantine | | | | |
| | | | *Melyvonnea erubescens* (Foslie) Athanasiadis & D.L.Ballantine | | | M | b |
| | Nemaliales | | | | | | |
| | | Galaxauraceae | | | | | |
| | | | *Actinotrichia* Decaisne | | | | |
| | | | *Actinotrichia fragilis* (Forsskål) Børgesen | | | M | b |
| * | | | *Actinotrichia* sp. | F32 | | G | a |
| | | | *Dichotomaria* Lamarck | | | | |
| * | | | *Dichotomaria marginata* (J.Ellis & Solander) Lamarck | | | M | a, b |
| | | | *Dichotomaria obtusata* (J.Ellis & Solander) Lamarck | | | M | b |
| * | | | *Dichotomaria* sp. | F33 | | G | a |
| | | | *Galaxaura* J.V.Lamouroux | | | | |
| * | | | *Galaxaura rugosa* (J.Ellis & Solander) J.V.Lamouroux | F31 | | G | a, b |

**Table 2** (continued)

| | | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|---|
| | | | *Gloiophloea* J.Agardh | | | | | |
| | | | | *Gloiophloea articulata* Weber Bosse | | | M | b |
| | | | *Trichogloea* Kützing | | | | | |
| | | | | *Trichogloea requienii* (Montagne) Kützing | | | M | b, ah |
| | | | | *Tricleocarpa fragilis* (Linnaeus) Huisman & R.A.Townsend | | | M | b |
| | | Liagoraceae | | | | | | |
| | | | *Liagora* J.V.Lamouroux | | | | | |
| | | | | *Liagora ceranoides* J.V.Lamouroux | | | M | b |
| | | | | *Liagora engleriana* Zeh | | | M | b |
| | | | | *Liagora voeltzkowii* Zeh | | E | M | b |
| * | | | | *Liagora* sp. 1 | F36 | | G | a |
| * | | | | *Liagora* sp. 2 | | | M | a |
| | | | *Macrocarpus* Showe M.Lin, S.-Y.Yang & Huisman | | | | | |
| * | | | | *Macrocarpus* sp. | F34 | | G | a |
| | | | *Neoizziella* S.-M.Lin, S.-Y.Yang & Huisman | | | | | |
| * | | | | *Neoizziella asiatica* S.-M.Lin, S.-Y.Yang & Huisman | F35 | | G | a |
| | | | *Titanophycus* Huisman, G.W.Saunders & A.R.Sherwood | | | | | |
| | | | | *Titanophycus validus* (Harvey) Huisman, G.W.Saunders & A.R.Sherwood | | | M | b |
| | | Scinaiaceae | | | | | | |
| | | | *Scinaia* Bivona-Bernardi | | | | | |
| | | | | *Scinaia japonica* Setchell | | | M | b |
| | | | | *Scinaia moniliformis* J.Agardh | | | M | b |
| | | | | *Scinaia setchellii* W.R.Taylor | | | M | b |
| | Nemastomatales | | | | | | | |
| | | Nemastomataceae | | | | | | |
| | | | *Predaea* G.De Toni | | | | | |

**Table 2** (continued)

| | | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|---|
| | | | | *Predaea feldmannii Børgesen* | | | G | u |
| | | Schizymeniaceae | | | | | | |
| | | | *Platoma* Schousboe ex F.Schmitz | | | | | |
| | | | | *Platoma gelatinosum* (M.Howe) C.W.Schneider, McDevit, G.W.Saunders & C.E.Lane | | | G | v |
| | | | *Titanophora* (J.Agardh) Feldmann | | | | | |
| | | | | *Titanophora pikeana* (Dickie) Feldmann | | | M | b, ai |
| | | | | *Titanophora weberae* Børgesen | | | M | b, ai |
| | Peyssonneliales | | | | | | | |
| | | Porphyridiaceae | | | | | | |
| | | | *Erythrolobus* J.L.Scott, J.B.Baca, F.D.Ott & J.A.West | | | | | |
| | | | | *Erythrolobus madagascarensis* E.C. Yang, J.L. Scott & J.A. West | | E | G | z |
| | Porphyridiales | | | | | | | |
| | | Peyssonneliaceae | | | | | | |
| | | | *Peyssonnelia* Decaisne | | | | | |
| | | | | *Peyssonnelia conchicola* Piccone & Grunow | | | M | b |
| | | | | *Peyssonnelia coxalocalcificata* Farghaly | | | M | b |
| | | | | *Peyssonnelia foveolata* (Weber Bosse) Denizot | | | M | b |
| | | | | *Peyssonnelia guadalupensis* E.Y.Dawson | | | M | b |
| | | | | *Peyssonnelia indica* (Weber Bosse) Denizot | | | M | b |
| | | | | *Peyssonnelia mariti* (Weber Bosse) Denizot | | | M | b |
| | | | | *Peyssonnelia nordstedtii* Weber Bosse | | | M | b |
| | | | | *Peyssonnelia obscura* Weber Bosse | | | M | b |
| | | | | *Peyssonnelia orientalis* (Weber Bosse) Cormaci & G.Furnari | | | M | b |
| | | | | *Peyssonnelia thomassinii* Marcot-Coqueugniot & Boudouresque | | E | M | b |
| | | | *Sonderophycus* Denizot | | | | | |
| * | | | | *Sonderophycus capensis* (Montagne) M.J.Wynne | F11 | | G | a, b |

