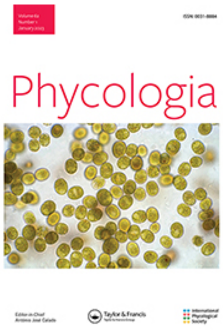

Phycologia

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/uphy20

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To cite this article: Cibele Conceição dos Santos, José Marcos de Castro Nunes, Gabriel do Nascimento Santos, Edilene Maria dos Santos Pestana, Valéria Cassano & Goia de Mattos Lyra (2023) Taxonomic changes in the Lomentariaceae (Rhodymeniales, Rhodophyta): *Yendoa gen. nov*. and *Ceratodictyon sanctae-crucis sp. nov.*, Phycologia, 62:1, 19-28, DOI: 10.1080/00318884.2022.2133269

To link to this article: https://doi.org/10.1080/00318884.2022.2133269

PHYCOLOGIA
2023, VOL. 62, NO. 1, 19–28
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Taxonomic changes in the Lomentariaceae (Rhodymeniales, Rhodophyta): *Yendoa gen. nov.* and *Ceratodictyon sanctae-crucis sp. nov.*

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ABSTRACT

The Lomentariaceae, previously treated as subfamily Lomentarioideae in the family Champiaceae, is one of the six families currently classified in the Rhodymeniales. Relationships within the family are not well-established, and new genera have been segregated from *Lomentaria*, a notoriously polyphyletic taxon as currently circumscribed. The lack of access to molecular data of type specimens has limited the taxonomic clarifications within the Lomentariaceae. Using new collections from Brazil, historical collections and data available in GenBank, we generated *rbc*L and COI-5P phylogenies of the Lomentariaceae, and we used species delimitation methods to assess the species-level diversity among sequences. A nuclear LSU rDNA phylogeny, although less representative in number of taxa, confirmed our findings. Our results recovered *Ceratodictyon* and *Semnocarpa* as monophyletic, whereas *Lomentaria* was polyphyletic. Integrating phylogenetic analyses, analyses of genetic variance, and morphological analyses, we revealed a new species, *Ceratodictyon sanctae-crucis sp. nov*., collected on the coast of Bahia (northeastern Brazil). Having included a newly generated sequence of the holotype of *Lomentaria sinensis*, a heterotypic synonym of *L. hakodatensis*, and a sequence from a sample collected near the type locality of *L. hakodatensis*, we propose the new genus *Yendoa gen. nov*. to accommodate this species. Our results support a more phylogenetically coherent taxonomic scheme for the Lomentariaceae, which now includes only monophyletic genera.

ARTICLE HISTORY
Received 10 November 2021
Accepted 04 October 2022

KEYWORDS
COI-5P; *Lomentaria hakodatensis*; Molecular phylogeny; Nuclear-encoded LSU rDNA; *rbc*L

INTRODUCTION

Lomentariaceae Willkomm *emend.* I.K. Lee is currently one of the six families classified in the Rhodymeniales F. Schmitz. The taxon has been treated as a subfamily, Lomentarioideae Kylin, within the Champiaceae Kützing (Kylin 1931). Lee (1978) made an emendation of the Lomentariaceae on the basis of vegetative and reproductive characters, and classified it in the Rhodymeniales. Early taxonomic studies of Rhodymeniales emphasized the presence of longitudinal filaments limiting the hollow parts of the thallus as a relevant character for delimiting families (Bliding 1928; Sparling 1957). The first broad molecular study of Rhodymeniales used sequences of the small subunit of ribosomal DNA and included 56% of the known genera of the order, but only two species (in one genus) of Lomentariaceae (Saunders *et al.* 1999). Recently, Filloramo & Saunders (2016) demonstrated in a multigene phylogeny that, as presently circumscribed, *Lomentaria* Lyngbye, the most diverse genus in the family, is not monophyletic. Efforts have been made to resolve the taxonomic problems of Lomentariaceae, with the attribution of generic status to clades distantly related to its type species (Filloramo & Saunders 2016; Wynne *et al.* 2019). Studies on Lomentariaceae rarely connected molecular data with detailed morphological analyses. Therefore, the lack of clarity on relevant characters to delimit genera and species is a source of taxonomic challenges (Gavio *et al.* 2005; Le Gall *et al.* 2008; Sherwood *et al.* 2010; Filloramo & Saunders 2016; Freshwater *et al.* 2017). *Ceratodictyon* Zanardini, the second most diverse genus, is monophyletic (Filloramo & Saunders 2016), whereas the seven remaining genera are either mono- or bi-specific and are represented by few specimens to date.

Ceratodictyon (= *Gelidiopsis* F. Schmitz) has a history of taxonomic changes and different circumscriptions. Before being classified in the Lomentariaceae (Saunders *et al.* 1999), it was placed in the Gigartinales (Norris 1987) and in the Rhodymeniaceae (Price & Kraft 1991). *Gelidiopsis* was considered a synonym of *Ceratodictyon* on the basis of molecular analyses (Le Gall *et al.* 2008). *Ceratodictyon* is distributed worldwide, with nine accepted species (Guiry & Guiry 2022).

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Supplemental data for this article can be accessed online at https://doi.org/10.1080/00318884.2022.2133269

The use of barcoding techniques has shown that the diversity of red algae in Brazil has been underestimated, especially in the under-sampled northeastern coastline (Soares *et al.* 2015; Lyra *et al.* 2016, 2021; Jesus *et al.* 2018; Pestana *et al.* 2020, 2021; Santos *et al.* 2020). However, species delimitation methods have not been applied to the Lomentariaceae in Brazil, and the actual diversity of this family remains unexplored.

In this study we addressed the long-standing problem of the polyphyly of *Lomentaria*, adding newly generated sequences, including sequences of the holotype of *Lomentaria sinensis* M. Howe, a heterotypic synonym of *L. hakodatensis* Yendo (Okamura 1936, *fide* Lee 1978), to phylogenetic analyses. We also investigated the diversity of *Ceratodictyon* in Bahia, Brazil, applying barcoding analyses based on COI-5P and *rbc*L gene datasets, and species delimitation methods.

