Large-scale diversity reassessment, evolutionary history, and taxonomic revision of the green macroalgae family Udoteaceae (Bryopsidales, Chlorophyta)

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Short running title: Diversity, evolution, and taxonomy of Udoteaceae

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Abstract:

Udoteaceae is a morphologically diverse family of the order Bryopsidales. Despite being very widespread geographically, this family is little known compared to the closely related Halimedaceae or Caulerpaceae. Using the most extensive Udoteaceae collection to date and a multilocus genetic dataset (*tufA, rbcL* and 18S rDNA), we reassessed the species diversity of the family, as well as the phylogenetic relationships, the diagnostic morpho-anatomical characters and evolutionary history of its genera, toward a proposed taxonomic revision. Our approach included a combination of molecular and morphological criteria, including species delimitation methods, phylogenetic reconstruction and mapping of trait evolution. We successfully delimited 62 species hypotheses, of which 29 were assigned (existing) species names and 13 represent putative new species. Our results also led us to revise the genera *Udotea* s.s*., Rhipidosiphon* s.s. and *Chlorodesmis* s.s., to validate the genus *Rhipidodesmis* and to propose three new genera: *Glaukea* gen. nov., *Ventalia* gen. nov*.,* and *Udoteopsis* gen. nov. We also identified two large species complexes, which we refer to as the "*Penicillus-Rhipidosiphon-Rhipocephalus-Udotea* complex" and the "*Poropsis-Penicillus-Rhipidodesmis* complex". Using a time-calibrated phylogeny, we estimated the origin of the family Udoteaceae at Late Triassic (ca 216 Ma), whereas most of the genera originated during Paleogene. Our morphological inference results indicated that the thallus of the Udoteaceae ancestor was likely entirely corticated and calcified, composed of a creeping axis with a multisiphonous stipe and a pluristromatic flabellate frond. The frond shape, cortication and calcification are still symplesiomorphies for most extant Udoteaceae genera and represent useful diagnostic characters.

Key words: Chlorophyta; macroalgae; species delimitation; phylogeny; trait evolution

1.INTRODUCTION

Udoteaceae J. Agardh is a family of green siphonous macroalgae belonging to the order Bryopsidales J. H. Schaffner. The family has a worldwide distribution with representatives occurring in tropical, subtropical and temperate regions throughout the Atlantic, Indian and Pacific oceans as well as in the Red Sea and the Mediterranean Sea. Udoteaceae species are most abundant in reef ecosystems where they play an important ecological function as primary producers, contribute to carbonate fluxes and provide shelter and food to other organisms (Goreau, 1963 ; Wray, 1977 ; Ries, 2006 ; Payri, 2000 ; Granier, 2012). Currently, the family, which includes both calcified and non-calcified taxa, accounts for eight extant genera and 64 species (Guiry & Guiry, 2020), if we exclude: 1) synonymized or invalid genera (*Ancestria, Neseae, Coralliodendron, Corallocephalus, Espera* (syn. of *Penicillus*); *Decaisnella* and *Geppina* (syn of. *Udotea*); *Flabellaria* J. V. Lamouroux (syn. of *Flabellia*); *Rhipidodesmis* (syn. of *Chlorodesmis*); *Poropsis* Nizamuddin (uncertain) and *Flabellaria* Lamarck (nom. illeg.)) ; and 2) genera previously shown to be unrelated to the Udoteaceae (*e.g., Botryodesmis, Pseudochlorodesmis* and *Siphonogramen* (Verbruggen et al. 2009a); *Boodleopsis*, *Callipsygma* and *Johnson-sea-linkia* (Cremen et al., 2019); *Chloroplegma* (syn. of *Avrainvillea*; Wade et al 2018), *Rhipiliella* (probably belonging to Rhipiliaceae; Dragastan et al., 1997). A total of 20 species included in these genera can then be subtracted from the overall species diversity previously included in the Udoteaceae.

Although they are all siphonous and composed of a unique giant and multinucleate tubular cell, Udoteaceae genera are remarkable for their morphological diversity. Their forms range from dichotomous filaments, single or grouped in tufts, to more complex thalli with characteristic frond morphologies (*e.g.,* capitate for the genus *Penicillus* or flabellate for *Udotea*).

Since its publication by Agardh (1887), the most comprehensive work on Udoteaceae was published by Gepp & Gepp (1911). Several authors have subsequently contributed to improving knowledge of species diversity (Farghaly, 1980; Meinesz, 1980; Littler & Littler, 1990a and b; Vroom et al., 1998;

Collado-Vides et al., 2009), and with the discovery of new species and the increase in morphological information, several authors have discussed the need to redefine genera (Agardh, 1887; Gepp & Gepp, 1911; Nizamuddin, 1963; Farghaly, 1980; Littler & Littler, 1990a; Dragastan et al., 1997). The few molecular-based studies conducted on Udoteaceae have highlighted conflicts between morphological and molecular information, revealing polyphyletic genera (*i.e., Chlorodesmis, Penicillus, Poropsis, Rhipocephalus, Rhipidosipon* and *Udotea*) and unresolved phylogenetic relationships for most taxa (Kooistra, 2002; Lam & Zechman, 2006; Curtis et al.; 2008; Verbruggen et al., 2009a and b; Coppejans et al., 2011; Lagourgue et al., 2018; Wade & Sherwood, 2018; Cremen et al., 2019). When reassessing the classification of the order Bryopsidales using the chloroplast genome, and to avoid proliferation of new families with a parsimonious and practical purpose, Cremen et al. (2019) proposed to abandon the Udoteaceae family in favor of tribe Udoteae, which the authors placed in family Halimedaceae Link together with other families such as Rhipiliaceae Kützing and Pseudocodiaceae L. Hillis-Colinvaux, and the genus *Halimeda*. However, we believe that this decision overlooked morpho-anatomical variability and existing genera and species diversity in the clade that we therefore prefer to maintain as the family Udoteaceae. Indeed, studies on closely related families (Halimedaceae, Caulerpaceae Kützing) revealed unexpected species diversity (Verbruggen et al., 2005a and b; Sauvage et al., 2013) and highlighted the existence of new lineages at the family level with low morphological differentiation (Sauvage et al., 2016; Verbruggen et al., 2017, Cremen et al., 2019). This contrasts sharply with the family Udoteaceae, whose rich species and genus diversity remains to be reassessed. The genetic data available for Udoteaceae is fragmentary (122 sequences for *tufA, rbcL* and 18S rDNA) and is limited to 26 of the current 64 species, often with only one sequenced marker per specimen and some level of misidentification. Numerous tools have been developed to assess diversity and delimitate species that are now largely applied across various macroalgal taxa. These include tree-based methods such as the General Mixed Yule Coalescent (GMYC) (Pons et al., 2006) and its Bayesian implementation, bGMYC (Reid & Carstens, 2012), the Poisson tree process model (PTP, Zhang et al., 2013) and the Multi-rate version,

mPTP (Kapli et al., 2017), as well as methods directly relying on genetic distances, such as the Automatic Barcode Gap Discovery (ABGD, Puillandre et al., 2012a). For robust species hypothesis, several authors have recommended to search for congruence between the different methods applied to several genes (Carstens et al., 2013; Carstens & Knowles, 2007; Dupuis et al., 2012; Leliaert et al., 2014; Puillandre et al., 2012b; Rannala, 2015) and to compare molecular-based partitions with non-genetic data (Carstens et al., 2013; Carstens & Knowles, 2007; Fujita et al., 2012; Talavera et al., 2013; Wiens, 2007).

Additionally, the large morphological diversity of Udoteaceae genera and species illustrates a complex pattern of diversification within the Bryopsidales, which has led to several hypotheses on the morphology of its ancestor (Gepp & Gepp, 1911; Littler & Littler, 1990a; Vroom et al., 1998; Kooistra, 2002). To date, these hypotheses remain untested (*e.g.,* calcified or uncalcified ancestor), and the family represents an original and interesting case study for an evolutionary approach. Analytical methods, including statistics (Dubois, 2007; Rabosky et al., 2013) make it possible to analyze the phylogenetic evolution of morphological characters and the genotype/phenotype correlation by measuring, for example, the phylogenetic signal of morphological characters. The phylogenetic inference of trait evolution is another relevant approach, which has been little used for the study of macroalgae, with only three studies applied to green siphonous macroalgae (*Codium* (Verbruggen et al., 2007); *Halimeda* (Verbruggen et al., 2009c) and *Pseudocodium* (Payri & Verbruggen, 2009)). By using this approach, it is possible to explore the evolution of morpho-anatomical characters both in time and across lineages and to test hypotheses about the ancestral state of various characters. It is then possible to highlight relevant characters to discriminate groups of species or specific morphological patterns, which together allow a better understanding of the evolutionary history of the taxa studied. Phylogenetic inference of trait evolution is therefore of particular interest, among others, for integrative taxonomy approaches based on data of various origins (molecular, morphological, ecological, functional data, etc.) (Dayrat, 2005; Schlick-Steiner et al., 2010; Garbino, 2018).

Using the largest Udoteaceae taxon sampling to date and a multilocus genetic dataset (*tufA, rbcL* and 18S rDNA), we aim to reassess the species diversity of the family, the phylogenetic relationships, the diagnostic morpho-anatomical characters of its genera, as well as the morphological and evolutionary history of the lineages, and to provide the necessary taxonomic revisions. To reach these objectives, we use a combination of molecular and morphological approaches, including species delimitation methods, phylogenetic reconstruction, time-calibrated analyses and inference on the evolution of morpho-anatomical characters.

2. Material and Methods

2.1 Sampling

Samples were collected using SCUBA down 60 m deep or snorkeling from various localities worldwide including in the Atlantic, Indian and Pacific oceans as well as the Red Sea and the Mediterranean Sea. A total of 644 samples were processed in this study, including 527 samples collected by the authors and 117 obtained through collaborations (Table S1 in Supporting Information). Vouchers were pressed-dried on herbarium sheets and housed in various herbariums, including NOU in New Caledonia, PC in France and GENT in Belgium (herbarium abbreviations follow Thiers (2019), continuously updated). Subsamples of the fresh specimens were preserved in a 5% formaldehyde solution in sea water for later morpho-anatomical observations and both in 95% ethanol and silica gel for later DNA extractions.

2.2 Morphological characters and analyses

Morpho-anatomical observations were made on fragments preserved in formaldehyde or directly on herbarium specimens. Calcified specimens were previously treated with a 5% hydrochloric acid solution for 1 to 2 hours. Observations and measurements were made using an A2 Imager microscope (Axio) fitted with a Canon EOS-100D camera. Photos of macroscopic characters were

made using a binocular microscope (Wild M3Z) equipped with a Canon EOS-700D camera. All morpho-anatomical characters reported in previous studies were considered (Gepp & Gepp, 1911; Littler & Littler, 1990a, b; Ducker, 1967; Coppejans et al., 2011). A selection of 30 discrete (10 binary and 20 multivariate) and two continuous characters were analyzed, including morphological (*e.g*., thallus, stipe, frond shape, attachment type) and anatomical characters (*e.g.,* siphon diameter and form, branching type, secondary structures). For each species, the different states of character were encoded into a matrix without ordination or weight. All character states are synthesized in Supporting Information (Data S1).