**Table 2** (continued)

| | | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|---|
| | | | *Ramicrusta* Zhang Derui & Zhou Jinghua | | | | | |
| | | | | *Ramicrusta calcea* (Heydrich) K.R.Dixon | | | M | b |
| | Plocamiales | | | | | | | |
| | | Plocamiaceae | | | | | | |
| | | | *Plocamium* J.V.Lamouroux | | | | | |
| | | | | *Plocamium corallorhiza* (Turner) J.D.Hooker & Harvey | | | M | b |
| | | | | *Plocamium cornutum* (Turner) Harvey | | | M | b |
| | | | | *Plocamium glomeratum* J.Agardh | | | M | b |
| | | | | *Plocamium suhrii* Kützing | | | M | b |
| | | Sarcodiaceae | | | | | | |
| | | | *Sarcodia* J.Agardh | | | | | |
| | | | | *Sarcodia montagneana* (J.D.Hooker & Harvey) J.Agardh | | | M | b |
| | Rhodachlyales | | | | | | | |
| | | Rhodachlyaceae | | | | | | |
| | | | *Rhodachlya* J.A.West, J.L.Scott, K.A.West, U.Karsten, S.L.Clayden & G.W.Saunders | | | | | |
| | | | | *Rhodachlya madagascarensis* J.A.West et al | | E | G | w |
| | Rhodymeniales | | | | | | | |
| | | Champiaceae | | | | | | |
| | | | *Champia* Desvaux | | | | | |
| | | | | *Champia irregularis* (Zanardini) Piccone | | | M | b |
| | | | | *Champia parvula* (C.Agardh) Harvey | | | M | b |
| * | | | | *Champia* sp. | F15 | | G | a |
| | | | *Coelothrix* Børgesen | | | | | |
| | | | | *Coelothrix irregularis* (Harvey) Børgesen | | | M | b |
| * | | | | *Coelothrix* sp. | F16 | | G | a |
| | | Faucheaceae | | | | | | |
| | | | *Fauchea* Montagne & Bory | | | | | |

**Table 2** (continued)

| | | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|---|
| | | | | *Fauchea madagascariensis* Farghaly | | E | M | b |
| | | | *Gloiocladia* J.Agardh | | | | | |
| | | | | *Gloiocladia profunda* (Borgesen) N.Sánchez & Rodríguez-Prieto | | | M | b |
| | | | | *Gloiocladia spinulosa* (Okamura & Segawa) N.Sánchez & C.Rodríguez-Prieto | | | M | b |
| | | Hymenocladiaceae | | | | | | |
| | | | *Hymenocladia* J.Agardh | | | | | |
| | | | | *Hymenocladia kallymenioides* (Holmes) F.Schmitz | | | M | b |
| | | Lomentariaceae | | | | | | |
| | | | *Ceratodictyon* Zanardini | | | | | |
| | | | | *Ceratodictyon variabile* (J.Agardh) R.E.Norris | | | M | b |
| * | | | | *Ceratodictyon spongiosum* Zanardini | F17 | | G | a, b |
| | | Rhodymeniaceae | | | | | | |
| | | | *Botryocladia* (J.Agardh) Kylin | | | | | |
| | | | | *Botryocladia botryoides* (Wulfen) Feldmann | | | M | b |
| | | | | *Botryocladia leptopoda* (J.Agardh) Kylin | | | M | b |
| | | | | *Botryocladia madagascariensis* G.Feldmann | | | M | b, ab |
| | | | | *Botryocladia skottsbergii* (Børgesen) Levring | | | M | b |
| | | | | *Botryocladia sonderi* P.C.Silva | | | M | b |
| | | | *Chamaebotrys* J.M.Huisman | | | | | |
| | | | | *Chamaebotrys boergesenii* (Weber Bosse) Huisman | | | M | b |
| | | | *Halichrysis* (J.Agardh) F.Schmitz | | | | | |
| | | | | *Halichrysis micans* (Hauptfleisch) P.Huvé & H.Huvé | | | M | b |
| | | Rhodymeniales incertae sedis | | | | | | |
| | | | *Sciadophycus* E.Y.Dawson | | | | | |
| | | | | *Sciadophycus stellatus* E.Y.Dawson | | | M | b |
| | Sporolithales | | | | | | | |

**Table 2** (continued)

| | | Cluster | E | Id | References |
|---|---|---|---|---|---|
| | Sporolithaceae | | | | |
| | *Sporolithon* Heydrich | | | | |
| | *Sporolithon crassiramosum* (Pilger) P.C.Silva | | E | M | b |
| | *Sporolithon sibogae* (Weber Bosse & Foslie) P.C.Silva | | | M | b |
| | Ulvophyceae (34) | | | | |
| | Bryopsidales | | | | |
| | Bryopsidaceae | | | | |
| | *Bryopsis* J.V.Lamouroux | | | | |
| | *Bryopsis corymbosa* J.Agardh | | | M | b |
| | *Bryopsis hypnoides* J.V.Lamouroux | | | M | b |
| | *Bryopsis myosuroides* Kützing | | | M | b |
| | Caulerpaceae | | | | |
| | *Caulerpa* J.V.Lamouroux | | | | |
| * | *Caulerpa brachypus* Harvey | UR6, UT7 | | G | a, b |
| | *Caulerpa chemnitzia* (Esper) J.V.Lamouroux | | | M | b |
| | *Caulerpa chemnitzia* var. *turbinata* (J.Agardh) Fernández-García & Riosmena-Rodríguez | | | M | b |
| * | *Caulerpa cupressoides* (Vahl) C.Agardh | UR5, UT9 | | G | a, b |
| | *Caulerpa cupressoides* var. *lycopodium* Weber Bosse | | | M | b |
| | *Caulerpa lentillifera* J.Agardh | | | M | b |
| | *Caulerpa mexicana* Sonder ex Kützing | | | M | b |
| | *Caulerpa mexicana* f. *laxior* (Weber Bosse) W.R.Taylor | | | M | b |
| * | *Caulerpa racemosa* (Forsskål) J.Agardh | UR7, UT8 | | G | a, b |
| | *Caulerpa racemosa* f. *condensata* Weber Bosse | | | M | b |
| | *Caulerpa scalpelliformis* (R.Brown ex Turner) C.Agardh | | | M | b |
| | *Caulerpa serrulata* (Forsskål) J.Agardh | | | M | b |
| | *Caulerpa serrulata* var. *hummii* (Díaz-Piferrer) Farghaly | | | M | b |