MATERIAL AND METHODS

Sixty-one specimens were sampled in the intertidal at 12 locations along the extensive coastline of Bahia state, the longest in the littoral of Brazil (Table S1), covering almost seven degrees of latitude (from 11°28.4496′S to 18°19.0928′S).

For the molecular analyses, 20–40 mg of dried fragments were used for DNA extraction using 2% CTAB (modified from Doyle & Doyle 1987) or the extraction kits NucleoSpin Plant II (Macherey-Nagel, Düren, Germany) and PureLink Plant (Invitrogen, Waltham, Massachusetts, USA). For amplification of *rbc*L we used various combinations of the primer sets: F*rbc*Lstart–R492, F*rbc*Lstart–R492a and F*rbc*LStart–R753; F492–R1150 and F492a–R1150a; F993–R*rbc*S Start and F753–R*rbc*S Start (Freshwater & Rueness 1994; Cassano 2009).

PCR cycles for both genes included: initial denaturation at 94°C for 4–5 min; 34 or 35 cycles at 94°C for 30 s to 1 min; 45–47°C for 1 min; 72°C for 1.5–2 min extension, and a final extension at 72°C for 7 min. Amplified DNA samples were sequenced using the BigDye Terminator v3.1 Cycle Sequencing Ready Reaction (Applied Biosystems, Waltham, Massachusetts, USA) following the manufacturer's protocol. Forward and reverse DNA sequences were obtained for each gene.

We analysed the holotype of *Lomentaria sinensis*, deposited in the New York Botanical Garden (NY), New York, USA: NY00900337, *N.H.Cowdry* 556, collected 29 July 1920 from Chefoo, China (labelled *Lomentaria hakodatensis*), and sampled it for DNA extraction. *Rbc*L, COI-5P and LSU sequences were also obtained for two of our samples, *Ceratodictyon intricatum* (C. Agardh) R.E. Norris ALCB132899 and *L. sinensis* NY00900337, from Next Generation Sequencing (NGS), Raw reads were mapped to selected references of each gene using Geneious v9.1.8 (Kearse *et al.* 2012), thereby obtaining the aimed sequences for each sample. NGS was performed at the FAS Center for Systems Biology at Harvard University, using the Illumina NextSeq 500 (Illumina, Inc., San Diego, California, USA) with 150 bp, paired-end.

Additional *rbc*L, LSU and COI-5P sequences were obtained from GenBank (Table S1). The most appropriate model of sequence evolution was selected using jModeltest v2.1.10 (Darriba *et al.* 2012) under the Akaike Information Criterion (AIC). The GTR+I +G model of sequence evolution was selected for all datasets. ML analyses were performed as single partitions on the online server CIPRES Science Gateway v3.3 (Miller *et al.* 2010), using the tree inference interface and sequence alignment in the XSEDE RaxML v8.2.0 (Stamatakis 2014), with 1,000 bootstrap replicates. BI analyses were performed using MrBayes v3.0 (Huelsenbeck & Ronquist 2001). The parameters for the BI analysis were the following: four chains of the Markov chain Monte Carlo for two independent runs were performed (one hot and three cold), sampling one tree every 1,000 generations for 10,000,000 generations, starting with a random tree. We discarded the first 50,000 generations in both runs as the burn-in to build the consensus tree. We used *Botryocladia* (J. Agardh) Kylin (Rhodymeniaceae) sequences as an outgroup for all three datasets.

We calculated intra- and interspecific variation among specimens using Geneious for our *rbc*L and COI-5P datasets, which had the broadest taxon sampling. For these datasets, we also applied the Automated Barcode Gap Discovery (ABGD) method of Puillandre *et al.* (2012) using JC69 (Jukes & Cantor 1969) and K2P (Kimura 1980) models. We used optimum parameter settings as follows: $P_{\min} = 0.001$, $P_{\max} = 0.10$, P steps = 10, a relative width gap (x–value) of 1.5, minimum slope = 0.001, number of bins = 20, and JC69 Jukes-Cantor MinSlope = 1.5 (Jukes & Cantor 1969). ABGD calculates a single, model-based, one-sided confidence limit for intraspecific divergences observed across the entire alignment. The test determines a threshold level of genetic diversity from the first significant gap beyond this limit and uses it to partition the data into phylogenetic species hypotheses (Puillandre *et al.* 2012). We also applied the Assemble Species by Automatic Partitioning (ASAP method of Puillandre *et al.* 2021), using default settings for the JC69 (Jukes & Cantor 1969) and K2P (Kimura 1980) models. ASAP is a new method to build species partitions from single locus sequence alignments, based on pairwise genetic distances, providing a score for each defined partition (the lower the score, the better the partition) (Puillandre *et al.* 2021). We also applied the Statistical Parsimony Network (SPN) analyses developed by Templeton *et al.* (1992) for the COI-5P and *rbc*L matrices, using the TCS software v1.21 (Clement *et al.* 2000), in which the minimal number of mutational steps is calculated, and sequences of the same species are joined with a confidence limit >95%. Using species delimitation methods, we compared the different Primary Species Hypotheses (PSHs) with phylogenetic and morphological analyses to support our taxonomic decisions.

For the morphological analyses, specimens were fixed in 4% formalin/seawater. Transverse and longitudinal hand sections were performed with a razor blade, and stained with acidified aniline blue (1% aqueous solution). Voucher specimens were deposited in the Alexandre Leal Costa Herbarium (ALCB) at the Universidade Federal da Bahia, Brazil, and isotypes were deposited in the Universidade de São Paulo Herbarium (SPF). We contrasted our morphological and phylogenetic species hypotheses, and our taxonomic decisions were undertaken considering the interpretation of results and the congruence among methods.