2.3 DNA sequencing and alignment

Samples were extracted using either the Plant mini Kit (Qiagen Inc, Valencia, CA, USA) (for *Chlorodesmis*), the Blood and Tissue Kit (Qiagen Inc, Valencia, CA, USA) (for calcified genera*, i.e., Udotea, Penicillus, Rhipocephalus, Tydemania*) or the CTAB protocol (for *Rhipidosiphon* and *Poropsis*). Two chloroplast markers were targeted, *tufA* and *rbcL*, as well as the 18S rDNA nuclear gene using previously published primers (Händeler et al., 2010; Kooistra, 2002; Lam & Zechman, 2006; Verbruggen et al., 2009b) (see Table S2). PCR reactions were conducted in a final volume of 25 µL including 12.5 µL of AmpliTaq Gold 360 Master Mix (Applied Biosystems), 1 µL of each primer (10 µM), 0.75 µL of dimethylsulfoxyde (DMSO), 1 µL of bovine serum albumin (BSA), 2.5 µL of DNA and 6.25 µL of ultra-pure water. PCR programs follow Lagourgue et al. (2018). The Sanger sequencing reaction was carried out using 20 µL of PCR product by Genoscreen (Lille, FRANCE). Sequences were then edited in Geneious version 7.1.9 (http://www.geneious.com, Kearse et al., 2012) and aligned for each marker separately using the MUSCLE algorithm available in the software. Sequences obtained from collaborators and Genbank were added to our dataset. As far as possible, a maximum of specimens from the type localities have been included in the analyses. When none was available, Genbank sequences that did not come from the type localities were considered with caution for the risk of misidentification by previous authors.

164 **2.4 Composition of the datasets**

165 The two chloroplasts markers, *tufA* and *rbcL,* known for their discriminatory power at the species
166 level in green macroalgae (Leliaert et al., 2014; Saunders & Kucera, 2010; Verbruggen et al., 2009b)
167 were selected for species delimitation analyses. Maximum Likelihood (ML) and Bayesian ultrametric
168 trees were reconstructed from single marker alignments, after removing identical haplotypes using
169 the Collapsetypes v4.6 perl script (Chesters, 2013). Outgroup taxa (see Table S3) were also removed
170 before running species delimitation analyses.

171 In addition, two different concatenated multilocus matrices (*tufA*, *rbcL* and 18S rDNA) were compiled
172 to perform phylogenetic analyses. The first was composed of several specimens per species, for
173 which at least two of the three markers were available, to assess the taxonomic position and
174 composition of the different Udoteaceae genera. The second dataset corresponded to a selection of
175 one specimen per species (as defined by the species delimitation approach) and was intended for
176 evolutionary analyses and time-calibrated phylogeny. A total of ten outgroup species were added to
177 the second dataset to ensure proper phylogenetic calibration (see Table S3).

178 **2.5 Tree inference**

179 Prior to the phylogenetic analyses, each dataset was analyzed with Partition Finder v1.1.0 (Lanfear et
180 al., 2012) to determine the best partition schemes and the most suitable evolutionary models based
181 on the Akaike information criterion (AIC). As the sequencing success was uneven between the two
182 parts of the *rbcL* gene, we chose to consider them separately (as *rbcL5'* and *rbcL3*') to improve the
183 modelling.

184 For each dataset, ML trees were reconstructed using RAXML (Stamatakis, 2014) through the CIPRES
185 web portal (Miller et al., 2010). ML analyses were launched using the "rapid bootstrapping and
186 search for the best-scoring ML tree" algorithm, the GTR+I+G evolutionary model and 1,000 bootstrap
187 (bs) iterations (Stamatakis et al., 2008).

188 Bayesian ultrametric trees (for species delimitation analyses) were estimated using BEAST
189 (Drummond et al., 2012) through the CIPRES web portal. Two independent analyses of 30 and 40
190 million generations were run for *tufA* and *rbcL*, respectively, and sampled every 1,000 generations.
191 The Likelihood ratio test, using MEGA 6 (Tamura et al., 2013), rejected the null clock hypothesis;
192 trees were, therefore, estimated using a relaxed lognormal molecular clock (Drummond et al., 2006)
193 with a coalescent constant size tree prior as recommended by Monaghan et al. (2009).

194 The Bayesian inference (BI) on the multilocus matrix (*tuf*A, *rbc*L, and 18S) composed of several
195 specimens per species, was performed using MrBayes v.3.2 (Ronquist & Huelsenbeck, 2003) through
196 the CIPRES portal. The analysis was carried out in two independent runs of four incrementally heated
197 chains of 50 million generations, sampled every 1,000 generations, with a burn-in set at 10 %.

198 The time-calibrated phylogeny was carried out using BEAST v.2.5.0 (Bouckaert et al., 2014) through
199 the CIPRES web portal. It was estimated under a Calibrated Yule model (Heled & Drummond, 2012)
200 and a relaxed lognormal molecular clock (Drummond et al., 2006). Two independent analyses were
201 run for 75 million generations and sampled every 10,000 generations.

202 For all Bayesian analyses, each run output was checked in Tracer v.1.5 (Rambaut & Drummond, 2007)
203 to confirm the convergence of the Markov Chains Monte Carlo (MCMC) and that effective sample
204 size (ESS) values were all above 200, before computing a consensus topology and posterior
205 probabilities. For Beast trees, the outputs were combined using Log Combiner (included in the BEAST
206 package), removing the first 10% generations as burn-in. The Maximum Clade Credibility Tree (MCCT)
207 was calculated using Tree Annotator (included in the BEAST package).

208 Outgroup taxa, partition schemes, evolutionary models, and reconstruction parameters for all ML
209 and BI trees are detailed in Table S3 (Supporting Information).

210 **2.6 Species delimitation methods**

Five species delimitation methods were used to assess the Udoteaceae species diversity based on the chloroplast markers: ABGD, GMYC, bGMYC, PTP and mPTP. The species delimitation process then consists of comparing the different primary species hypotheses (PSHs) resulting from the species delimitation methods, and searching for congruence between the different markers analyzed to define secondary species hypotheses (SSHs). In case of conflicts, a majority rule was applied, and the most prevalent PSH was selected. Morpho-anatomical observations were then compared to molecular-based species hypotheses to confirm SSHs, as well as to assign species names when possible.

The ABGD method was applied to both *tufA* and *rbcL* alignments through the website: http://www.abi.snv.jussieu.fr/public/abgd/abgdweb.html. The Kimura model (relative minimum gap width (X) = 1) was used for the *tufA* analysis, while the JC (X = 0.5) and the SD models (X= 1) were preferred for analysing the *rbcL*5' and *rbcL*3' fragments, respectively. All other parameters were used with default values. GMYC was performed using the package "splits" in R (R Development Core Team, 2019) on bayesian MCCTs. The bGMYC method was applied using the "bGMYC" package (Reid & Carstens, 2012) also in the R environment on a subsample of 100 BEAST trees. The analyses were carried out on 10,000 and 15,000 MCMC generations, sampled every 100 generations, for *tufA* and *rbcL*, respectively. The PTP method was conducted through the Exelixis Lab web server (http://sco.h-its.org/exelixis/web/software/PTP/index.html) on the ML rooted tree and run for 500,000 generations for both *tufA* and *rbcL*, sampling every 1,000 generations and without considering the outgroups. Finally, mPTP was carried out on the mPTP web server (http://mPTP.hits.org) both on bayesian MCCTs and ML rooted tree with default settings for all parameters.

2.7 Time calibration points

For reconstruction of the time-calibrated phylogeny, three calibration points derived from fossil information were used (Table S4): 1) *Halimeda soltanesis* - 250 million of years (Ma) (Poncet, 1989), 2) *Caulerpa* sp. - 280 Ma (Gustavson & Delevoryas, 1992), and 3) *Pseudopenicillus aegaeicus* - Late

Triassic (Dragastan et al., 1997). Due to the lack of convergence of runs and low ESS values during preliminary analyses, likely because of bias in paleontological dating and/or erroneous phylogenetic placement, we choose not to consider the age of the fossil *Udotea palmetta* (Fiore, 1936). These calibration points were set with uniform distributions and minimal age corresponding to the estimated age of the fossil (*cf.* Table S4). Three additional calibration points were selected from the study of Verbruggen et al. (2009b): 1) Bryopsidales root – 456 Ma, 2) Crown of Core Halimedineae – 391 Ma, and 3) Crown of Halimedaceae + Pseudocodiaceae + Udoteaceae – 273 Ma. They were constrained using corresponding ages and normal distributions (*cf.* Table S4 for more details).

2.8 Phylogenetic signal and correlation analyses

The phylogenetic signal is based on the assumption that phylogenetically related organisms tend to resemble each other phenotypically. In this study, the phylogenetic signal was measured to identify whether a morphological trait followed this trend or appeared more labile and unpredictable. Our aim was to assess the relevance of each trait to provide revised morphological descriptions. For the continuous characters, the phylogenetic signal (PS) was estimated with Blomberg's K (Blomberg et al., 2003) and Pagel's λ (Pagel, 1999) statistics using the "phylosig" function of the phytools package (Revell, 2012) in R. These two measures quantify trait variation with respect to the "random walk" model of the Brownian motion (BM). If K=1, the PS is strong and in accordance with the BM model; if K<1, the PS is lower than under the BM model; if K=0, there is no PS (the trait evolves independently of the phylogeny); if K>1, the PS is stronger than expected under the BM model (close species are more similar than expected under the BM). If λ equals or is close to 0, there is no PS; if λ=1, the PS is strong (the trait evolves following the BM model); if 0< λ<1, a PS exists, but the trait does not evolve according to the BM model and probably follows another process (*e.g.,* Ornstein-Uhlenbeck, OU). The evolutionary model best adapted to the trait evolution (BM, OU or the "early-bust" model) was tested using the "geiger" package (Harmon et al., 2008). For discrete characters, the PS was estimated with the phylogenetic D statistic (Fritz & Purvis, 2010) using the function "phylo.d" of the

261 "caper" package (Orme et al., 2013) in R. The D statistic calculates the ratio between the sum of the
262 sister clade differences, from which the BM expectation is extracted, and the difference between a
263 random estimate and the BM expectation. If D<0, the trait has a strong PS; if D>0, the trait has a PS
264 lower than expected with the BM model.

265 The correlation between discrete characters was computed using the function "fitpagel" of the
266 "phytools" package (Revell, 2012). For continuous characters, the phylogenetic generalized least
267 squares (PGLS) was calculated with the "nmle" package.

268 Multivariate discrete characters were converted to binary for estimating the D statistic (PS) and
269 Pagel's test of correlation (see Data S1 for transformation).

270 **2.9 Ancestral states reconstruction**

271 To infer trait evolution on the phylogeny, we used the time-calibrated phylogeny of the family
272 reconstructed from the concatenated multilocus matrix and the characters matrix produced from the
273 morpho-anatomical observations. Ancestral state estimations were computed using the "phytools"
274 package (Revell, 2012). The "contMap" function was used for the continuous characters, while
275 estimations for discrete (binary and multivariate) characters were calculated using the
276 "make.simmap" function with 1,000 simulations. Equal probability was applied to each state of
277 character that was either missing or had a non-applicable (N.A.) value.