**Table 2** (continued)

| | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|
| | | | *Caulerpa sertularioides* (S.G.Gmelin) M.Howe | | | M | b |
| | | | *Caulerpa taxifolia* (M.Vahl) C.Agardh | | | M | b |
| | | | *Caulerpa verticillata* J.Agardh | | | M | b |
| | | | *Caulerpa webbiana* Montagne | | | M | b |
| | | | *Caulerpa webbiana* var. *pickeringii* (Harvey & Bailey) Eubank | | | M | b |
| | Codiaceae | | | | | | |
| | | *Codium* Stackhouse | | | | | |
| | | | *Codium acuminatum* O.Schmidt | | | M | b |
| | | | *Codium arabicum* Kützing | | | M | b |
| * | | | *Codium arenicola* M.E.Chacana & P.C.Silva | UT12 | | G | a, x |
| * | | | *Codium capitatum* P.C.Silva | | | M | b |
| | | | *Codium cicatrix* P.C.Silva | | | G | x |
| | | | *Codium decorticatum* (Woodward) M.Howe | | | G | x |
| | | | *Codium duthieae* P.C.Silva | | | G | x |
| | | | *Codium dwarkense* Børgesen | | | G | b, x |
| | | | *Codium extricatum* P.C.Silva | | | G | x |
| * | | | *Codium geppiorum* O.C.Schmidt | | | M | a |
| | | | *Codium lucasii* subsp. *capense* P.C.Silva | | | G | x |
| | | | *Codium madagascariense* Farghaly | | E | M | aj |
| | | | *Codium mozambiquense* P.C.Silva | | | G | x |
| | | | *Codium prostratum* Levring | | | G | x |
| | | | *Codium repens* P.Crouan & H.Crouan | | | G | x |
| | | | *Codium spongiosum* Harvey | | | G | x |
| * | | | *Codium taylorii* P.C.Silva | UT11 | | G | a, x |
| | | | *Codium tomentosum* Stackhouse | | | M | b |
| | Dichotomosiphonaceae | | | | | | |
| | | *Avrainvillea* Decaisne | | | | | |

**Table 2** (continued)

| | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|
| * | | | *Avrainvillea erecta* (Berkeley) A.Gepp & E.S.Gepp | UR10 | | G | a, b |
| | | | *Avrainvillea rawsonii* (Dickie) M.Howe | | | M | b |
| | Halimedaceae | | | | | | |
| | | *Halimeda* J.V.Lamouroux | | | | | |
| | | | *Halimeda copiosa* Goreau & E.A.Graham | | | M | b |
| | | | *Halimeda cuneata* Hering | | | M | b |
| | | | *Halimeda cylindracea* Decaisne | | | M | b |
| * | | | *Halimeda discoidea* Decaisne | UR1, UT1 | | G | a, b |
| * | | | *Halimeda distorta* (Yamada) Hillis-Colinvaux | UR4, UT3 | | G | a |
| | | | *Halimeda fragilis* W.R.Taylor | | | M | b |
| | | | *Halimeda incrassata* (J.Ellis) J.V.Lamouroux | | | M | b |
| | | | *Halimeda lacrimosa* M.Howe | | | M | b |
| | | | *Halimeda macroloba* Decaisne | | | M | b |
| | | | *Halimeda micronesica* Yamada | | | M | b |
| * | | | *Halimeda minima* (W.R.Taylor) Hillis-Colinvaux | UR3, UT4 | | G | a |
| | | | *Halimeda opuntia* (Linnaeus) J.V.Lamouroux | | | M | b |
| | | | *Halimeda renschii* Hauck | | | M | b |
| | | | *Halimeda tuna* (J.Ellis & Solander) J.V.Lamouroux | | | M | b |
| | Pseudocodiaceae | | | | | | |
| | | *Pseudocodium* Weber Bosse | | | | | |
| | | | *Pseudocodium devriesii* Weber Bosse | | | M | b |
| | Rhipiliaceae | | | | | | |
| | | *Rhipiliopsis* A.Gepp & E.S.Gepp | | | | | |
| | | | *Rhipiliopsis madagascariensis* Farghaly & Denizot | | E | M | b |
| | Udoteaceae | | | | | | |
| | | *Chlorodesmis* Harvey & Bailey | | | | | |
| | | | *Chlorodesmis hildebrandtii* A.Gepp & E.S.Gepp | | | M | b |

**Table 2** (continued)

| | | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|---|
| | | | | *Chlorodesmis major* Zanardini | | | M | b |
| * | | | | *Chlorodesmis* sp. | UR9, UT5 | | G | a |
| | | | *Udotea* J.V.Lamouroux | | | | | |
| | | | | *Udotea argentea* Zanardini | | | M | b |
| | | | | *Udotea glaucescens* Harvey ex J.Agardh | | | M | b |
| | | | | *Udotea indica* A.Gepp & E.S.Gepp | | | M | b |
| * | | | | *Udotea orientalis* A.Gepp & E.S.Gepp | UR8, UT6 | | G | a, b |
| | Cladophorales | | | | | | | |
| | | Anadyomenaceae | | | | | | |
| | | | *Anadyomene* J.V. Lamouroux | | | | | |
| | | | | *Anadyomene wrightii* Harvey ex J.E.Gray | | | M | b |
| | | | | *Anadyomene pavonina* (J.Agardh) Wille | | | M | b |
| * | | | | *Anadyomene stellata* (Wulfen) C.Agardh | | | M | a, b |
| | | | *Microdictyon* Decaisne | | | | | |
| | | | | *Microdictyon boergesenii* Setchell | | | M | b |
| | | | | *Microdictyon tenuius* J.E.Gray | | | M | b |
| | | | | *Microdictyon thiebautii* Setchell | | | M | b |
| | | | | *Microdictyon umbilicatum* (Velley) Zanardini | | | M | b |
| * | | | | *Microdictyon* sp. | | | M | a |
| | | Boodleaceae | | | | | | |
| | | | *Acrocladus* Nägeli | | | | | |
| | | | | *Acrocladus herpesticus* (Montagne) Boedeker | | | M | b |
| | | | *Boodlea* G.Murray & G.De Toni | | | | | |
| * | | | | *Boodlea composita* (Harvey) F.Brand | | | M | a, b |
| | | | *Nereodictyon* Gerloff | | | | | |
| | | | | *Nereodictyon imitans* Gerloff | | | M | b |
| | | Chladophoraceae | | | | | | |