RESULTS

Our *rbc*L Lomentariaceae dataset, including 12 newly generated sequences and 24 additional sequences, was 1,165 bp long. Our LSU dataset included two newly generated sequences and thirteen additional sequences, and was 2,829 bp long. Our COI-5P dataset included 20 newly generated sequences and 24 additional sequences, and was 583 bp long. We included newly generated sequences from the holotype of *L. sinensis* in each of the three datasets. Our *rbc*L phylogeny (Fig. 1) was the most robustly supported among the three, and the topologies from the COI-5P (Fig. 2) and LSU rDNA (Fig. S1) trees were not in conflict with the *rbc*L tree. The new species of *Ceratodictyon* is represented only in the *rbc*L dataset.

Our *rbc*L phylogeny (Fig. 1) produced a fully supported *Ceratodictyon* clade with *Fushitsunagia catenata* (Harvey) Filloramo & G.W. Saunders as a well-supported sister group. A strongly supported *Lomentaria* clade included the type species *L. articulata* (Hudson) Lyngbye. It was distinct from other genera and distantly related to samples identified as *L. hakodatensis*. The sequences of *L. hakodatensis* formed a fully supported clade in all three phylogenies.

Sequences from the holotype of *L. sinensis*, a taxonomic synonym of *L. hakodatensis*, clustered with the other *L. hakodatensis* sequences in the phylogenies of the three sampled genes (Figs 1, 2, S1). Importantly, the *rbc*L phylogeny included a sequence from a specimen collected near the species type locality (Sumiyoshi, Hakodate, Hokkaido, AB793780), and all the sequences of *L. hakodatensis* had 0%–0.69% intraspecific divergence. Based on our results, we propose here a new genus, *Yendoa gen. nov.*, to accommodate the species *Lomentaria hakodatensis* (see below).

In our *rbc*L phylogeny, sequences of *Ceratodictyon variabile* (J. Agardh) R.E. Norris were placed in a clade (79% BP, 1.00 PP) that also included samples of *C. repens* (Kützing) R.

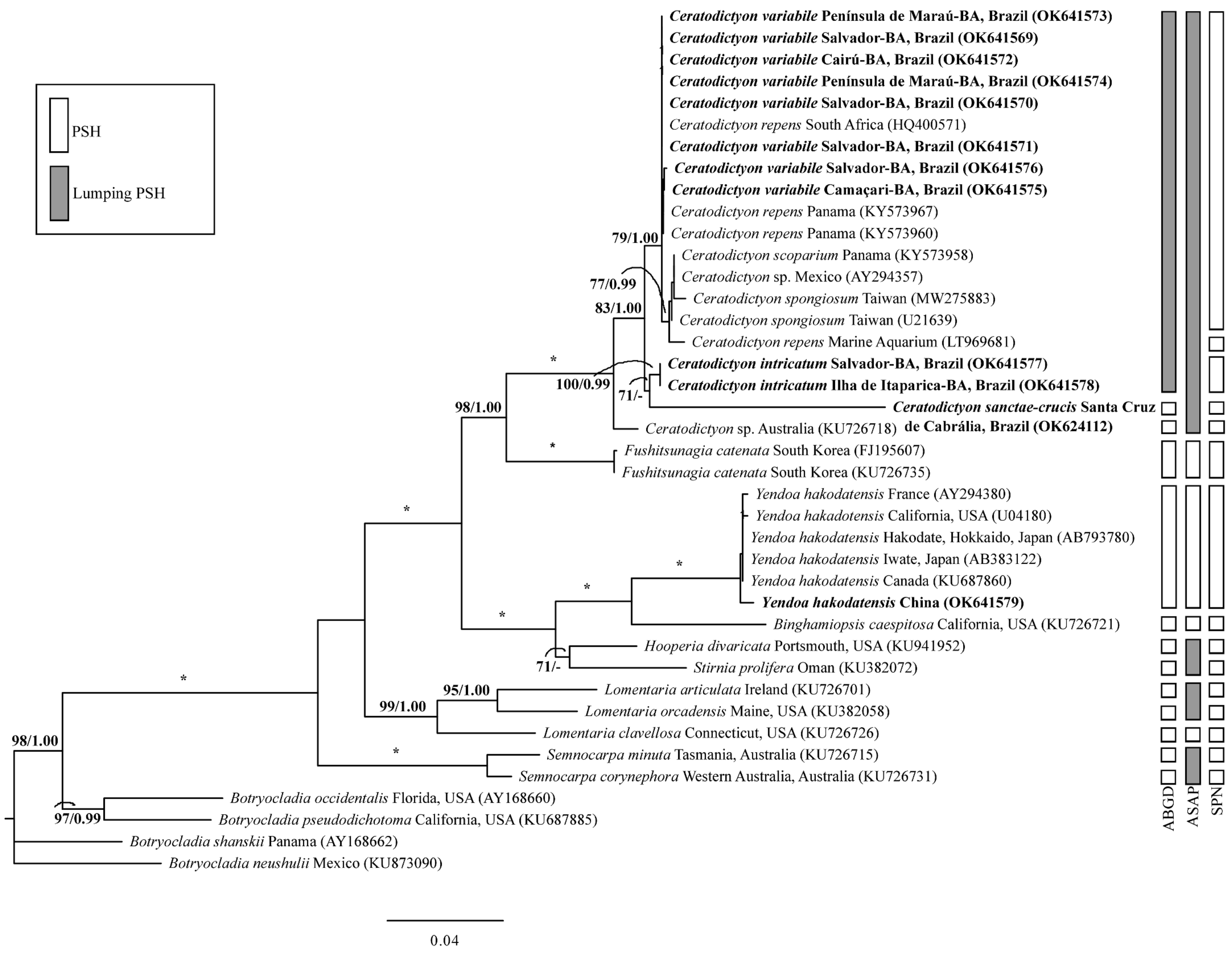


Fig. 1. Maximum likelihood (ML) tree based on *rbc*L sequences of Lomentariaceae. Bootstrap percentages and Bayesian posterior probabilities (BP/PP) are shown at the nodes. Sequences generated in this study are in bold. (-), values lower than 70% BP/0.95 PP; *, 100% BP/1.0 PP. Inset displays ABGD, ASAP and SPN reconstructions of hypothesized species based on the dataset. White bars are in agreement with the Primary Species Hypothesis (PSH) and grey bars represent lumping PSH. Sequence of the holotype of *Lomentaria sinensis* in bold (OK641579).