278 Based on the combination of molecular and morpho-anatomical data and using a likelihood criterion
279 and a defined number of iterations, these analyses reconstruct the ancestral state estimated at each
280 node for each character selected. The ancestral state estimation, therefore, represents the
281 probability of the different states of a given character at each node of the tree. This allows
282 identifying the status and taxonomic relevance of the morphological characters studied.
283 Synapomorphies (*i.e.*, derived states shared by at least two taxa and inherited from a common
284 ancestor) are useful in the taxonomic review process at genus-level and for documenting diagnoses.
285 Homoplasies (*i.e.*, similar states of character found between different species, which do not originate

from the same ancestor) cannot be used for species diagnoses, but provide information on the evolutionary history of a particular trait and allow to explore its evolutionary pattern.

3. RESULTS

3.1 Genetic variability

A total of 1,056 sequences were obtained in this study, including 518 *tufA* sequences (852 base pairs, bp), 397 *rbcL* sequences (1,365 bp-long, including 763 bp of the *rbcL*5' fragment and 602 bp of the *rbcL*3' fragment), and 141 18S rDNA sequences (1,226 bp). The *tufA* dataset had 179 unique haplotypes and 482 variables sites (57.24 %). The *rbcL* dataset had 139 unique haplotypes and 496 variables sites (36.3 %), with the *rbcL*5' and *rbcL*3' fragments accounting for 287 (37.61%) and 209 variable sites (34.72%), respectively. Finally, the 18S rDNA dataset had 222 variables sites (18.10%). From our dataset, *tufA* appeared more variable than *rbcL*. The *rbcL5'* fragment was more variable than the *rbcL*3' fragment, which corroborates the results of Lagourgue et al. (2018) for the Caribbean Udoteaceae species, and contrasts with other studies on Bryopsidales families, for which the *rbcL3'* fragment appeared more variable and informative than *rbcL5'* (Saunder & Kucera, 2010).

A total of 422 sequences have been submitted to the Genbank under accession numbers MT324398-MT324484 for 18S rDNA sequences, MT339592-MT339713 and MT456567-MT456591 for *rbcL* sequences and MT340305-MT340496 for *tufA* sequences (see Table S1).

3.2 Species delimitation and name assignment

3.2.1 Primary Species Hypotheses (PSHs): Results obtained with the five delimitation methods for the *tufA* and *rbcL* datasets are summarized in Table 1 and are available in more detail in Supporting Information (Figures S1 & S2 and Data S2). The PSHs support values of the hPTP method and the *a posteriori* probabilities (PP) of bGMYC partitions are also given in Supporting Information (Data S3 & S4 and Tables S5 & S6, respectively). The five methods recovered between 39 and 53 PSHs for *tufA*, and between 48 and 56 PSHs for *rbcL*. Among those, a total of 23 and 35 PSHs were shared between

the five methods for *tufA* and *rbcL*, respectively. Several incongruences were found between the five methods results for *tufA* as well as for *rbcL* (Figures S1 and S2 respectively). For the *tufA* dataset, most discrepancy was found for the delimitation of *Udotea* spp. (clades 24 to 29 and clades 38 & 39) and *Chlorodesmis* spp. (clades 17 & 59) (Fig. S1). Similarly, for the *rbcL* dataset, most incongruences were also found for delimitating some *Udotea* spp. (clades 26 to 29) and *Chlorodesmis* species (clades 17, 21,22 and 59) (Fig. S2). For both markers, the GMYC and bMGYC methods were the most conservative, whereas hPTP tended to over-split clades.

3.2.2 Secondary Species Hypotheses (SSHs) and assignment: Based on the common PSHs of the five species delimitation methods (see Table S7) or the majority rule**,** a total of 50 and 54 SSHs were retained for *tufA* and *rbcL*, respectively, out of which 42 SSHs were common between the two markers. Most of them (24) were congruent between markers and with morpho-anatomical observations and were, therefore, retained as valid species hypotheses. Some of the remaining SSHs, which were not congruent between markers, were resolved using morpho-anatomical observations (15), while others require further data and analysis (3). Table S8 (Supporting Information) provides details on the incongruence resolution process, conclusions and species assignment.

Altogether, 62 SSHs were retained for the two markers combined. Among these, 29 SSHs were identified to species level, five SSHs still require confirmation, and 13 SSHs could represent species new to science. Another 15 SSHs were represented by sequences downloaded from the Genbank or provided by collaborators, for which morpho-anatomical data were unavailable to confirm species name assignment. Genera and species name assigned to the different SSHs are detailed in the Supporting Information (Figures S1 & S2, Table S1).

3.3. Phylogenetic relationships and evolution

Our concatenated multilocus matrix (3,443 bp) included sequences for a total of 145 specimens, which represented 43 genetically delimited species from several localities around the world from which specimens had never been sequenced. The ML and BI phylogenies resulting from our analyses

(Fig. 1) provide new insights into the phylogenetic relationships of Udoteaceae taxa. They produced a total of ten well supported "terminal" clades corresponding to five Udoteaceae genera recorded as current taxonomically by Guiry & Guiry (2020) (*i.e., Udotea, Rhipidosiphon, Chlorodesmis, Tydemania, Flabellia*). Our results confirmed the polyphyly and paraphyly of the genera *Udotea, Chlorodesmis, Rhipidosiphon, Rhipocephalus,* and *Penicillus* as already pointed out in previous studies (Kooistra, 2002; Lam & Zechman, 2006; Curtis et al.; 2008; Verbruggen et al., 2009a and b; Coppejans et al., 2011; Lagourgue et al., 2018; Wade & Sherwood, 2018; Cremen et al., 2019). Only *Tydemania* and the monospecific genus *Flabellia* were monophyletic. The genus *Poropsis* is represented by only one species in this multilocus phylogeny, therefore we could not confirm its monophyly (but see the multiples *Poropsis* lineages retrieved in gene trees used for species delimitation analyses (Fig. S1 & S2), and which do not form a monophyletic clade). Although similar conclusions were reported in the literature previously, limited data and unresolved phylogenetic relationships prevented the authors from drawing taxonomic conclusions (Kooistra, 2002, Curtis et al., 2008, Lam & Zechman,2006; Verbruggen et al., 2009b, Lagourgue et al., 2018). In our analyses, the family Udoteaceae was monophyletic (as defined in the introduction) with high node support (bs: 93; PP: 1) (Figure 1.A). This result contrasts with previous studies where *Tydemania* was more closely related to Pseudocodiaceae than Udoteaceae (Verbruggen et al., 2009b; Sauvage et al., 2016) but corroborates the results of Cremen et al. (2019) (see nevertheless the differences between the chloroplast genes tree (*tufA* and *rbcL*) (Figures S3) which is similar to the concatenated multilocus topology (Fig. 1), and the nuclear 18S rDNA gene tree (Figure S4), where Udoteaceae is not monophyletic (*Tydemania* and *Flabellia* branch with *Pseudocodium* species, although not supported). Here, using node support, the phylogenetic position of type species, the congruence of morphological characters, original diagnoses, published observations and/or proposals, as well as the ancestral character reconstruction, we selected nine clades (A-I, collapsed in Figure 1.B) on which we based our taxonomic revision proposal. Our findings led us to consider clades A, B, D and F, which contained type species for *Tydemania*, *Udotea, Chlorodesmis* and *Rhipidosiphon*, respectively, as

representatives of current genera, for which we propose to redefine the taxonomic boundaries. Our data also indicate that clades C, E, and G represent lineages requiring the establishment of new genera (*Glaukea* gen. nov*., Ventalia* gen. nov. and *Udoteopsis* gen. nov., respectively), while the taxonomic status of clades H and I (the "*Penicillus-Rhipidosiphon-Rhipocephalus-Udotea* (PRRU) complex" and the "*Poropsis-Penicillus-Rhipidodesmis* (PPR) complex", respectively) remains unclear (see further below for discussion and diagnoses).

The time-calibrated phylogeny of the family Udoteaceae was reconstructed from the concatenated multilocus matrix (*tufA*, *rbcL* and 18S rDNA) and results are shown in Figure 2. This tree is similar to that shown in Figure 1 and node support is higher for the Bayesian inference than the maximum likelihood method. The revised and new genera (*Chlorodesmis* s.s., *Rhipidosiphon* s.s., *Udotea* s.s., *Glaukea* gen. nov., *Ventalia* gen. nov. and *Udoteopsis* gen. nov.) were all monophyletic with strong node support (bs > 90; PP >0.98) (but see the nuclear tree, where *Rhipidosiphon* is polyphyletic; Fig S4)). Results indicate a divergence between the families Halimedaceae and Pseudocodiaceae/Udoteaceae around 288 Ma (Permian, Paleozoic), while the divergence between the families Pseudocodiaceae and Udoteaceae is around 246 Ma (Late Triassic, Mesozoic). The origin of the Udoteaceae is estimated at about 216 Ma (Late Triassic), but its diversification began around 109 Ma (Early Cretaceous). The most recent speciation event is dated at 3.5 Ma, but most of the extant species originated from diversification events during the Cenozoic (from ca 59 Ma) (Figure 2).

3.4. Phylogenetic signal, correlation and ancestral reconstructions of morpho-anatomical characters

The analysis of morphological characters according to the phylogeny and the ancestral reconstructions allowed us to understand the ancestral character states better and to identify those relevant for our taxonomic proposal and revision.

Analysis of the phylogenetic signal for the two continuous traits by the Pagel's λ test indicated the presence of a strong phylogenetic signal following a BM model for the stipe siphon diameter and a

386 phylogenetic signal according to a model other than a BM for the frond siphon diameter (Tables S9).
387 The Blomberg's K test also found a phylogenetic signal for both traits, but weaker than in a BM model
388 (Table S9). Of the 27 discrete characters, 17 had a phylogenetic signal (Table S10), while 10 had no or
389 weak phylogenetic signal. The highest scores (D statistics) were found for: growth mode, type of
390 constrictions and absence or presence of a stipe (-2.05, -1.25 and -0.96, respectively); the lowest PS
391 values were found for: stipe ramification (1.04), type of dichotomies (1.36) and stipe siphon aspect
392 (1.79). Overall, the phylogenetic signal analyses revealed strong correlations with the phylogeny for
393 the majority of characters studied. Still, several of those traditionally used to distinguish between
394 Udoteae genera had a weak PS, including stipe shape, frond composition, branching pattern, siphon
395 aspect, type of dichotomy and presence or absence of constrictions. On the other hand, the external
396 habit or the type of constriction, which are characters rarely considered, appeared remarkable for
397 their strong phylogenetic signal. Similarly, calcification and thallus cortication also had strong PS,
398 which confirms their taxonomic relevance for the classification of Udoteaceae genera.

399 Our analyses of trait correlations also provided several interesting results which are detailed in Table
400 S11 and Data S5 (Supporting Information).