**Table 2** (continued)

| | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|
| | | *Chaetomorpha* Kützing | | | | | |
| | | | *Chaetomorpha aerea* (Dillwyn) Kützing | | | M | b |
| | | | *Chaetomorpha antennina* (Bory) Kützing | | | M | b |
| | | | *Chaetomorpha linum* (O.F.Müller) Kützing | | | M | b |
| | | *Cladophora Kützing* | | | | | |
| | | | *Cladophora prolifera* (Roth) Kützing | | | M | b |
| | | | *Cladophora saviniana* Børgesen | | | M | b |
| | | | *Cladophora sibogae* Reinbold | | | M | b |
| | | | *Cladophora vagabunda* (Linnaeus) Hoek | | | M | b |
| * | | | *Cladophora* sp. | | | M | a |
| | | *Pseudorhizoclonium* Boedeker | | | | | |
| | | | *Pseudorhizoclonium africanum* (Kützing) Boedeker | | | M | b |
| | | | *Pseudorhizoclonium mangroviorum* Boedeker, Leliaert & A.R.Sherwood | | | M | y |
| | | *Rhizoclonium* Kützing | | | | | |
| | | | *Rhizoclonium implexum* (Dillwyn) Kützing | | | M | b |
| | Siphonocladaceae | | | | | | |
| | | *Boergesenia* Feldmann | | | | | |
| * | | | *Boergesenia forbesii* (Harvey) Feldmann | | | M | a, b |
| | | *Chamaedoris* Montagne | | | | | |
| | | | *Chamaedoris delphinii* (Hariot) Feldmann & Børgesen | | | M | b, ak |
| | | *Dictyosphaeria* Decaisne | | | | | |
| * | | | *Dictyosphaeria cavernosa* (Forsskål) Børgesen | | | M | a |
| * | | | *Dictyosphaeria versluyisii* Weber Bosse | | | M | a |
| | | *Siphonocladus* F.Schmitz | | | | | |
| | | | *Siphonocladus tropicus* (P.Crouan & H.Crouan) J.Agardh | | | M | b |
| | Valoniaceae | | | | | | |

**Table 2** (continued)

| | | | | | Cluster | E | Id | References |
|---|---|---|---|---|---|---|---|---|
| | | | *Valonia* C.Agardh | | | | | |
| * | | | | *Valonia aegagrophila* C.Agardh | | | M | a |
| * | | | | *Valonia fastigiata* Harvey ex J.Agardh | | | M | a, b |
| | | | | *Valonia macrophysa* Kützing | | | M | b |
| | | | | *Valonia utricularis* (Roth) C.Agardh | | | M | b |
| * | | | | *Valonia ventricosa* J.Agardh | | | M | a |
| | | | *Valoniopsis* Børgesen | | | | | |
| * | | | | *Valoniopsis pachynema* (G.Martens) Børgesen | | | M | a, b |
| | Dasycladales | | | | | | | |
| | | Dasycladaceae | | | | | | |
| | | | *Bornetella* Munier-Chalmas | | | | | |
| * | | | | *Bornetella nitida* Munier-Chalmas ex Sonder | UR12 | | G | a |
| | | | | *Bornetella oligospora* Solms-Laubach | | | M | b |
| * | | | | *Bornetella sphaerica* (Zanardini) Solms-Laubach | UR11 | | G | a, b |
| | | | *Neomeris* J.V.Lamouroux | | | | | |
| | | | | *Neomeris annulata* Dickie | | | M | b |
| | | | | *Neomeris dumetosa* J.V.Lamouroux | | | M | b |
| * | | | | *Neomeris van-bosseae* M.Howe | UR13 | | G | a |
| | | | | *Neomeris* sp. | UR14 | | G | |
| | Trentepohliales | | | | | | | |
| | | Trentepohliaceae | | | | | | |
| | | | *Trentepohlia* C.Martius | | | | | |
| | | | | *Trentepohlia chinensis* (Harvey) Hariot | | | M | b |
| | Ulotrichales | | | | | | | |
| | | Gayraliaceae | | | | | | |
| | | | *Gayralia* K.L.Vinogradova | | | | | |
| | | | | *Gayralia oxysperma* (Kützing) K.L.Vinogradova ex Scagel & al | | | M | b |

**Table 2** (continued)

| | | Cluster | E | Id | References |
|---|---|---|---|---|---|
| | Ulvales | | | | |
| | Ulvaceae | | | | |
| | *Ulva* Linnaeus | | | | |
| | *Enteromorpha juergensii* Kützing | | | M | B |
| | *Ulva enteromorpha f. caespitosa* Le Jolis | | | M | B |
| | *Ulva flexuosa* Wulfen | | | M | B |
| * | *Ulva lactuca* Linnaeus | UT13 | | G | a, b |
| | *Ulva linza* Linnaeus | | | M | B |
| | *Ulva paradoxa* C.Agardh | | | M | B |
| | *Ulva reticulata* Forsskål | | | M | B |
| | *Ulva rigida* C.Agardh | | | M | B |
| * | *Ulva* sp. 1 | UR22 | | G | A |
| * | *Ulva* sp. 2 | UR21, UT14 | | G | A |