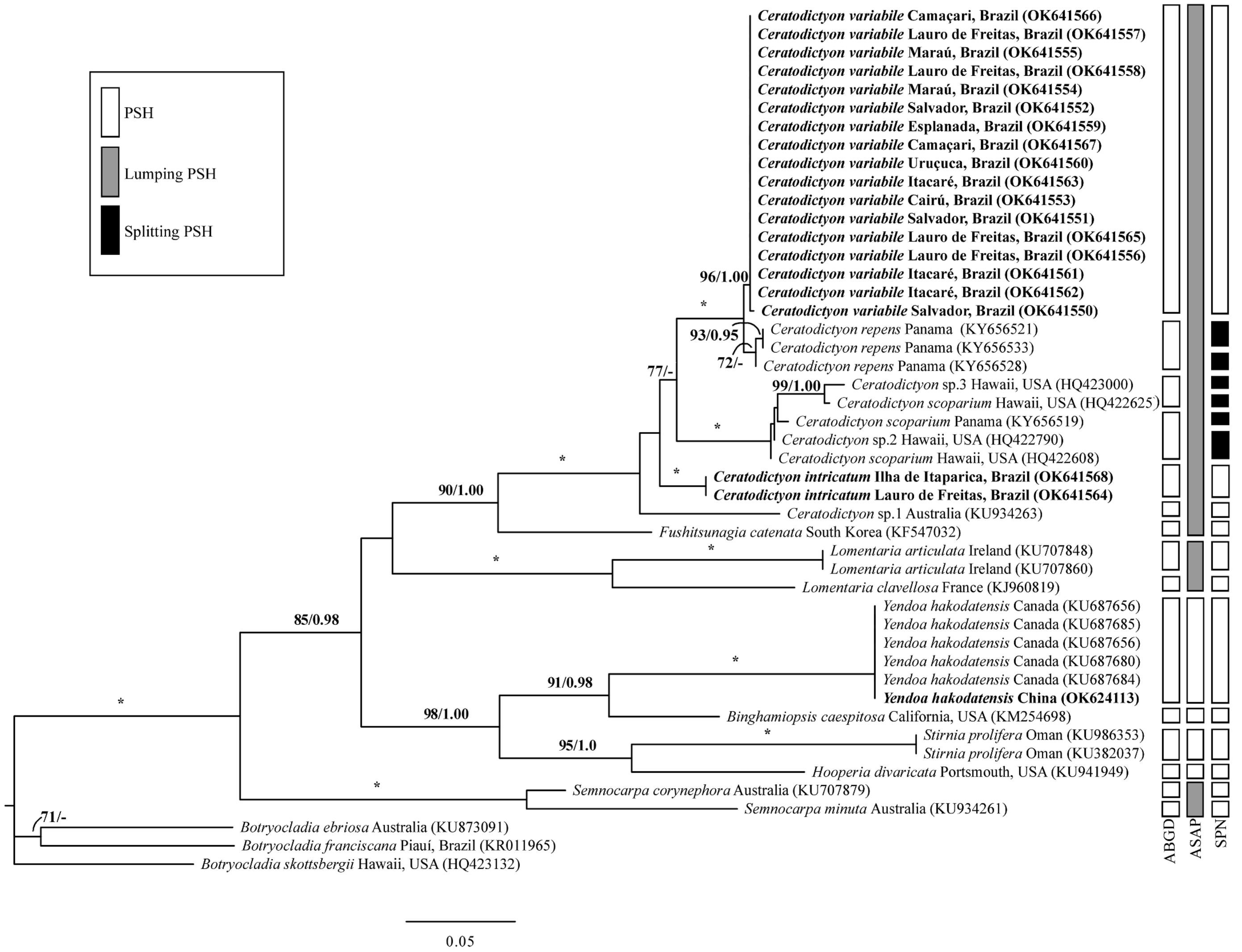


Fig. 2. Maximum Likelihood (ML) tree based on COI-5P sequences of Lomentariaceae. Bootstrap percentages and Bayesian posterior probabilities (BP/PP) are shown at the nodes. Sequences generated in this study are in bold. (-), values lower than 70% BP/0.95 PP; *, 100% BP/1.0 PP. Inset displays ABGD, ASAP and SPN reconstructions of hypothesized species based on the dataset. White bars are in agreement with the Primary Species Hypothesis (PSH), grey bars represent lumping PSH and black bars represent splitting PSH. Sequence of the holotype of *Lomentaria sinensis* in bold (OK624113).

E. Norris from South Africa, from Panama and from a marine aquarium, samples of *C. spongiosum* Zanardini from Taiwan, one sample of *Ceratodictyon* sp. from Mexico, and one sample of *C. scoparium* (Montagne & Millardet) R.E. Norris from Panama (Fig. 1). We identified a distinct sequence from Brazil, sampled in Santa Cruz de Cabrália, southern Bahia (Fig. 1), weakly supported (71% BP) as sister to *C. intricatum*. The genetic divergences for taxa considered in this study are shown in Tables S2, S3.

ABGD results for the *rbc*L (Fig. 1) and COI-5P (Fig. 2) matrices (P = 0.001) did not vary between the models used (JC69 or K2P). ABGD results for *rbc*L formed a single group of all sequences of *Ceratodictyon intricatum, C. repens, C. scoparium, C. spongiosum, C. variabile* and *Ceratodictyon* sp. from Mexico, except for *Ceratodictyon sp. nov*. from Brazil and *Ceratodictyon* sp. from Australia. ABGD results for the *rbc*L matrix, in which *Ceratodictyon sp. nov*. was represented, supported our taxonomic decision to propose a new species. Results for COI-5P split sequences of these samples into six separate groups. ABGD results for both COI-5P and *rbc*L formed a single entity including the *L. sinensis* holotype sequence with other *L. hakodatensis* sequences.