401 Finally, the ancestral state reconstruction results are provided in Supporting Information (Data S5)
402 with a summary of correlated characters, ancestral state estimation and the putative
403 synapomorphies, symplesiomorphies or homoplasies. Table 2 reports the results for discrete
404 characters that are the most relevant because 1) they show a PS; 2) the ancestral state could be
405 estimated for the Udoteaceae ancestor; and 3) homoplasies, synapomorphies or symplesiomorphies
406 could be identified (see Table S12 for these results for all the characters studied). Figure 3 presents
407 ancestral state reconstruction of four characters, that we consider the most important for
408 understanding the evolution of the Udoteaceae and revising the taxonomy of its genera. Frond shape
409 (Fig.3. A), thallus cortication (Fig 3.B), presence or absence of calcification (Fig. 3.C) and secondary
410 structures on frond siphons (Fig. 3.D) (all other characters are presented in Data S5).

411 The ancestral state (plesiomorphic) was identified for a total of 26 characters (Table S12). We also
412 found several homoplasies (convergent or parallel), as well as cases of regression or
413 synapomorphies, providing important information on the evolutionary trajectories of the different
414 characters. Additionally, we found that several characters states traditionally referenced in genus
415 diagnoses appeared to represent varying degrees of homoplasy. This is particularly true for the
416 presence of pores on the calcified surface of siphons (*e.g.*, *Rhipidosiphon* s.s.*, Penicillus, Poropsis*),
417 the alignment of dichotomies (*Rhipidosiphon*), the capitate frond of "*Penicillus*" (Figure 3.A), or some
418 characters used to identify species such as the branching of the stipe (*e.g.*, *Flabellia petiolata, Udotea*
419 *dixonii*, etc.), and the presence of descending lateral siphons (*Udotea glaucescens*, *R.*
420 *lewmanomontiae*) (Data S5). Our results also reveal, for the first time, that many states of character,
421 which used to be considered relevant and diagnostic of genera in previous Bryopsidales studies (*e.g.,*
422 the flabellate form, the presence of a stipe, total cortication, or total calcification) actually represent
423 symplesiomorphies within the family Udoteaceae (*i.e.,* states inherited from the family's ancestor
424 and maintained throughout evolution) (Fig. 3. A. to D and Data S5). The presence of these ancestral
425 states (plesiomorphic) is contrasted between genera, but they often still represent the majority of
426 the states observed. The most symplesiomorphic genera are *Flabellia, Udotea* s. s. and *Glaukea* gen.
427 nov. Conversely, the genera with the most derived states (homoplasies and synapomorphies) are
428 *Tydemania, Chlorodesmis* s.s. and *Rhipidodesmis* s.s.

429 All major findings for taxonomical purpose are reported for each genus in the following sections (4.3)
430 and corresponding figures (see Figures 4, 6, 7 and 9) and are also discussed in sections 4.2.1 to 4.2.5.

431

432 **4. DISCUSSION**

433 **4.1. Udoteaceae phylogenic evolution and diversity**

434 The topology of the time-calibrated phylogeny (Figure 2), based on one representative per species,
435 appeared similar to our comprehensive ML phylogeny (Fig. 1) and the proposed revised genera were

436 all monophyletic with strong node support (bs > 90; PP> 0.98). According to our results, the origin of
437 Udoteaceae dates back to about 216 Ma (Late Triassic), which corroborates the work of Verbruggen
438 et al. (2009b) and the calibration points used for the reconstruction. The divergence between the
439 families Halimedaceae and Udoteaceae/Pseudocodiaceae is estimated to about 288 Ma, which
440 corresponds to the Permian (Paleozoic) and Udoteaceae latter diverged from Pseudocodiaceae
441 during the Late Triassic (ca 246 Ma, Mesozoic). Most of the Udoteaceae genera originated during the
442 Paleogene (*i.e.*, between ca 66 and 23 Ma) and the most recent speciation event was estimated
443 around 3.5 Ma (Figure 2).

444 Our results also shown that for taxa of the family Udoteaceae, *tufA* and *rbcL*5' alone appear sufficient
445 to assess the variability at species-level and can be used as "barcodes". However, for a larger genetic
446 or phylogenetic analysis (several families or the order Bryopsidales), we recommend using *tufA,* and
447 the whole *rbcL* marker (or the *rbcL*3' fragment instead of the *rbcL*5') so that results can be compared
448 to previous studies. In contrast, the 18S rDNA was less variable than the chloroplast markers and,
449 therefore, does not represent a good choice for species delimitation analyses.

450 Our results also demonstrate that the family Udoteaceae has high morphological complexity and
451 large species diversity, although this is not homogeneous across clades. Kooistra (2002) had already
452 pointed out to different genetic and morphological patterns within the family Udoteaceae with: 1)
453 fully corticated taxa being morphologically similar ("poor" in diversity), and corresponding to older
454 lineages with slower phenotypic diversification; and 2) uncorticated genera showing rapid
455 cladogenesis with considerable phenotypic changes between related species. This latter case of
456 diversification is found mainly in the "PRRU complex". The complex is monophyletic and
457 geographically restricted. However, it has many homoplasies with other taxa outside the clade that
458 are geographically disconnected, which illustrates parallel genetic and morphological evolutions. The
459 large morphological diversity of the Udoteaceae could thus be interpreted as a phenotypic

evolvability (*i.e.,* the ability of lineages to evolve with the production of morphological and ecological novelties) that promotes speciation (Pigliucci, 2008; Adamowicz et al., 2008).

Finally, the analysis of the evolutionary history of the Udoteaceae provides a better understanding of its very significant diversity, both in terms of species and genera, which has long been underestimated but which is demonstrated here, through our results. Although there is no family or tribe concept that is commonly accepted, we question the need for the revisions proposed by Cremen et al. (2019), where such a species and genus rich family as Udoteaceae was downgraded to tribe. Ultimately, whether one prefers Udoteaceae or Udoteae should not jeopardize the following proposed taxonomic revision of the genera.

4.2. Morphological evolution

Through phylogenetic signal and correlation analyses, as well as the inference of morpho-anatomical trait evolution on phylogenies, seven characters appeared as the most relevant for taxonomic purposes as well as for the macroevolutionary models they represent. These characters (and their most relevant states) are: the frond shape (particularly the “flabellate”, “capitate” and “caespitose” states) (Fig.3. A.), the thallus cortication (particularly the “total thallus cortication” state) (Fig. 3. B), the presence or absence of calcification (both states) (Fig. 3. C), the presence or absence of stipe (both states), the presence or absence of pores on calcified siphons sheath (both states), the secondary structures on frond siphons (particularly the “appendages” state) (Fig. 3. D) and, finally, the type of supra-dichotomial constrictions (the “symmetrical” and “asymmetrical” states).

In the following sections, we use these characters and other results of our study to discuss various hypotheses about the evolution of the family Udoteaceae.

4.2.1 ***What did the Udoteaceae ancestor look like?*** According to our results (*cf.* Data S5), the Udoteaceae ancestor may have had a creeping axis with a multisiphonous non-ramified stipe and a

484 single pluristromatic flabellate frond (Fig. 3. A), all continuously joined together. It may have been
485 entirely corticated (stipe and frond) (Fig. 3. B) and calcified (Fig. 3. C), but the siphons' sheath may
486 have been non-porous. The siphons' ramifications may have been dichotomous and arranged in a
487 single plan, with unaligned isomorphic dichotomies and asymmetric supra-dichotomial constrictions.
488 Frond and stipe siphons may have been parallel to subparallel and may have had appendages (Fig. 3.
489 D). We estimated the average diameters of the frond and stipe siphons to be 95 µm and 70 µm,
490 respectively. We have no precise estimation for the attachment system.

491 This ancestral morphology is close to the description of the fossil genus *Pseudoudotea* (calcified,
492 flabellate frond and siphons with "finger-like" appendages at the margin) described by Dragastan et
493 al. (1997). *Pseudoudotea* belongs to the family Pseudoudoteaceae, with other fossil genera such as
494 *Hydra* or *Garwoodia*. Missing information, such as the attachment system or stipe morphology,
495 makes a thorough comparison of their morphology with that of the putative Udoteaceae ancestor
496 impossible, but our results suggest that the morphological characters shared by *Pseudoudotea* and
497 the putative Udoteaceae ancestor could be the inheritance of a common ancestor between the two
498 families.

499 Dragastan et al. (1997) proposed to consider the fossil *Pseudopenicillus aegaeicus* as representative
500 of the former family Udoteaceae. The external morphology of the fossil is similar to the extant genus
501 *Penicillus*, with a stipe whose siphons bear dichotomously branched "secondary siphons"
502 (appendages) and a capitulum with free siphons. Although the age of the fossil (Early Triassic)
503 coincides with the temporal origin of the putative Udoteaceae ancestor, most of the fossil's
504 morphological characters differ from those inferred for the putative Udoteaceae ancestor. Based on
505 these observations, we believe that *Pseudopenicillus* represents an extinct genus of family
506 Udoteaceae and does not represent the most recent common ancestor of the entire family.

507 **4.2.2** ***Is the modern form inherited from a simple or a complex morphology?*** Various hypotheses
508 have been put forward regarding the morphology of the most recent Udoteaceae ancestor. Some

509 authors argue for a simple, filamentous and uniaxial primitive form (Hillis-Colinvaux, 1984, Meinesz,
510 1980) or an uncorticated frond (Littler & Littler, 1999; Dragastan et al., 1997) from which genera with
511 more complex morphologies may have evolved through successive acquisitions of derived states.
512 Others prefer a complex ancestral form from which simpler forms may have emerged through
513 successive secondary losses of character states (Kooistra, 2002; Verbruggen et al., 2009b). Our
514 results tend to support the second hypothesis, where the common ancestor to all Udoteaceae
515 species may have had a complex morphology, including the presence of a stipe, and a thallus calcified
516 and corticated throughout (*i.e*., appendages on both the frond and stipe siphons). The simpler forms
517 may represent derived states, which appeared several times throughout the evolutionary history of
518 the family; *i.e.,* these simpler morphologies represent innovations or ecological adaptations rather
519 than reversions towards a more ancestral state.

520 This is well illustrated by the morphological character “cortication”, which is often seen as a complex
521 feature but is also very relevant for the taxonomic classification of Udoteaceae. Cortication can be
522 restricted to the stipe or present throughout the thallus (*i.e.,* also on the frond). For Kooistra (2002),
523 total cortication may be ancestral because it occurs in basal lineages (*e.g., Flabellia petiolata* or
524 *Udotea flabellum*) and could even predate the Udoteaceae ancestor. For this author, total thallus
525 cortication could correspond to an undifferentiated (stipe and frond similarly corticated) and
526 "primitive" state. In contrast, the presence of cortication in the stipe only may be the differentiated
527 and derived state. This hypothesis contrasts with that of other authors who consider total thallus
528 cortication to be a more evolved and complex state derived from a primitive uncorticated state
529 (Littler & Littler, 1990a). In our study, the characters related to cortication and types of secondary
530 structures (in stipe or frond) all show strong phylogenetic signals, but the total thallus cortication of
531 the ancestor appears poorly represented within the family (Fig. 3. B). Indeed, our results indicate that
532 the loss of frond cortication occurred several times independently during the evolutionary history of
533 the family and could represent convergent homoplasic evolution. This character state was
534 maintained throughout subsequent speciation events and, although more recent evolution towards

535 incomplete cortication is seen for some species (*e.g.,* in *Ventalia* gen. nov, Fig. 3. B), no reversion to
536 total cortication was observed from an uncorticated state.