*Indicates the species identified in this study; Clusters: *P#* Phaeophyceae *rbc*L lineage in Fig. S1, *F#* Florideophyceae *rbc*L lineage in Fig. S2, *UR# & UT#* Ulvophyceae *rbc*L and *tuf*A lineage in Fig. S3, *Endemism (E) E* species endemic to Madagascar, Identification (Id.): *G* based on molecular and morphological data, *M* based on morphological data only. †indicate groups (genus or species) potentially involved in community phase-shifts

*a* this study, *b* in Silva et al. (1996), *c* Steen et al. (2015), *d* Mattio and Payri (2010), *e* Mattio et al. (2015), *f* Dixon et al. (2014), *g* Won et al. 2009, *h* De Jong et al. (1999), *i* Sekimoto et al. (2009), *j* West et al. (2006), *k* Hernandez-Kantun et al. (2016), *l* Kato and Baba (2019), *m* Boo et al. (2015), *n* Boo et al. (2016), *o* Boo et al. (2018), *p* Tronchin et al. (2003), *q* Le Gall et al. (2015), *r* Manghisi et al. (2014), *s* Manghisi et al. (2015), *t* De Clerck et al. (2005b), *u* Gabriel et al. (2009), *v* Gabriel et al. (2010), *w* West et al. (2008), *x* Verbruggen and Costa (2015), *y* Sherwood et al. (2019); *z* Yang et al. (2010), *aa* Zuccarello et al. (2010), *ab* Feldmann (1945), *ac* Wynne (1982), *ad* Wynne (2013), *ae* Chamberlain and Norris (1994), *af* Santelices (1994), *ag* Kraft (1977), *ah* Coppejans et al. (2000), *ai* Schils and Coppejans (2002), *aj* Farghaly (1980), *ak* Leliaert and Coppejans (2004)

(85 Phaeophyceae; 1 Compsopogonophyceae; 240 Florideophyceae; 116 Ulvophyceae), 165 genera (25; 1; 110; 29), 79 families (11; 1; 50; 17) and 31 orders (7; 1; 17; 6).

### DNA amplification and sequencing

A total of 210 sequences (103 *rbc*L sequences for Phaeophyceae, 53 Florideophyceae, 33 Ulvophyceae; 21 *tuf*A for Ulvophyceae) were generated corresponding to 89 genetic groups: 30 Phaeophyceae, 36 Florideophyceae, and 23 Ulvophyceae (Table S3, Figs. S1-S3). For the Ulvophyceae, 23 and 14 groups were identified with *rbc*L and *tuf*A, respectively, including 11 groups in common, six specific to *rbc*L and three specific to *tuf*A.

### BLAST results

BLAST analyses with *rbc*L sequences returned a 100% similarity match for 1% of the Phaeophyceae sequences, 4% of the Florideophyceae and 8% of the Ulvophyceae (Table S4). BLAST results returned the highest percentage of matches across classes for a percentage of identity comprised between 99% and 100%, with 27%, 36% and 43% of the Phaeophyceae, Florideophyceae and Ulvophyceae, respectively (Table S4). BLAST analyses with *tuf*A sequences returned 100% and 99% matches for 33% and 57% of the Ulvophyceae sequences, respectively. A total of 51%, 49% and 35% of the Phaeophyceae, Florideophyceae and Ulvophyceae, respectively, had less than 98% similarity matches (Table S4).

Among the 56 genera identified in this study, six genera do not have *rbc*L sequences on GenBank including five Cladophorales genera (*Anadyomene*, *Boergesenia*, *Dictyosphaeria*, *Microdictyon*, *Valoniopsis*) and one Fucales (*Polycladia*); and 10 Ulvophycean genera do not have *tuf*A sequences including eight Cladophorales genera (*Anadyomene*, *Boergesenia*, *Boodlea*, *Cladophora*, *Dictyosphaeria*, *Microdictyon*, *Valonia*, *Valoniopsis*) and one Dasycladales (*Bornetella*). Nineteen genera have less than 10 *rbc*L sequences on GenBank (Table S5). Among the 56 genera identified, the average of the ratio [number of *rbc*L sequenced species/number of species described] is 52%, 43% and 19% for the Phaeophyceae, Florideophyceae and Ulvophyceae, respectively; and 15% for *tuf*A (Ulvophyceae).

We were unable to amplify either *rbc*L or *tuf*A sequences for any of the Cladophorales species; nor *tuf*A sequences for any of the Dasycladales species. Sequences generated from all Cladophorales specimens all corresponded to unidentified Ulvales taxa (Fig. S3) probably epiphytic on the Cladophorales. We generated the first *rbc*L sequence for the Fucales genus *Polycladia*.

We were unable to classify to the genus level the sample MADA18ALG043 (Fig. S8); BLAST (max 90% similarity) and phylogenetic analyses (Fig. S9) indicated that the alga belongs to the Order Nemastomatales and to the family Schizymeniaceae, and is sister to *Schizymenia* and *Platoma* (Fig. S9). Further morphological and molecular analyses in progress could clarify its nomenclatural identity.

## Discussion

Present results provide new data for the Malagasy marine flora and we discuss the limits of DNA-barcoding given the present reference dataset. Complemented by previous records, we provide the first comprehensive and taxonomically updated checklist for the Malagasy marine flora. We discuss specific threats to biodiversity on Madagascar's coastal reefs from both anthropic and anthropogenic activities and possible conservation strategies.