ASAP results for both *rbc*L and COI-5P lumped in a single group all the sequences of *Ceratodictyon*, and in the COI-5P results, *Ceratodictyon* sequences were also lumped with sequences of *Fushitsunagia catenata*. Also, for both matrices, the results from ASAP distinguished species in the *Lomentaria* clade and lumped sequences of *L. hakodatensis* (including the sequence from the holotype of *L. sinensis*) into a single entity.

Finally, for both datasets, SPN results lumped all the sequences of *L. hakodatensis* into a single group. *Ceratodictyon* sequences were split into nine groups in the COI-5P dataset, and into five groups in the *rbc*L dataset, with our new sample from Santa Cruz de Cabrália, Brazil, split from other known *Ceratodictyon* species.

Based on our findings, we propose a new species for the distinct *Ceratodictyon* sample collected in Brazil, and a new genus for the '*Lomentaria*' *hakodatensis* clade. Nomenclature and synonyms followed AlgaeBase (Guiry & Guiry 2022).

Ceratodictyon sanctae-crucis C.C. Santos, Lyra, Cassano & J.M.C. Nunes *sp. nov.*

Figs 3–6

DESCRIPTION: Plants erect, forming large tufts, brownish, up to 6.5 cm high, entangled, attached to the sandy substrate by a prostrate stoloniferous branch system. The thallus branches into several cylindrical to compressed axes, which divide irregularly or alternately into dichotomies or trichotomies; apices flexible, delicate and acute (Fig. 3). Lower portion of thallus with anastomosing branches (Fig. 4). Axes of thallus 250–385 µm wide in transverse section. Multiaxial growth, outer cortex composed of small cells and medulla composed of larger cells that are loosely aggregated (Fig. 5). The cortical region consists of 1–2 layers of cells (Fig. 5). In transverse section, the cortical cells are rounded to elongated (7–13 µm long and 8–12 µm wide) and gradually increase in size towards the medullary region. Medullary region of 8–9 layers of cells (Fig. 5). In cross section, the medullary cells are roundish, 17–20 µm long and 22–26 µm wide. In longitudinal section, the outer cortex shows a single-layer and the medulla has densely aggregated filaments, bearing solitary gland cells (Fig. 6). Reproductive structures were not observed. GenBank accession for *rbc*L sequence: OK624112.

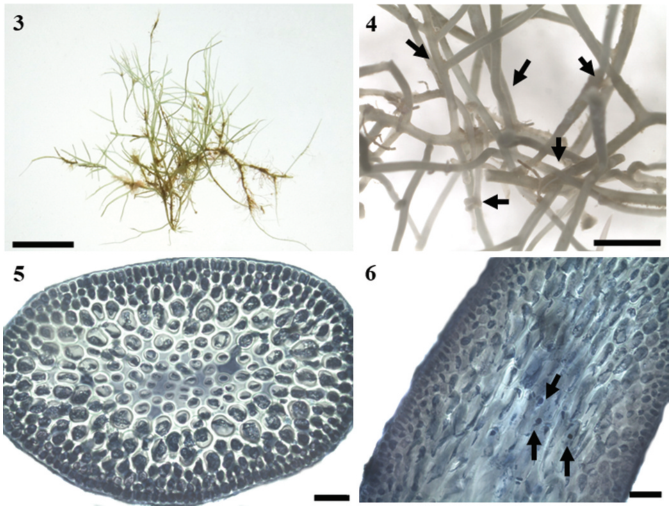
HOLOTYPE: ALCB132919, collected 17 May 2018 by C.C. Santos, deposited in Alexandre Leal Costa Herbarium (ALCB), Bahia, Brazil.

ISOPTYPES: SPF58671, SPF58672, deposited in the Universidade de São Paulo Herbarium (SPF), São Paulo, Brazil.

TYPE LOCALITY: Camurugi River, Arakakaí, Santa Cruz de Cabrália, Bahia, Brazil, 16°16.93′S, 39°1.23′W; specimens (holotype and isotypes) were collected in the intertidal zone, in a protected reef close to the meeting point between the sea and the river, growing in sandy substratum.

ETYMOLOGY: The species was named in honour of the city of Santa Cruz de Cabrália (Bahia) for its historical value for Brazil.

COMMENTS: *Ceratodictyon sanctae-crucis* differs from *C. intricatum* in habitat and thallus construction (*C. sanctae-crucis* is found in sandy substrate forming large entangled tufts, whereas *C. intricatum* is found in rocky substrate forming holdfast cushions, with very narrow thalli), in the height of the thallus (longer in *C. sanctae-crucis*, 6.0–6.5 cm, and shorter in *C. intricatum*, 2–3 cm), and in the shape of the outermost cortical cells (rounded to elongated in *C. sanctae-crucis* and oval in *C. intricatum*). *Ceratodictyon sanctae-crucis* differs from *C. repens* in gross morphology of the thallus (cylindrical to compressed in *C. sanctae-crucis* and flattened to palmate in *C. repens*), and in the absence of anastomosed branches in *C. repens. Ceratodictyon sanctae-crucis* differs from *C. variabile* by the consistency of the thallus (flexible and delicate in *C. sanctae-crucis* vs. rigid and wiry in *C. variabile*), and by the absence of anastomosed branches in *C. variabile.*



Figs 3–6. *Ceratodictyon sanctae-crucis sp. nov.*

Fig. 3. Thallus habit. Scale bar = 2 cm.

Fig. 4. Habit of the thallus showing tangled branches that anastomose to other branches (arrows). Scale bar = 2 cm.

Fig. 5. Cross section of the thallus showing the larger medullary cells and loosely aggregated and the cortical cells slightly elongated to rounded. Scale bar = 30 µm.

Fig. 6. Longitudinal section of the axis showing the densely aggregated medullary filaments and gland cells occurring solitary (arrows). Scale bar = 30 µm.