537 The shape of the frond is also an important character, which has often been discussed when
538 considering the morphological complexity of Udoteaceae. Because the flabellate frond is the most
539 common character among the current Udoteaceae genera, Vroom et al. (1998) considered that the
540 hypothesis of an ancestor with a flabellate frond was more parsimonious than the hypothesis of
541 multiple independent appearances of flabellate fronds proposed by Hillis-Colinvaux (1984). Vroom et
542 al. (1998) proposed that the ancestral frond morphology may be a single flabellate frond, like those
543 of *Udotea.* This early frond may have evolved successively into three different forms: (i) the multiple
544 flabellate fronds arising from a single axis of *Rhipocephalus*, (ii) a deconstruction of the flabellate
545 frond into free siphon fronds seen in *Penicillus*, and finally in a last evolutionary jump (iii) the
546 segmented morphology of *Tydemania*. Our results indicate that the ancestral state (or plesiomorphy)
547 may have been a flabellate frond, and although it is found in most genera, this character state is
548 important for differentiating them (Fig. 3. A). The free siphons frond shape appeared several times as
549 a derived state but led to different forms simultaneously and not successively as proposed by Vroom
550 et al. (1998). In addition, while the capitulum form is homoplasic, the caespitose form or the form
551 with multiple structures (glomeruli/flabella) arising from a single axis are taxonomically informative
552 and synapomorphic for genera (Fig. 3. A). Overall, the evolution from a flabellate form to a free
553 siphon form requires further analyses before it is confirmed or refuted. In addition, these
554 evolutionary scenarios will need to be further studied to determine whether it is the result of
555 environmental adaptations (changes in environmental conditions, colonization of new ecological
556 niches), or whether it corresponds to an evolutionary advantage favored by selection.

557 The loss of character states previously considered as derived and complex (*e.g.,* presence of a stipe,
558 calcification and cortication) appear to be frequent and progressive events throughout the
559 Udoteaceae evolutionary history. Forms considered “simple”, such as *Chlorodesmis*, may be extreme

cases of secondary loss of complex character states. Indeed, studies have argued that the very simple morphology of *Chlorodesmis* could be a case of regression to a simple primitive ancestral state or, a case of neoteny for which the non-calcified "juvenile" stages may have become fertile (Meinesz, 1980; Kooistra, 2002).Genomic efforts combined with transcriptomics could be used to explore the genes involved in morphogenesis. The observation of reproductive structures in some *Chlorodesmis* species (Gepp & Gepp, 1911; Ducker, 1965, 1967) has shown that they are fertile forms and not filamentous life stages of more complex and unknown species.

4.2.3 *Could the Udoteaceae ancestor have been calcified?* Calcification is another diagnostic character for distinguishing between Udoteaceae genera. Our results show that the putative Udoteaceae ancestor may have been calcified and that this character state remained as a symplesiomorphy among most of the extant genera and species (Fig. 3. C). Calcification loss occurred several times independently in the family's evolutionary history. It appears as a homoplasic derived state (parallel evolution) in a few genera including *Chlorodesmis* s.s*, Rhipidodesmis* and *Flabellia.* This result is in agreement with several published hypotheses (Kooistra, 2002; Curtis et al., 2008; Verbruggen et al., 2009b). However, other studies have proposed that the Bryopsidales ancestor was uncalcified. Calcification may then have been a derived state resulting from two independent evolutionary events, in the suborders Halimedineae (to which Udoteaceae belongs) and Bryopsidineae (*Pedobesia*) (Lam & Zechman, 2006; Verbruggen et al., 2009b). A broader phylogenetic analysis and reconstruction of ancestral character states, including the Halimedineae suborder or other members of the Bryopsidales, is needed to assess if calcification is a plesiomorphy (as for Udoteaceae) and if the absence of cortication is an homoplasic derived state or a reversion to an older ancestral state (*e.g.,* Bryopsidales ancestor).

Because it makes algae less palatable and the whole thallus stronger, particularly the siphon's structures, calcification was considered as an ecological advantage against herbivores (Hay et al., 1994, Littler & Littler, 1990a) or when facing physical environmental pressures (Littler & Littler,

585 1990a). The occurrence of calcified and non-calcified Udoteaceae taxa was also linked to
586 environmental conditions, especially the concentration and type of environmental organic matter,
587 which is likely to influence algal metabolism through $CaCO_3$ precipitation (Kooistra, 2002). This could
588 explain the seasonal and alternate occurrence of calcified and non-calcified forms of *Penicillus*
589 *capitatus* in the Mediterranean (non-calcified form: *P. capitatus* f. *mediterraneus* ex- "*Espera*")
590 (Meinesz, 1980). However, the occurrence of both calcified and non-calcified taxa within the same
591 habitat (*e.g.*, Geep & Gepp (1911), Farghaly (1980), Littler & Littler (2000), Coppejans et al. (2001),
592 etc.) indicates that calcification does not only depend on the environment. Culture experiments are
593 needed to explore the link between calcification and environmental conditions.

594 Finally, our results highlight the correlation between calcification and the presence of a stipe (Fig. 3.
595 C, Data S5, Table S11). This corroborates observations made in some species whose calcified forms
596 have a stipe while the filamentous and non-calcified forms have none (*e.g.,* see the work on *Penicillus*
597 by Friedman & Roth (1977) or Meinesz (1972, 1975, 1980)). The presence of a stipe is known to be
598 related to the type of anchoring substrate. Species with a stipe are most often encountered in soft
599 substrates, where calcification could help to remain erect from substrate. Soft substrates are usually
600 found in open environments exposed to grazing, where calcification could also represent a defense
601 strategy (even if the grazing pressure is lower than in the reef environment).

602 **4.2.4** ***Are pores and appendages functional traits?*** The "window" function was introduced by Gepp
603 & Gepp (1911) for pores visible on the calcified surface of siphons or the secondary structures on
604 siphons. These two structures are believed to promote and increase contact with the surrounding
605 environment and facilitate the flow of nutrients and light inside the siphon. Like Littler & Littler
606 (1990a), we observed that species with appendages or protuberances do not have pores on the
607 surface of siphons (*e.g.,* species of *Udotea* s.s. and *Ventalia* gen. nov.). In contrast, pores are present
608 in calcified species with naked siphons (*e.g.,* species of *Penicillus* or *Rhipidosiphon* s.s.). Additionally,
609 our correlation tests confirmed that the presence and absence of pores and the secondary structures

610 of the frond siphons are two correlated characters (Table S11). Similarly, ancestral reconstructions
611 have shown that, in most cases, these characters are linked to evolutionary processes (pores appear
612 when appendages are lost) (Fig. 3. D and Data S5). However, some calcified species of *Ventalia* gen.
613 nov. do not have secondary structures or pores. The combination of low calcification and very thin
614 frond could explain why particular structures, such as pores and appendages which facilitate
615 exchanges with the environment, are not necessary (N.B.: Although the genus *Rhipidosiphon* s.s. is
616 monostromatic, the strong frond calcification could explain the presence of pores on the siphons
617 surface).

618 Our analysis also revealed that the presence or absence of pores and secondary structures (or
619 cortication) on the siphons were correlated (among others) to the shape and thickness of the frond
620 or to the diameter and arrangement of siphons (in one or several planes) (Table S11). This result
621 corroborates the notion of "windows" (Gepp & Gepp, 1911) and their function for the continuity of
622 exchanges between the surrounding environment and the inside of the siphon. In conclusion, the
623 presence of pores on the calcified surface of the siphons, which represents a parallel homoplasic
624 evolution (Data S5), may correspond to a functional homoplasy. In contrast, the presence of
625 appendages, which represents a symplesiomorphy (Data S5), may be a functional plesiomorphy.

626 **4.2.5** ***Are constriction type indicator of generic boundaries?*** The type of dichotomy constrictions also
627 had a strong phylogenetic signal, and ancestral reconstruction highlighted it as an important
628 diagnostic character at the genus level (Data S5). The only exception is the genus *Chlorodesmis* s.s.,
629 which has species with various types of dichotomy constrictions. Gepp & Gepp (1991) and Littler &
630 Littler (1990a) discussed the distinct geographical patterns of this trait in *Udotea* species of the
631 Caribbean and Indo-Pacific regions. However, this pattern was less evident in our study. We found
632 that all Caribbean taxa have symmetrical constrictions, except *Udotea* s.s. species, while Indo-Pacific
633 species of *Udotea* s.s., *Glaukea* gen. nov. and *Ventalia* gen. nov have asymmetrical constrictions

634 above the dichotomies. Despite its high phylogenetic signal, the evolution and geographical
635 distribution of this character state remains difficult to explain.

636 For Farghaly (1980), this character is of no taxonomical importance because whether the
637 constrictions are “aligned” or “mismatched” (*i.e.,* symmetrical or asymmetrical, respectively)
638 accounts for the regular or irregular siphon growth rates, respectively. From our observations, we
639 believe the constrictions appear long after the branches are fully grown, and this is why apical
640 dichotomies (on the siphons margin) generally do not have constrictions yet.

641 Functionally, the constrictions help to limit the loss of cytoplasm during grazing by herbivores by
642 allowing rapid occlusion of the siphons (Duffy & Hay, 1990; Menzel et al., 1998; Vroom et al., 2001).
643 As Udoteaceae species are found in environments with different grazing pressures, the arrangement
644 of constrictions (on one or two levels) may be the result of various evolutionary adaptations to
645 specific environments.

646

647 **4.3. Systematics revisions and taxonomic treatment**

648 In this section, we discuss the revised clades (as delimited in Figure 1.B) individually, based on both
649 the molecular (species delimitation and phylogeny) and morphological (observations and
650 phylogenetic inference of character) results. We include details about the proposed systematic and
651 taxonomic revisions, species diversity, geographical distribution and diagnostic morphological
652 characters. The genera *Tydemania* (Clade A) and *Flabellia* are not detailed here, as no taxonomic
653 changes have been applied to them (but see Lagourgue et al. (2019) for more details about the
654 morphology, diversity and distribution of *Tydemania* species).

655

656 **4.3.1 *Udotea* sensu stricto (*Udotea* group 1- Clade B)**

Clade B is strongly supported (bs: 97; PP: 0.98) and contains six *Udotea* species, including the type-species *U. flabellum (J.* Ellis & Sollander) M. Howe, and therefore represent *Udotea* s.s. It is composed of species found in the Caribbean (*U. dixonii, U. dotyi, U. occidentalis*) and the Pacific (*U. geppiorum, U.* sp1) (Figure 4). *Udotea* is strongly calcified and characterized by a stubby thallus with a pluristromatic flabellate frond. The frond can be lobed and entire or divided or segmented, with segments inserted in each other in a 'tongue and groove' arrangement (Sauvage et al., 2020). The rhizoidal system is well-developed and bulbous. The frond siphons have well-developed secondary structures called appendages. These latter are either dichotomously divided or lobed, and all have numerous well-defined apices. The cortication is complete, *i.e.*, appendages are present throughout the stipe and the frond. The specific symplesiomorphies and synapomorphies of the *Udotea* genus are shown in Figure 4.