## Diversity

Madagascar is well known for its high degree of diversity and endemicity of terrestrial animals and plants (Goodman and Benstead 2003, 2005). However, the marine flora remained relatively poorly known with previous estimates only reporting approximately 200 species (Goodman and Benstead 2005). Contradicting previous reports that the seaweed diversity was well-known (Goodman and Benstead 2005), updated species numbers provided in our study double previous estimates. These differences between the estimates of Goodman and Benstead (2003, 2005) and our study are partly due to new collections since 2005, but mostly a result of inadequate research of past literature. Moreover, a relatively high number of taxa (29, or 6.5%) represented endemic species; while this is still significantly short of the rate of endemism for the terrestrial flora and fauna (37 to 100%; CBD 2020), it is to be taken into consideration that with some exceptions (e.g., *Portieria*; Leliaert et al. 2018) marine algae are generally more widely distributed into the world's oceans. However, a more comprehensive sampling may significantly increase this number. This study provides the first comprehensive catalogue of Malagasy seaweeds with a total 442 species (Table 2). Our sampling in northern Madagascar resulted in the identification of 110 species including 72 new species records for Madagascar (ca. 16% of Malagasy seaweeds species diversity). The diversity uncovered from northern Madagascar represents ca. 25% of the Malagasy seaweeds diversity, and molecular-based taxonomic studies are needed to obtain a better picture of the marine algal species diversity; in this respect the present study contributes significantly to our knowledge of the marine flora of North Madagascar. Currently, the identification of 148 species (52 Phaeophyceae, 62 Florideophyceae, 34 Ulvophyceae) is supported by molecular data, which represent only a third (ca. 33%) of the known algal diversity from Madagascar. Molecular studies are therefore also needed to confirm previous records solely based on morphological identification. Several algal species previously recorded from Madagascar are probably misidentifications, as it is the case for the only two species of *Lobophora* previously reported based on morphological data: *L. variegata* and *L. papenfussii*. Recent molecular-based taxonomic studies showed that *L. variegata* is restricted to the Greater Caribbean and *L. papenfussii* to the Central Indo-Pacific (Vieira et al. 2017, 2016, 2020); and these two species have neither been identified by Steen et al. (2015) nor in this study.

In terms of novelty, several groups gave a low BLAST score, which either indicates that these groups are new genera or that no sequences for the corresponding species were yet available in the reference library. Among the 89 unique taxa identified 32 (ca. 36%) could only be identified to species level. For instance, among the nine species of *Lobophora* identified from northern Madagascar, only one matched a taxonomically accepted species and the remaining eight corresponded to new species. But as discussed further below, this could also be an artifact of sequence availability. Further taxonomic analyses are recommended to explore the taxonomic novelty of these samples with low BLAST score. One specimen in particular (MADA18ALG043, Figs S8, S9) may belong to a new genus of Florideophyceae belonging to the Schizymeniaceae, Nemastomatales, and will be described elsewhere. Several species were only provisionally named based on morphological characters, and additional analyses are required to confirm their identity.

It is fairly evident that the seaweeds diversity uncovered so far from Madagascar is only the "tip of the iceberg". As the fourth largest island in the world, with 5600 km of coastline, Madagascar is characterized by a diverse range of bioclimatic zones and is under the influence of several major ocean currents that support unique marine habitats and ecosystems encompassing coral reefs, mangroves, seagrass beds, estuaries, and coastal marshes. Consequently, the checklist of 442 species compiled in this study, comprising no less than 110 species identified from a limited number of localities in northern Madagascar, may represent only a fraction of the marine algal species diversity of Madagascar, and more are expected to be found with increased sampling effort, including possible further endemic species. A comprehensive sampling across these ecosystems and at greater depths would significantly increase these numbers, with a molecular approach being an essential tool to fully assess the scope of this algal diversity.

## DNA-barcoding

The present study offers an exercise in seaweeds species barcoding and exposes the limits of such approach in seaweeds. Contrary to other groups such as fishes, where species identification is quite efficient since the reference libraries are comprehensive and comprise validated and maintained DNA barcodes (COI) (Costa et al. 2012), the DNA barcode reference library for seaweeds remains fragmentary and to some extent not curated. We highlight specific issues in DNA barcoding analyses that we encountered in our study: *(1) Completeness*: comparing the number of species for which sequences are available on GenBank to the numbers of currently taxonomically accepted species for the 57 genera identified in this study, we had an average of 38% completeness for all seaweeds: 19% for the Ulvophyceae, 52% for the Phaeophyceae and 43% for the Florideophyceae (Table 2). In other words the reference library is missing 62% of the known diversity. Six and nine genera respectively out of the 57 identified in our study did not have *rbc*L and *tuf*A sequences available on GenBank, while 18 had less than 10 sequences. As a result, a DNA-barcoding approach would fail to identify a large part of the diversity; *(2) Non-labeled sequences*: in some cases, sequences matched most closely with sequences unidentified at the species-level labeled only as "sp." in the databases. Others were labeled with the Latin abbreviation "cf." (*confer*, *conferatur*) implying that they are comparable to, and probably belong to the given name (Turland et al. 2018). These taxa are yet to be taxonomically examined and confirmed. *Codium*, *Halimeda* are examples of green algal genera with a considerable number of incompletely identified sequences (ca. 35% of *Codium* sequence unique names were labeled either with "cf." or "sp."). Those are usually the well-studied genera. Within the Florideophyceae, the genus *Portieria* is the best example with 298 sequences labeled as *Portieria* cf. *hornemannii* out of 354 *rbc*L available sequences on GenBank, representing 84% of the sequences for that taxon. The sequencing of type or authentic material from the type locality would help to solve this problem; *(3) Mis-identified sequences*: mislabeling results either from misidentification or recent changes of names. Misidentification may also be caused by the presence of cryptic species and the unawareness of such presence. These numbers may be overestimated since some names are in synonymy. Mislabeled sequences are difficult to identify, and they can induce downstream errors since new sequences are typically annotated using existing ones. The cosmopolitan green algal genus *Ulva* represents by far the most confusing group with ca. 30% of *Ulva* names available on GenBank not currently taxonomically accepted and ca. 10% of *rbc*L and *tuf*A unique haplotypes assigned with more than one name; *(4) Limited resolution*: in some groups such as the brown algal genus *Sargassum* or the green algal genus *Ulva*, the *rbc*L marker is poorly differentiating species apart; it is not clear how much percentage similarity is necessary to assign a sequence to a species. As seen in Fig. S1, polytomies encompasses several distinct species within the *Sargassum* group. These highlight the limitations of the *rbc*L marker for this genus and the need to complement the algal GeneBank reference library with mitochondrial markers (*cox*1, *cox*3; Mattio and Payri 2010).