To help resolve the current polyphyly of the genus *Lomentaria*, we propose a new genus to accommodate *Lomentaria hakodatensis.*

Yendoa C.C. Santos, Lyra & J.M.C. Nunes *gen. nov.*

DESCRIPTION: Plants with thallus intertangled, forming spherical to hemispherical masses in tuft, brownish-purple, 5–10 cm high, attached to the substratum by a stoloniferous discoid holdfast; hollow, very gelatinous and flaccid thallus. The thallus branches three to five times into several cylindrical to flattened axes, which divide in braches strictly opposite, verticillate or rarely alternate; with numerous anastomosing branches. Cortical and medullary layers surrounding a central cavity interrupted by multirowed cellular septa at definite intervals, gland cells attaching to innermost cells, solitary or aggregated. Tetrasporangia are tetrahedrally divided, elliptical to round, occurring in sori on inflated intersepta of branches, surrounded by filaments of modified medullary cells, which form a poorly marked network. Cystocarps scattered mostly on upper portion of the frond of the lateral branches, solitary or in groups of two or three, sessile, mammiform, spherical to pear-shaped, with prominent pores and with pericarp of stellately modified cells. Carpogonial branch three-celled, carposporangia polygonal to round, gonimoblast cells making fusion cells of trunk-like column. Spermatangia developing in sori over the whole thallus surface and developing terminally on mother cells, hemispherical to elliptical (Yendo 1920; Lee 1978; Curiel *et al.* 2006). GenBank accessions: *rbc*L, OK641579; LSU rDNA, OL348326; COI-5P, OK624113.

TYPE SPECIES: *Yendoa hakodatensis* (Yendo) C.C. Santos, Lyra, & J.M.C. Nunes *comb. nov.*

ETYMOLOGY: The generic name honours the author of the type species, *L. hakodatensis*, Dr. Kichisaburo Yendo, for his valuable contributions to phycology.

Yendoa hakodatensis (Yendo) C.C. Santos, Lyra & J.M.C. Nunes *comb. nov.*

BASIONYM: *Lomentaria hakodatensis* Yendo 1920, *Botanical Magazine, Tokyo [Shokubutsu-gaku zasshi]* 34, p. 6.

HETEROTYPIC SYNONYM: *Lomentaria sinensis* M. Howe (1924, p. 139, pl. 1, fig. 1).

LECTOTYPE: Hawkes (1986, p. 332) designated as lectotype of the species a specimen with the following annotation by Yendo: '*Lomentaria hakodatensis* Yendo, specimen original, forma typica, note No. 196, Oshoro, July 1908', deposited at the time in the University of Tokyo Herbarium (TI), Tokyo, Japan. The specimen is currently deposited at the herbarium of the Faculty of Science, Hokkaido University (SAP), Hokkaido, Japan.

TYPE LOCALITY: Oshoro, Hokkaido, Japan.

COMMENTS: According to Hawkes (1986), Yendo (1920) did not designate a holotype for *Lomentaria hakodatensis*, and the syntypes reported by him could not be located in the University of Tokyo Herbarium (TI). Thus, Hawkes (1986) designated the specimen mentioned above, from Oshoro, Hokkaido, Japan, as lectotype.

A second lectotypification was made by Yoshida (1998). Yoshida's proposed lectotype has the same no. 196, and is deposited in the herbarium of the Faculty of Science, Hokkaido University (SAP) with a different date and locatity: Yachigashira, Hakodate, Hokkaido, May 1903. However, the lectotypification by Hawkes (1986) has priority over the one proposed by Yoshida (1998). We examined images of both specimens, provided by the director of the Faculty of Science Hokkaido University's herbarium. We included a *rbc*L sequence of *L. hakodatensis* (AB793780) collected near the lectotype locality (Oshoro, Hokkaido, Japan), at Sumiyoshi, Hakodate, Hokkaido. The sequence obtained from the holotype of the heterotypic synonym *L. sinensis* was placed in the same clade as the sequence from Hakodate in the *rbc*L phylogeny, supporting the indication by Okamura (1936, *fide* Lee 1978) that *L. sinensis* and *L. hakodatensis* represent the same species.

DISCUSSION

Our results corroborate those obtained by Filloramo & Saunders (2016), showing that *Ceratodictyon, Semnocarpa* Huisman, Foard & Kraft, *Fushitsunagia* Filloramo & G.W. Saunders, *Hooperia* J. Agardh and *Stirnia* M.J. Wynne are monophyletic. *Lomentaria* was recovered as polyphyletic, with species separated into two distant clades, as previously observed (Filloramo & Saunders 2016; Wynne *et al.* 2019). One of those clades corresponded to the true *Lomentaria* clade, as it included the type species, *L. articulata*, whereas the other included sequences previously identified as *L. hakodatensis*; this clade receives generic status here, as *Yendoa gen. nov.*, and the new combination *Y. hakodatensis comb. nov.* is established for the type species. ABGD, ASAP and SPN species delimitation results from both *rbc*L and COI-5P matrices grouped all sequences of *Lomentaria hakodatensis*, including the sequence from the holotype of *L. sinensis*, considered synonymous with *L. hakodatensis*, as a single entity. Therefore, our results corroborate the synonymy of *L. sinensis* and *L. hakodatensis*, and resolve the monophyly of *Lomentaria*, with our proposal for a new genus. The new genus was placed, in our phylogenies, in a well-supported sister relationship with *Binghamiopsis caespitosa* I.K. Lee, J. A. West & Hommersand. The main character that distinguishes *Yendoa* from *Binghamiopsis* I.K. Lee, J.A. West & Hommersand is the construction of the thallus. *Binghamiopsis* lacks cellular septa and lacunae surrounded by medullary cells, whereas they are present in *Yendoa* as multirowed cell septa (Lee 1978; Lee *et al.* 1988; Curiel *et al.* 2006; Filloramo & Saunders 2016).