Considering these species as part of distinct lineage is not entirely new but had never been formalized nor verified molecularly. Previous authors proposed to consider some of these species in a proper group, named in turns "corticatae" (Agardh, 1887; *U. flabellum* only), an unnamed group by Gepp & Gepp (1911; *U. flabellum, U. argentea, U. occidentalis, U. verticillosa* and *U. wilsonii*), "completely corticated blade" (Nizamuddin, 1963), "Udotea" (Farghaly, 1980; *U. flabellum, U. argentea* and *U. occidentalis*), "Flabellum" (Littler & Littler, 1990a; including only the Caribbean species *U. flabellum, U. dixonii, U. dotyi, U. occidentalis* and *U. norrisii*), and "complete corticated species" (Dragastan et al., 1997; *U. flabellum*).

Futhermore, Tseng & Dong (1975) described several *Udotea* species from China. Despite very brief descriptions, they mention species with long and dichotomously ramified lateral branches on siphons, which could refer to appendages, and could correspond to *Udotea* s.s. species (*U. reniformis, U. tenax, U. tenuifolia, U. velutina* and *U. xishaensis).* Nevertheless, morphological and molecular verification is needed for confirmation.

Species of the genus *Udotea* s.s. are characterized by limited morphological variations compared to other ex-*Udotea* species, as previously noticed by Kooistra (2002), who considered this lineage to be ancestral. Results of our time-calibrated phylogeny confirmed that *Udotea* s.s. was indeed one of the oldest genera to diverge in the family (ca 109 Ma, *cf.* Figure 2). This morphological resemblance between the species *in situ* could explain several erroneous identifications that have led to an overestimation of their distribution range. The genus has a wide geographical repartition, but the distribution range of species is more restricted than previously reported. For example, *U. flabellum* does not occur worldwide, but appears limited to the western tropical Atlantic (Figure 4). Similarly, we found that the Atlantic species, *U. occidentalis,* has a sister species in the Pacific, *U.* sp1 (bs: 100; PP: 1), which is close morphologically (lobed aspect of the frond appendages and similar siphon diameter but different stipe appendages).

Udotea J. V. Lamouroux

Diagnosis: Lamouroux JVF. 1812. Sur la classification des polypiers coralligènes non entièrement pierreux. *Nouveaux Bulletin des Sciences, Societé philomatiques de Paris* 3: 181–188.

Type species*: U. flabellum* (J. Ellis & Solander) M. Howe; Type: unknown; Type locality: West Indies, Basionym: *Corallina flabellum*, Ellis & Solander; Synonyms: *Udotea flabella* J.V. Lamouroux; *Udotea halimeda* Kützing

List of species (as per this study): *U. flabellum*, *U. occidentalis, U. geppiorum, U. dotyi, U. dixonii,* and *U.* sp1 (new species to be described).

Morphological description emended from Lamouroux (1812) and Gepp & Gepp (1911)): Flabellate, pluristromatic, corticated and highly calcified frond; Multisiphonous, corticated and calcified stipe; Continuous stipe-frond junction; Bulbous holdfast and well-developed rhizoidal system; Frond and stipe siphons with appendages, either dichotomously divided or lobed, with numerous well-defined

705 apices; Siphons dichotomously branched; Dichotomies isomorphic and not aligned; Asymmetrical
706 supra-dichotomial constriction; Non-porous siphons sheath.
707 **Geographic distribution (confirmed using DNA sequencing)**: Atlantic Ocean: Caribbean Is.
708 (Lagourgue et al., 2018; This study), Mexico (Lam and Zechman, 2006), Bermuda (Lagourgue et al.,
709 2018), Florida (Lagourgue et al., 2018), Bahamas (Lagourgue et al., 2018), Honduras (Kooistra, 2002),
710 Panama (Kooistra, 2002; Kooistra et al., 2002; Lagourgue et al., 2018), Jamaica (Lagourgue et al.,
711 2018); Pacific Ocean: Hawai'i (Sauvage et al., 2016), Papua New Guinea (This study); Solomon (This
712 study), Tonga, Fiji (Sauvage et al., 2019; This study), New Caledonia (Grande Terre, Surprises Is.,
713 Chesterfield Is.) (This study).
714
715 **4.3.2 *Glaukea* gen. nov. (*Udotea* group 2 - Clade C)**
716 The new genus *Glaukea* (bs*:* 100; PP: 1, Fig. 1) is proposed to accommodate specimens previously
717 assigned to *Udotea argenta* Zanardini (Figure 1). The genus *Glaukea* is characterized by a flabellate
718 and zonate frond, entire or more or less divided, siphons with diameter < 80 µm and lobed
719 appendages with rounded, swollen and convex apices (Figure 5). Our results indicate that the genus
720 is composed of two genetically distinct species (bs*:* 100; PP: 1 for both; Fig. 1) that both match the
721 very brief original diagnosis of *U. argentea* (Zanardini, 1858). However, we were unable to confirm
722 the identity of the two species for two reasons: 1) we have no specimen from the type locality (Suez,
723 Egypt); and 2) we could not locate the type specimen. The resolution of this case requires
724 observations of the type specimen and the sequencing of samples from the type locality for
725 lectotypification. This new genus is thus a complex of species that we refer to as *Glaukea argentea* 1
726 and *G. argentea* 2 until further study provides clarification to confirm species name. In any case, this
727 clade can no longer be considered as *Udotea* in the present assessment, considering the topology of
728 the tree.
729 The genus *Glaukea* has retained several ancestral states and has many symplesiomorphies including
730 a flabellate pluristromatic frond, a plurisiphonous stipe that is not ramified, with a continuous stipe-

731 frond junction, calcified siphons sheath without pores, thallus cortication, complete cortication of the
732 frond and stipe, dichotomously ramified siphons that are arranged in one plan, and parallel to
733 subparallel in the frond, random and isomorphic dichotomies, with asymmetrical supra-dichotomial
734 constrictions, and appendages on frond and stipe siphons. Two synapomorphies were also
735 highlighted including a bulbous holdfast and the presence of an erect axis. The current distribution of
736 the genus is Indo-Pacific, with *G. argentea* 1 distributed throughout the area while *G. argentea* 2
737 seems restricted to Madagascar.

738

739 *Glaukea* Lagourgue & Payri *gen. nov.*
740 **Type species**: *Glaukea argentea* (Zanardini) Lagourgue & Payri comb. nov.; Type: unknown; Type
741 locality: Suez, Egypt; Basionym: *Udotea argentea* Zanardini, J. 1858. Plantarum in mari Rubro
742 hucusque collectarum enumerato (juvante A. Figari). *Memoirie del Reale Istituto Veneto di Scienze,*
743 *Lettere ed Arti* 7: 209-309, pls III-XIV.
744 **List of species (as per this study)**: *Glaukea argentea, G*. sp1. Comment: Since the type specimen is
745 unknown and no specimen of type locality could be sequenced, further studies are needed to clarify
746 the taxonomic status of the two *Glaukea* taxa.
747 **Etymology:** from the Greek "glaukos" meaning a green color with a blue tinge, in connection with the
748 color of the thallus *in situ*.
749 **Morphological description emended from Zanardini (1858) and Gepp & Gepp (1911):** Flabellate,
750 sub-reniform to lobed frond, more or less cut out, striated, zonate and pluristromatic, entire or
751 eroded upper margin, pale green-grey to ashy green; Short and not-ramified stipe, plurisiphonous,
752 with a continuous stipe-frond junction; Bulbous holdfast; The thallus is calcified with non-porous
753 siphon sheath; Siphons ramify in dichotomy and are arranged in one plan, parallel to subparallel in
754 the frond; The dichotomies are not aligned and isomorphic with asymmetrical supra-dichotomial
755 constrictions; Siphons diameter < 80 µm with decreasing size towards the apex in the blade and 25-

100 µm in the stipe; Total cortication of the thallus through the presence of appendages on siphons; In the frond, siphons have numerous pyriform and lobed appendages (100-200 µm long), alternately or distically arranged, constricted at the base and with rounded, swollen and convex apices; In the stipe, siphons appendages (300 -800 µm long) are dischotomously ramified (1-4 times) and digitate ("finger-like") and with obtuse or swollen apices.

Geographical distribution (confirmed using DNA sequencing): Indian Ocean: Mayotte (This study), Scattered Islands (Glorioso Is., Juan de Nova Is.) (This study), Madagascar (This study); Pacific Ocean: Guam (Kooistra, 2002), Papua New Guinea (Cremen et al., 2019; This study). For more detailed distributions in Indo-Pacific and Red Sea, see Guiry & Guiry (2020). However, others distribution reported by solely morpho-anatomical data (Guiry & Guiry, 2020) need further verification by DNA sequencing, due to potential confusion with some *Udotea* species (*e.g., U. flabellum, U. geppiorum).*

4.3.3 *Chlorodesmis* sensu stricto (Clade D)

Based on our results, we propose to circumscribe the genus *Chlorodesmis* s.s. to the clade containing the type species *C. fastigiata* (bs: 92; PP: 0.8). This clade includes five other species, three of which are probably new (*C.* sp2, *C.* sp3, *C.* sp5), while the identification of the two others requires further verification (*C.* cf. *hildebrandtii* and *C.* cf. *major*, Figure 6). We exclude the species *C. caespitosa,* which was recovered in Clade I, and *C. baculifera*, which grouped outside of the family Udoteaceae (preliminary analyses, publication in prep). Molecular analyses of the *Chlorodesmis* species not included in our study (*C. papenfussii, C. dotyi, C. haterumana, C. mexicana* and *C. sinensis*) are needed to confirm their status, particularly since their morphological descriptions are relatively short (Taylor, 1945; Trono, 1971; Itono, 1973; Tseng & Dong, 1978), which makes it impossible to discuss their possible status.

The genus *Chlorodesmis* is characterized by an uncalcified thallus in tufts, composed of a discoid base from which arise free and interwoven siphons dichotomously divided and constricted. The symplesiomorphies and synapomorphies characterizing the genus and shown in Figure 6, are useful

for distinguishing the genus from other filamentous species, particularly the caespitose tufted blade, the absence of cortication or the presence of supra-dichotomial constrictions. Indeed, due to their relatively simple morphology, there are only few diagnostic characters available to identify *Chlorodesmis* species, and this has most likely led to misidentifications in the past. Many non-calcified and tufted filamentous forms belonging to other lineages and families could have been confused with *Chlorodesmis* and reassessing these records, using the diagnostic characters highlighted here, could reveal very different geographical distribution patterns.