Among the Ulvophyceae, the genus *Ulva* represents today the most problematic group affected by most issues aforementioned. The genus, characterized by a simple and yet extensively plastic morphology (e.g., Blomster et al. 1999), accounts over 100 currently taxonomically accepted names (Guiry and Guiry 2020). The recent use of molecular tools unveiled a rampant cryptic diversity within this genus, which taxonomists have trouble linking to existing names (e.g., Hofmann et al. 2010). The extensive mislabeling on GenBank has resulted in numerous polytomic species names. Additionally, the reference library is biased towards temperate region, and potentially misses the diversity from tropical regions, where taxonomic efforts are still limited, and which may differ from temperate regions. In the light of these issues, we refrained from putting names on the sequences that returned no close match to any *Ulva* sequences on GenBank.

Finally, for the Ulvophyceae, while today there are slightly more sequences of *tuf*A available on GenBank, in our study we were able to amplify more *rbc*L than *tuf*A sequences for the same specimens, while some taxa were only successfully amplified in *tuf*A. While Saunders and Kucera (2010) recommended the use of *tuf*A to standardize barcode inititives in the Chlorophyceae, our own results suggest that *rbc*L may be a more suitable marker than *tuf*A for DNA-barcoding in Ulvophyceae. We nevertheless recommend the usage of both markers until a better reference library is provided for either chloroplastic or mitochondrial genes as standard DNA-barcoding marker. Difficulty in amplifying chloroplast genes among Cladophorales is due to the nature of their chloroplast genome, which is entirely fragmented into hairpin chromosomes (Del Cortona et al. 2017). As for the reasons explaining the failures in amplifying mitochondrial genes some authors pointed to the presence of introns or primer mismatch (Saunders and Kucera 2010). Accordingly, only nuclear genes (e.g., internal transcribed spacers, 18S rDNA) should be used as DNA barcoding markers for Cladophorales taxa.

## Anthropic impacts and conservation strategies

Madagascar, due to its unique geographic isolation and extensive diversity of coral reef habitats, is well known as one of the top biodiversity hotspots on the planet (Brooks et al. 2006). This is even more remarkable knowing that the diversity and speciation seen today is only a fraction of the island's original species richness, its native forest cover having been destroyed to a large extent by human settlers for herding and agriculture by 1600 AD (Gade 1996). The marine algal flora falls no exception to this, with 29 species endemic to the island (Table 2). Marine biodiversity however, due to its inherently lower percentage of endemism than land-locked terrestrial species, does not receive as high a priority for conservation, such as in locally-managed marine areas (Harris 2011). Growing population number, poverty and the lack of efficient national environmental management policies (especially those concerning ecosystem services) are all factors leading to the demise of marine coral reef habitats. Principal anthropogenic stressors impacting coral reefs worldwide include sewage outfalls, sedimentation from deforestation, and various pollutants (Harper et al. 2007; Harris et al. 2010). In our study, the large number of fleshy algae found