In the past two decades, molecular research has elucidated the evolutionary relationships of *Ceratodictyon* species (Saunders *et al.* 1999; Gavio & Fredericq 2005; Le Gall *et al.* 2008; Sherwood *et al.* 2010; Filloramo & Saunders 2016; Freshwater *et al.* 2017). Our *rbc*L and COI-5P phylogenies robustly place *Fushitsunagia catenata* as sister to *Ceratodictyon*. This result corroborates previous findings (Le Gall *et al.* 2008; Filloramo & Saunders 2016). In terms of morphology, *Ceratodictyon* species have a compact medulla, in which the cells gradually increase in size and elongate towards the interior, where the inner cortex and medulla are indistinguishable (Norris 1987, 2014; Price & Kraft 1991; Kim 2013); *Fushtisunagia*, its sister clade, has multilayered cell septa (Lee 1978; Filloramo & Saunders 2016).

ABGD results from both datasets were largely consistent, with few exceptions. For *rbc*L, it lumped most *Ceratodictyon* PSH into a single entity, a lumping tendency that has also been observed for other red algae (Jesus *et al.* 2016, 2018; Lyra *et al.* 2021). ASAP results for both datasets lumped all *Ceratodictyon* sequences into a single entity, and for the COI-5P dataset also lumped *Ceratodictyon* sequences and *Fushitsunagia catenata*, which is not consistent with morphology. Therefore, ABGD was more sensitive than ASAP in differentiating species diversity in the *Ceratodictyon* clade. For the *rbc*L dataset, SPN delimited more species entities than ABGD and ASAP. However, in the *Ceratodictyon* clade, it lumped our PSH into a single entity. For the COI-5P dataset it oversplit our PSHs. Overlumping and oversplitting results for SPN has also been observed (Jesus *et al.* 2016: Lyra *et al.* 2021). Importantly, both ABGD and SPN methods applied to the *rbc*L dataset consistently confirmed our newly proposed species *C. sanctae-crucis*.

The different results of the species delimitation methods obtained in our study are more related to the different mutation rates of COI-5P and *rbc*L than to the approach used (Muangmai *et al.* 2014; Jesus *et al.* 2016, 2018). Jesus *et al.* (2016) and Martins *et al.* (2021) recommend the use of various methods, markers with different rates of evolution, well-sampled taxa, and an integrative approach, in order to facilitate taxonomic decisions. Among our datasets, *rbc*L was useful to assess relationships among genera, while species delimitation methods applied with COI-5P were more efficient in delimitating recently diverged lineages, especially in the *Ceratodictyon* clade.

Of the nine taxonomically accepted species of *Ceratodictyon* (Guiry & Guiry 2022), some have morphological characters rarely explored in the literature (Soares *et al.* 2018). Even more infrequent are detailed descriptions of the reproductive morphology of the species (Price et al. 1984; Norris 1987; Price & Kraft 1991). The taxonomic challenges in *Ceratodictyon* are due to the high variability of its thallus morphology, and the absence of robust characters to distinguish species (Norris 1987). It is difficult to determine which characters are useful to distinguish species (Norris 1987), although the presence of anastomosed branches and the branching pattern of the thallus have been used (Soares *et al.* 2018). The presence of anastomosed branches was very important in the identification of *C. sanctae-crucis*. Our results demonstrate that the presence of anastomosed branches are not exclusive to *C. intricatum* and *C. pannosum* (Grunow) R.E. Norris (Norris 1987). *Ceratodictyon pannosum* has not been reported from the Western Atlantic (Wynne 2017), and its original description is incomplete (Grunow 1874). In the past, specimens from the Indian Ocean have been identified as *Gelidium pannosum* Grunow (the basionym of *C. pannosum*), but were only mentioned in species lists (Feldmann 1931; Silva *et al.* 1996). While both

Table 1. Comparison of the morphological characters of *Ceratodictyon* species.

Character	*C. hachijoensis*[1]	*C. intricatum*[2]	*C. pannosum*[3]	*C. planicaule*[4]	*C. repens*[5]	*C. sanctae-crucis sp. nov.*	*C. scoparium*[6]	*C. spongiosum*[7]	*C. tenue*[8]	*C. variabile*[9]
Height of habit (cm)	3.0–7.0	2.0–3.0	unknown	8.0	2.5–3.5	6.0–6.5	2.0–4.0	5.0–15	2.0–6.0	4.0–16
Thallus	erect, densely caespitose, forms cushion, cylindrical to complanate	erect, short tufts, forms cushion, very narrow, not very rigid, cylindrical to compressed	erect, strongly interwoven tufts, forms cushion, narrow, very rigid, cylindrical to flattened	erect, tough, wiry, cylindrical at base, becoming compressed distally	erect, dense tufts, firm consistency, flattened to palmate	erect, large entangled tufts, flexible and delicate, cylindrical to compressed	erect, tufts, tough, wiry, cylindrical to compressed	erect, imbricate, forms irregular cushions, subcylindrical to compressed	erect, cylindrical to compressed	erect, rigid, wiry, resistant, cylindrical, compressed to slightly flattened
Branching	dichotomous or rarely trichotomous	dichotomous, irregular to alternate	irregular and sparse	irregular and sparse	dichotomous, irregular, apices deeply divided, 3 to 4	dichotomous to trichotomous, irregular to alternate	dichotomous, rarely irregular	subdichotomous to irregular	subdichotomous, irregular, alternate to sparse	subdichotomous, dichotomous to trichotomous, irregular, alternate to opposite
Diameter of axis (µm)	unknown	130–252	unknown	280–490	260–285	250–385	250–340	100–350	250–400	240–890
No. of cell layers in axis	unknown	7–8	unknown	9–11	7–8	8–9	12–14	unknown	unknown	10–15
Cell shape of outer cortical layer	unknown	ovate	unknown	ovate	elongated to rounded	rounded to elongated	spherical, ovate to irregular	cuboidal to rectilinear	unknown	elongated and narrow
Cortical cells layer (µm)	unknown	5–7 x 8–10	unknown	7.5–12.5 × 2.5–5	3–8 x 8–12	7–13 x 8–12	5–12.5 × 2.5–7.5	2.5–7.5 x 6–15	8	3–7 x 8–16
Medullary cells layer (µm)	unknown	12–14 x 11–13	unknown	10–20 x 80	11–17 x 17–20	17–20 x 22–26	11–20 x 15–30	12–30	8–30	10–22 x 12–32
Anastomosing branches	absent	present	present	absent	absent	present	absent	present (occasionally)	absent	absent