Overall, our study confirms that the genus does not occur in the Atlantic Ocean, and its geographical distribution extends throughout the Indo-Pacific. Some of the species have wide geographic distribution (*e.g.*, *C. fastigiata* and *C.* sp5), while others appear more restricted (*e.g., C.* sp2 and *C.* sp5 in the WIO region) (Figure 6).

Chlorodesmis Harvey & Bailey

Diagnosis: Harvey WH, Bailey JW. 1851. Description of seventeen new species of algae, collected by the United States Exploring Expedition. *Proc. Boston Soc. Nat. Sci*. 3: 370–373.

Type species = *Chlorodesmis fastigiata* (C. Agardh) S.C. Ducker; Type: LD #15661, Herb. Alg. Agardh (LD); Type Locality: Mariannes Is. (Micronesia); Basionym: *Vaucheria fastigiata* C. Agardh - Synonyms: *C. comosa* Harvey & Bailey; *Avrainvillea comosa* (Harvey & Bailey) G. Murray & Boodle.

List of species (as per this study): *C. fastigiata, C.* cf. *hildebrandtii, C.* cf. *major* and three new species to be described (*C.* sp2, *C.* sp3 and *C.* sp5).

Morphological description emended from Harvey & Bailey (1851) and Gepp & Gepp (1911):

Uncalcified thallus with a felted, spongious, colorless and discoid base, bearing a green tuft of free and interwoven siphons; Siphons cylindrical, dichotomously branched and with numerous constrictions (“pseudo-articulated” in original diagnose of Harvey & Bailey); Round or pointed apices; Dichotomies iso- or anisomorphic; Symmetrical or asymmetrical supra-dichotomous constrictions with ring of cell-wall for most of species.

Geographical distribution (confirmed using DNA sequencing): Indian Ocean: Mayotte (This study), Scattered Is. (Glorioso Is, Juan de Nova Is.) (This study), Madagascar (This study), Maldive Is. (This study); Pacific Ocean: Okinawa (Japan) (Sauvage et al., 2016), Guam (Verbruggen & Schils, 2012), Papua New Guinea (This study), Australia (Lizard Is.) (Kooistra, 2002), New Caledonia (Grande Terre, Surprises Is.) (This study), French Polynesia (Verbruggen et al., 2009b; This study).

4.3.4 *Ventalia* gen. nov. (*Udotea* group 3 - Clade E)

The new genus *Ventalia* is proposed to accommodate species of clade E (bs: 93; PP: 1, Fig. 7) formerly known as *Udotea orientalis*, *U. indica* and *U. papillosa*, as well as four additional taxa (*V.* sp1, *V.* sp2, *V.* sp3 and *V.* sp4) which may represent new species (Figure 7). Each of these new species are highly supported (bs: 100; PP: 1, Fig. 7), except *Ventalia* sp2. *Ventalia* has a flabellate mono or pluristromatic frond, uncorticated (naked siphons lacking secondary structures) or pseudo-corticated siphons (*i.e.,* with rounded or spinous protuberances all around or only on the external and exposed side of the siphon) (Figure 8). The rhizoidal system is limited. The stipe is mono- or plurisiphonous, corticated or pseudo-corticated, partially or fully calcified. In plurisiphonous stipes, siphons have appendages of various aspects ranging from simple swellings to more developed structures dichotoumously divided, or with terminal dichotomies only in stubby appendages (Figure 8). The siphons are thin (< 45 µm in diameter) with a porous surface and the dichotomies have asymmetrical constrictions (see Figure 7 for detailed symplesiomorphies and synapomorphies). These species are very similar morphologically and are difficult to distinguish without a thorough anatomical analysis. This is particularly true for the cryptic species without protuberances (*i.e.,* naked siphons; *V. orientalis, V.* sp3 and *V.* sp2), which would not be distinguished from each other without detailed anatomical or molecular analyses.

A similar grouping was informally proposed by several authors: Agardh (1887) subdivided species according to the stipe cortication and included *U. orientalis* in a “Palmattae” group; Nizammudin

(1963) created a group for species with partially corticated frond and pointed apices; Farghaly (1980) grouped *U. indica, U. palmetta* and *U. papillosa* but not *U. orientalis* in a lineage called "Decaisnella" (invalid name); Finally, Gepp & Gepp (1911) considered *U. indica, U. palmetta*, *U. papillosa* and *U. orientalis* as part of a same group without naming it.

Although we included no sample of *U. palmetta* in our study, we believe that its morphology, as described in other studies (Decaisne, 1842; Gepp & Gepp, 1911; Farghaly, 1980) could match this new genus. Tseng & Dong (1975) also described two *Udotea* species from China (*Udotea fragifolia* and *U. renuifolia)*. Despite very brief descriptions, they mention species with simple lateral branches on siphons, which could refer to protuberances, a diagnostic character of several *Ventalia* species. Morphological and molecular studies of these species are needed to confirm their transfer to *Ventalia*.

The geographical distribution of the genus is Indo-Pacific. The species are restricted either to the Indian Ocean (*V. papillosa, V. indica* but also *V.* sp2 only found in Madagascar) or to the Pacific Ocean (*V.* sp1 and *V.* sp4) (Figure 7). Although *U. orientalis* is recorded throughout the Indo-Pacific (Guiry & Guiry, 2020), we were only able to include Western Indian Ocean (WIO) specimens in our study. Given the possible misidentifications of the other records, further analyses of *V. orientalis* specimens from the rest of its distribution range are needed.

Ventalia Lagourgue & Payri **gen. nov**

Type species: *Ventalia indica* (A.Gepp & E.S.Gepp) Lagourgue & Payri **comb. nov**.

List of species (as per this study): The genus is composed of seven species: *V. orientalis, V. indica, V. papillosa* and four new species to be described (*V.* sp1, *V.* sp2, *V.* sp3 and *V.* sp4).

Etymology: from the Greek "ventália", with regard to the flabellate (fan-shaped) frond

Morphological description: Flabellate frond, mono or pluristromatic, uncorticated or pseudo-corticated, calcified without porous siphons sheath; Stipe mono- or plurisiphonous, corticated or

858 pseudo-corticated, partially or fully calcified; Stipe-frond junction continuous; Reduced rhizoidal
859 system reduced; Frond siphons parallel to subparallels, naked or with protuberances; diameter <45
860 µm; Siphon ramification by dichotomies, not aligned; Asymmetrical constrictions above dichotomies;
861 Stipe siphons with appendages and/or ascending laterals.
862 **Geographic distribution (confirmed using DNA sequencing):** Indian Ocean: Scattered Islands (Glorioso
863 Is., Juan de Nova Is.) (This study), Madagascar (This study); Pacific Ocean: Hawai'i (Wade & Sherwood,
864 2017), Papua New Guinea (This study), New Caledonia (Grande Terre, Chesterfield Is., Surprises Is.)
865 (This study).
866
867 *Ventalia indica* (A.Gepp & E.S.Gepp) Lagourgue & Payri **comb. nov**.
868 **Type:** holotype: J. A. Murray in Herb. Mus. Brit.; BM000515946
869 **Basionym:** *Udotea indica* A.Gepp & E.S. Gepp, 1911. The codiaceae of the Siboga Expedition, including
870 a monograph of Flabellarieae and Udoteaceae. *Siboga-Expeditie* 62: 1–150.
871 **Type locality**: Karachi, Pakistan
872 **Ethymology:** pertaining to India (Latin adjective)
873 **Morphological description:** see Gepp & Gepp (1911).
874 **Geographic distribution (confirmed using DNA sequencing)**: Indian Ocean: Madagascar (This study).
875 Guiry & Guiry (2020) report an Indo-Pacific distribution, but we did not find *U. indica* specimen in the
876 Pacific, and that should thus be genetically confirmed.
877 **List of vouchers from this study:** Madagascar, Nosy Hao, 2016**:** NOU203645, NOU203653.
878 **Comment**: *U. orientalis* is the most widespread species, but its type could not be located. Instead, we
879 have chosen *U. indica* to represent the type species of *Ventalia* because its type specimen is correctly
880 listed and deposited in BM.
881
882 Other species needing new combinations:
883 *Ventalia orientalis* (A.Gepp & E.S.Gepp) Lagourgue & Payri **comb. nov**.

884 **Basionym:** *Udotea orientalis* A.Gepp & E.S. Gepp, 1911. The codiaceae of the Siboga Expedition,
885 including a monograph of Flabellarieae and Udoteaceae. *Siboga-Expeditie* 62: 1–150.
886 **Synonym**: *Rhipidosiphon orientalis* (Gepp & Gepp) Farghaly
887 **Type:** n°s 261, 262, 263 (Siboga Expedition: Stat. 64. Island Tanah-Djampeah, 30 m.); Hildebrandt, n°
888 1918 (Lamu Harbour, Zanzibar coast, covered at low water) – Note that none of these specimens could
889 be located in a referenced Herbarium.
890 **Type locality**: syntypes localities - various in Indian and Pacific Oceans; Indonesia; Philippine Islands
891 **Ethymology:** eastern (Latin adjective)
892 **Morphological description:** see Gepp & Gepp (1911).
893 **Geographical distribution (confirmed using DNA sequencing):** Indian Ocean: Madagascar (This study).
894 *Ventalia orientalis* is recorded throughout the Indo-Pacific (Guiry & Guiry, 2020 as *Udotea orientalis*),
895 but only specimens from the Indian Ocean have been genetically verified. A molecular verification of
896 specimens recorded in the Pacific Ocean is required.
897 **List of vouchers from this study (limited to 2 per locality):** Madagascar, Nosy Mitsio, 2016:
898 NOU203674, NOU203676; Madagascar, Nosy Lava, 2016: NOU203678, NOU203680; Madagascar,
899 Radama, 2016: NOU203703, NOU203722; Madagascar, Nosy Sakatia, 2016: NOU203737; Madagascar,
900 Nosy Manitsa, 2010: PC0171887; Madagascar, Baravo Lagoon, 2010: PC0142723.
901
902 *Ventalia papillosa* (A.Gepp & E.S.Gepp) Lagourgue & Payri **comb. nov**.
903 **Basionym**: *Udotea papillosa* A. Gepp & E.S. Gepp, 1911. The codiaceae of the Siboga Expedition,
904 including a monograph of Flabellarieae and Udoteaceae. *Siboga-Expeditie* 62: 1–150.
905 **Synonym**: *Decaisnella papillosa* (Gepp & Gepp) Farghaly
906 **Type:** unknown
907 **Type locality**: syntype localities - various in Indonesia, including Noimini Bay (Teluk Noilmina), Timor.
908 **Ethymology:** papillate, covered with papillae (Latin adjective)
909 **Morphological description:** see Gepp & Gepp (1911) for the description of the species.