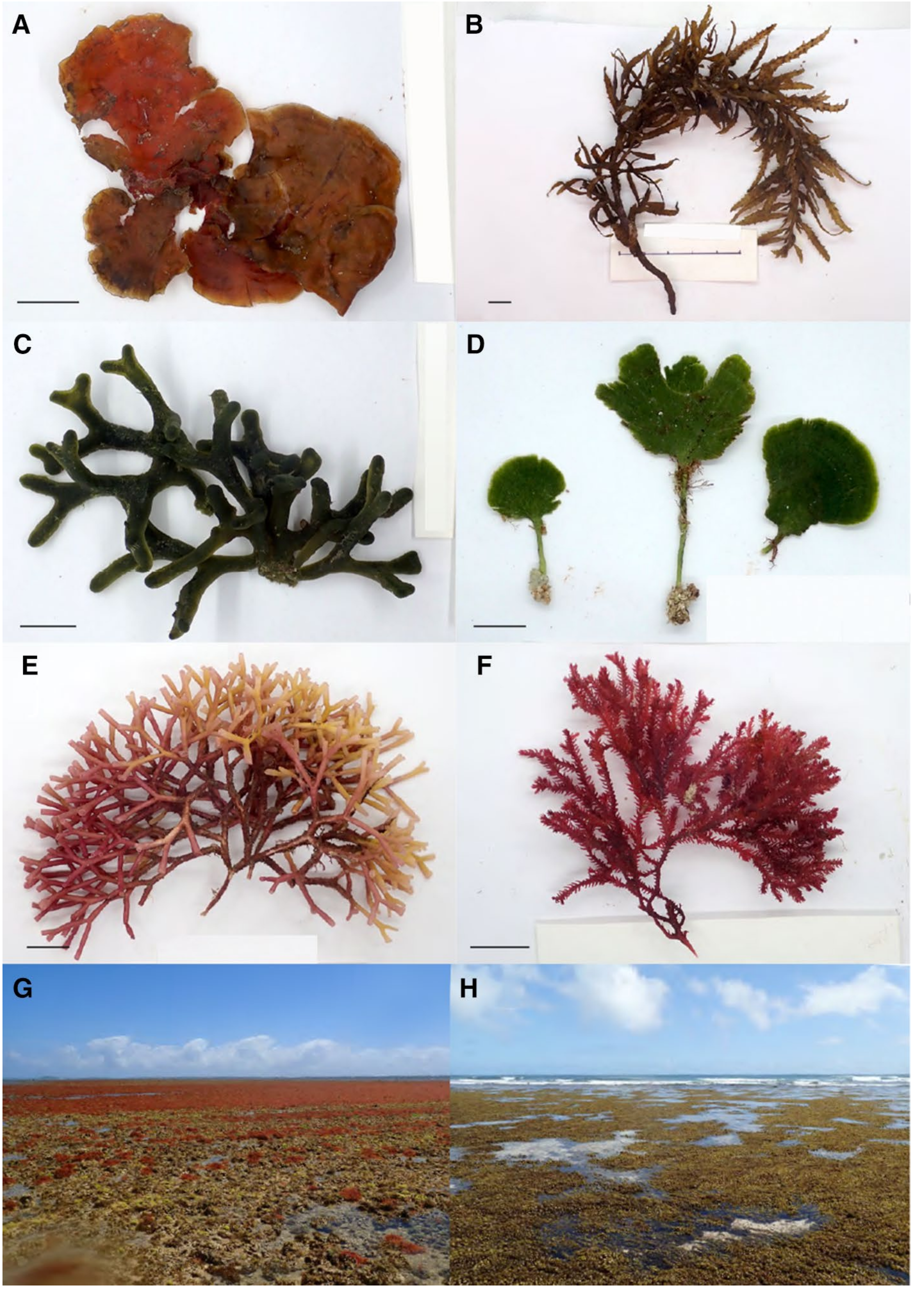


**Fig. 2** Representative seaweeds from Antsiranana Bay, northern Madagascar. *Ex situ* photographs of *Lobophora antsirananaensis* (MADA18ALG112) (**a**), *Sargassum* cf. *obovatum* (MADA18ALG588) (**b**), *Codium taylorii* (MADA18ALG139) (**c**), *Udotea orientalis* (MADA18ALG246) (d), *Galaxaura rugosa* (MADA18ALG048) (**d**), *Phacelocarpus tristichus* (MADA18ALG480) (**e**). *In situ* photographs of *Euchema denticulatum* extensive cover in the intertidal zone in the Petite Passe Orangea (**f**), *Sargassum* cf. *obovatum* extensive cover in the intertidal zone in the Mer d'Emeraude (**g**)

on the reefs (Fig. 2g, h) attests to the ecosystem phase shifts that are happening from coral-dominated to algae-dominated reefs (Arias-González et al. 2017; Brown et al. 2018). In the southwest Madagascar region near Andavadoaka, coral cover decline of over 80% with a dominance of the brown macroalgal genera *Dictyota*, *Sargassum* and *Turbinaria* were observed (Ahamada et al. 2004). In North-eastern Madagascar, abnormal imbalances in the biomass of *Dictyota*, *Acanthophora spicifera* and *Hypnea* spp. were noted on coastal flats subjected to high loads of terrigenous inputs and nutrients (Di Carlo and Tombolahy 2011). The same phenomenon, directly linked to human activity on land, was also reported for the Pacific island atoll of Tuvalu, subject to sustained sewage inputs into the lagoon leading to brown algal blooms (Fujita et al. 2013; N'Yeurt and Iese 2015; Nakamura et al. 2020) and in the central Pacific atoll of Kiribati, blooms of the red seaweed *Acanthophora spicifera* were reported (N'Yeurt, pers. obs.). While community-managed marine conservation areas have been implemented in the past in Madagascar (eg., Belle et al. 2009), in order to conserve the unique algal diversity of the highly threatened island, integrated land-sea planning that takes into consideration both anthropic terrestrial drivers such as deforestation, overpopulation, sewage inputs as well as marine ecosystem-based management approaches for mangroves, seagrass beds and coral reefs are essential (Brown et al. 2019). Such a Reef-to-Ridge (R2R) approach to biodiversity conservation has proven very successful in the Indo-Pacific region (Carlson et al. 2019) but is yet to occur in a systematic manner in Madagascar, and should be considered before the loss of endemic and keystone marine species reaches a critical state.

## Perspectives

Sampling in only a relatively small number of sites at shallow depths in Madagascar yielded over 110 species of seaweeds. This implies that future comprehensive marine algal biodiversity surveys across habitats and depths in Madagascar are needed to increase our knowledge of that island's diversity, with a potentially large number of endemic species. However, time is running out as much of the habitats under consideration are under threat from sedimentation, deforestation and unabated coastal development. Coupled with projected global increases in seawater temperature and ocean acidification, coral reef-building organisms of Madagascar could be subjected to multiple stressors to which they may not have time to adapt.

The present study provided an important contribution to algal DNA-barcoding through augmenting such molecular databases with sequences for species which were not yet available in the reference libraries (i.e., GenBank, BOLDSystems). It also provided meaningful insights into the usefulness and issues encountered in the choice of DNA barcodes for the identification of local algal floras. On the one hand, our results confirm to some extent the usefulness of the *rbc*L and *tuf*A genes as barcodes. However, the main problem to date is the completeness and accuracy of the reference libraries. This stresses the need for a detailed reference library comprising validated DNA barcodes. At present the Barcode of Life DataSystems (BOLD) and GenBank are the main public repositories of DNA barcode sequences. These reference libraries will need to mature and to be taxonomically validated.

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**Data availability** The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials.

**Code availability** Not applicable.

**Declarations**

**Conflict of interest** The authors declare no conflict of interests.

**Ethical approval** Not applicable.

**Consent to participate** All authors consent to participate.

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