References: 1) Yamada & Segawa 1953; 2) Kützing 1849; Norris 1987; Ballantine *et al*. 2011; Present study; 3) Grunow 1874; Schmitz 1895; 4) Littler & Littler 2000; Dawes & Mathieson 2008; Soares *et al*. 2018; 5) Nunes 2005; Nunes & Guimarães 2008; 6) Littler & Littler 2000; N'yeurt & Payri 2010; Soares *et al*. 2018; 7) Price *et al*. 1984; Price & Kraft 1991; 8) Setchell & Gardner 1924; Dawson 1953; Norris 2014; 9) Dawson 1953; Littler & Littler 2000; Dawes & Mathieson 2008; Norris 2014; Present study.

C. pannosum (as *G. pannosum*) and *C. sanctae-crucis sp. nov*. have anastomosed branches, the former has strongly interwoven tufts, forming a cushion, and wire-like axes (Schmitz 1895).

Of the nine accepted species of *Ceratodictyon*, three have been cited for the coast of Bahia: *C. planicaule* (W.R. Taylor) M.J. Wynne, *C. repens* and *C. variabile* (Nunes 2005; Nunes & Guimarães 2008). The specimens that we identified as *Ceratodictyon intricatum* have short, very narrow thalli, forming cushion and anastomosed branches, which are consistent with the South African specimens (Norris 1987). *Ceratodictyon intricatum*, therefore, constitutes a new occurrence for the Bahian coast.

Norris (1987) referred to two forms of *C. variabile* for Natal, South Africa. The first one was narrower, with cylindrical branches and also slightly compressed branches. The other form was quite flat, particularly in the median region of the thallus. Norris (1987) also examined specimens of *C. variabile* (from 'Ceylon', Sri Lanka) and *C. planicaule* (from Ilha do Governador, Rio de Janeiro, Brazil), and since he found no distinction to support different species, he proposed that the two names are synonymous. Thereafter, Littler & Littler (2000) described *C. variabile* and *C. planicaule* from the Caribbean as distinct species. Characters commonly cited for *C. planicaule* to differentiate it from *C. variabile* are the height of the thallus (above 8 cm) and the base of cylindrical and distally compressed thallus (Littler & Littler 2000; Dawes & Mathieson 2008; Soares *et al.* 2018). The descriptions of *C. variabile* vary greatly between authors and locations (Littler & Littler 2000; Nunes 2005; Dawes & Mathieson 2008; Coppejans *et al.* 2009; N'yeurt & Payri 2010; Kim 2013; Norris 2014). Although both *C. variabile* and *C. planicaule* have been reported for the coast of Bahia by Nunes (2005), we did not find *C. planicaule* among the specimens we analysed. The distinction between these two species requires further studies. In GenBank there are no *C. variabile* sequences available for COI-5P or *rbc*L, this study representing the first source of sequences of these genes for this species.

Across the Brazilian coast, *C. repens* is cited only for the coast of Bahia (Nunes & Guimarães 2008), and described as consisting of flattened, palmate and deeply divided bifurcating branches (2–4 dichotomy in the herbarium material analysed). These characters are similar to the specimens from the Fiji Islands (N'yeurt 2001). Coppejans *et al.* (2009) described *C. repens* from Sri Lanka, reporting the presence of 2–5 dichotomies in a single plane, giving the axes a typical pseudopalmate appearance. *Ceratodictyon repens* is a quite plastic species, whose characters differ greatly depending on the locality and habitat, as the morphological variability of *C. repens* appears to be controlled by environmental conditions (N'yeurt 2001).

The uniqueness of *C. sanctae-crucis* is clearly demonstrated by morphological characters. Habitat, height, morphology of the thallus and shape of the outermost cortical cells differ from *C. intricatum*, and the thallus habit and the lack of association with sponges distinguishes it from *C. pannosum*. Morphological characters of the 10 species of *Ceratodictyon* are summarized in Table 1.

Our results resolved taxonomic issues in the Lomentariaceae. Particularly, with the proposal of the new genus *Yendoa*, the currently recognized genera are rendered monophyletic. We also described a new species of *Ceratodictyon*, demonstrating the existence of added diversity of Lomentariaceae in the tropics, where intertidal and subtidal habitats are under-sampled. Investment on focused sampling of Lomentariaceae is essential to better understand their phylogenetic relationships and to identify morphological apomorphies for species delimitation within each genus, which also requires covering species distribution and environmental ranges.

ACKNOWLEDGEMENTS

We thank the Charles Davis' lab at Harvard University Herbaria for the infrastructure for obtaining plastid and mitochondrial sequences from *Ceratodictyon intricatum* and *Lomentaria sinensis*. We thank Prof. Dr. Tsuyoshi Abe of The Hokkaido University Museum and the director of the Faculty of Science Hokkaido University's herbarium, Prof. Dr. Kazuhiro Kogame, for sending us the digital images of the lectotype of *Lomentaria hakodatensis*. We also thank the reviewers for their useful comments and suggestions to improve the manuscript.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

FUNDING

This work was supported in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) under Grant 555 'Finance Code 001'. We thank Fundação de Amparo à Pesquisa da Bahia (FAPESB – RED 0006/2012; T.O. INT0001_2016), Programa de Apoio a Núcleos Emergentes (PRONEM TO PNE 0020/2011) and São Paulo Research Foundation (FAPESP – 2018/06085-1). CCS thanks Fundação de Amparo à Pesquisa da Bahia (FAPESB – T.O. B., N° BOL0416/2017) for a scholarship. VC and JMCN thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) 304141/2020-8, 308542/2018-5 for Productivity Fellowships, 304141/2020-8 and 308542/2018-5, respectively.

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