910 **Geographical distribution (confirmed using DNA sequencing)**: Indian Ocean: Scattered Islands
911 (Glorioso Is.) (This study), Madagascar (This study).
912 **List of vouchers from this study (limited to 2 per locality):** Madagascar, Sainte Marie Is., 2016:
913 NOU203581, NOU203595; Madagascar, Cap Masoala, 2016: NOU203602, NOU203603; Scattered
914 Islands, Glorioso Is., 2012: NOU087254
915

916 **4.3.5 *Rhipidosiphon* sensu stricto (Clade F)**

917 Clade F is well supported in the BI phylogeny (PP: 0.99; bs: 53) and includes the type-species *R.*
918 *javensis,* which led us to consider the clade as representative of *Rhipidosiphon* s.s. It also includes five
919 *Rhipidosiphon* taxa, two of which possibly correspond to new species (Figure 9). According to our
920 species delimitation analysis (Fig.S1 & S2 SI), and morpho-anatomical data (when available), it is
921 likely that *R.* sp2 (SSH34), *R.* sp3 (SSH 32), *R.* sp5 (SSH 55), *R*. sp 6 (SSH 56), *R.* sp8 (SSH 60) *R.* sp9 (SSH
922 61), and *Udotea* sp10 (SSH62) belong to *Rhipidosiphon* s.s. However, missing molecular data
923 prevented us from including them in the multilocus analysis.

924 The genus *Rhipidosiphon s.s.* is characterized by an uncorticated monostromatic flabellate frond, a
925 stipe, which is monostromatic at the base and, in some instances, becomes plurisiphonous near the
926 frond. The stipe is pseudo or fully uncorticated and partially calcified or fully uncalcified. A detailed
927 list of symplesiomorphies and synapomorphies characterizing the genus *Rhipidosiphon* is shown in
928 Figure 9. Based on our morphological and molecular results (Figures 9, S1 & S2), we propose to
929 transfer the species *Udotea glaucescens* to this genus. This was previously suggested by Nizammudin
930 (1963) and Farghaly (1980) but not validated (Guiry & Guiry, 2020). On the other hand, because it
931 clustered in clade H, we propose to exclude *R. floridensis* from *Rhipidosiphon* s.s.

932 We identified the type species, *R. javensis* among our samples collected in Bunaken Island (Sulawesi,
933 Indonesia), which is located near the type locality (Leiden Island, Nyamuk-besar, Java, Indonesia).
934 However, the sequence of our specimen did not match with the *rbcL* sequences recorded in the

Genbank under the same epithet (DML40128, DML40134). Due to the strong species crypticity of the genus *Rhipidosiphon,* we suspect that the specimens corresponding to the Genbank sequences could have been misidentified. Besides, these specimens were collected from the Great Astrolabe Reef in Fiji, which is more distant from the type locality.

The geographical distribution of the genus is strictly Indo-Pacific. According to Guiry & Guiry (2020), the most widespread species is *R. javensis,* for which records are available throughout the Indo-Pacific region. However, it is highly likely that some of these records represent erroneous identifications, such as the example cited above. Therefore, it is possible that the distribution of *R. javensis* is more restricted than previously thought, which is the case for most other species of the genus (*e.g.*, *R. glaucescens* and *R. lewmanomontiae* in the south and northwest Pacific, respectively) (Figure 9).

However, according to the results of the individual gene trees (*tufA*, *rbcL* and 18S rDNA) (see Figures S1, S2 and S4 respectively), where species do not form monophyletic clades, and due to the weak root node support in the ML multilocus tree, the genus *Rhipidosiphon*, as proposed in this study, remains to be confirmed. We recommend the sequencing of more species, more individuals per species, as well as neighbouring clades.

Rhipidosiphon Littler & Littler

Diagnosis: Montagne, J.F.C. 1842. Prodromus generum specierumque phycearum novarum, in itinere adpolum antarcticum…collectarum. Paris. 16 pp.

Type species: *R. javensis* Montagne; Type: PC, coll: Hombron; Type locality: Leiden Island (Nyamik-besar), near Jakarta, Java, Indonesia; Synonym: *Udotea javensis* (Montagne) A. Gepp & E.S. Gepp.

List of species (as per this study): *R. javensis, R. lewmanomontiae, R. glaucescens* comb. nov. and two other new species to be described (*R.* sp1 and *R.* sp4).

Morphological description emended from Littler & Littler (1990) and Gepp & Gepp (1911):
Flabellate, calcified, monostromatic and uncorticated frond; Monosiphonous (becoming plurisiphonous near the frond in some species), uncorticated or pseudo- corticated, partially or not calcified; Stipe-frond junction continuous; Fine hyaline rhizoids at the base; Frond siphons cylindrical, dichotomously branched, arranged in parallel to sub-parallel, without anastomosis but cemented by calcification; Isomorphic dichotomies with asymmetrical constrictions above; Porous siphon sheath.
Geographic distribution (confirmed using DNA sequencing): Indian Ocean: Mayotte (This study), Juan de Nova Is. (This study), Madagascar (This study), Maldive Is. (This study); Southeast-Asia: Thailand (Coppejans et al., 2011), Bunaken (This study); Pacific Ocean: Okinawa (Sauvage et al., 2016), Papua New Guinea (This study), Vanuatu (This study), New Caledonia (Grande Terre, Surprises Is.) (This study), Fiji (Coppejans et al., 2011; This study), Tonga (This study).

New combination proposed:
Rhipidosiphon glaucescens (Harvey ex J.Agardh) Lagourgue & Payri **comb.nov.**
Basionym: *Udotea glaucescens* Harvey ex. J. Agardh (Agardh J.G. 1887. Till Algernes Systematik.Nya bidrag. Acta Universitatis Lundensis 23: 1–174, 5 plates).
Type locality: Tonga
Type: Unknown
Ethymology: becoming glaucous (Latin adjective).
Morphological description: see J. Agardh (1887) and Gepp & Gepp (1911)
Geographical distribution (confirmed using DNA sequencing): Pacific Ocean: Vanuatu (This study) and Fiji (This study).
List of vouchers from this study: Fiji, Nagelelevu Lagoon, 2007: NOU087262; Fiji, Heemskercq reef, 2007: NOU087250; Fiji, Vanua Levu, 2007: NOU087256; Vanuatu, Bridgestock point, 2006.

4.3.6 *Udoteopsis* gen. nov. (*Udotea* group 4- Clade G)

985 The genus *Udoteopsis* is proposed to accommodate a new species represented by specimens
986 collected in Madagascar and Mayotte (WIO region). The monospecific genus is well-supported (bs:
987 100; PP: 1, Fig. 1) but its phylogenetic relationship to the genera *Chlorodesmis*, *Ventalia* gen.nov. and
988 *Rhipidosiphon* is weakly supported (bs: 67; PP: 0.93, Fig. 1). Additional sampling is needed to confirm
989 its phylogenetic relationships within the Udoteaceae (Figure 1). The genus is characterized
990 morphologically by a monostromatic calcified flabellate frond, irregular margins with growth zones
991 where siphons are free (no calcified cement) (Figure 10). The siphons are cylindrical, naked and
992 swollen at the apices. Isolated constrictions between the dichotomies are observed and more
993 numerous in the growth area. The siphons measure 100 µm in diameter and decrease in size towards
994 the apex (50-60 µm). The dichotomies have asymmetric constrictions, and some trichotomies are
995 also observed. The stipe is multisiphonous, entirely calcified and corticated with appendages on the
996 siphons. The stipe siphons are 100 µm in diameter for a total stipe width of 500-700 µm. The calcified
997 surface of the siphons is porous to with cracks (Figure 10). The genus has several symplesiomorphies:
998 a unique flabellate frond, calcification, a plurisiphonous stipe with a continuous stipe-frond junction,
999 dichotomous siphon ramifications, primary siphons arranged in one plane, random and isomorphic
1000 dichotomies, asymmetrical constrictions, appendages on the stipe's siphons and complete stipe
1001 cortication. Synapomorphies include a monostromatic frond, a reduced rhizoidal system, an erected
1002 axis, the presence or absence of supra-dichotomial constrictions and the absence of frond
1003 cortication. The new genus is exclusively found in the WIO region and so far, only known from
1004 Mayotte and Madagascar.
1005
1006 *Udoteopsis* Lagourgue & Payri **gen. nov.**
1007 **Type species**: *Udoteopsis maiottensis* Lagourgue & Payri sp. nov.
1008 **Ethymology:** named in reference to the morphological resemblance to the genus *Udotea.*
1009 **Morphological description:** Flabellate, monostromatic and calcified frond with irregular margin;
1010 Multisiphonous, calcified and corticated stipe (500-700 µm width); Continuous stipe-frond junction;

Reduced rhizoidal system; Frond siphons cylindrical and naked siphons branching dichotomously with supra-dichotomous constrictions; Stipe siphons with appendages; Porous siphons sheath.

Geographic distribution (confirmed using DNA sequencing): Western Indian Ocean: to date the genus is only known from Mayotte and Madagascar (This study).

Udoteopsis maiottensis Lagourgue & Payri sp. nov.

Types: holotype: NOU203562 (Mayotte, 2016); isotypes: NOU203560, NOU203561, NOU203570, NOU203580 (Mayotte, 2016), NOU204161 (Mayotte, 2010), PC0171655, (Madagascar, 2010)

Type locality: Mayotte; syntype locality: Madagascar

Ethymology: in reference to the species type-locality, Mayotte (Latin Maiotta)

Morphological description: Monostromatic, uncorticated, calcified, flabellate to feather-shaped frond, irregular margin with growth and free siphons (lacking calcification cement); Multisiphonous, corticated and calcified stipe; Stipe width of 500-700 µm; Continuous stipe-frond junction; Reduced rhizoidal system; Siphons cylindrical, naked and swollen at the apices in the frond, and highly constricted in growth zone; Siphons with appendages in the stipe; Siphons branching dichotomously; Some trichotomies; Isomorphic and not-aligned dichotomies; Asymmetrical constrictions above dichotomies; Siphons diameter of 100 µm (in frond and stipe) decreasing toward the apex (up to 50-60 µm) in the frond; Siphons surface porous to crack.

Geographical distribution (confirmed using DNA sequencing): Mayotte (This study), Madagascar (This study).

List of vouchers from this study: Mayotte, Tanaraki, 2016**:** NOU203560, NOU203561, NOU203562; Mayotte, N'gouja, 2016: NOU203570; Mayotte, Surprise Pass, 2016: NOU203580; Mayotte, 2010: NOU204161; Madagascar, Gallions Bey, 2010: PC0171655.

4.3.7 The "*Penicillus-Rhipidosiphon-Rhipocephalus-Udotea* (PRRU) complex" (Clade H)

Clade H, which is well supported (bs: 85; PP: 0.96, Fig. S5), includes specimens exclusively collected in the Western Tropical Atlantic (mostly in the Caribbean) and representing species only found in this region except for *Penicillus capitatus,* which distribution would also extend to the Mediterranean Sea (Meinesz, 1972 and 1975; see Guiry & Guiry, 2020 for more references) but this has to be confirmed genetically. Morphologically, all these species correspond to distinct and polyphyletic genera (*Udotea, Penicillus, Rhipidosiphon, Rhipocephalus*) (Figure S5), which results in high morphological diversity and discontinuities within this clade.

Few symplesiomorphies and synapomorphies were identified for this clade. The trait inference analysis did not support the grouping of these species under a single genus. Instead, splitting the clade into three genera would appear a better option (see Fig. S5). We discuss the resulting genus hypotheses below:

Genus hypothesis 1) This subclade is fully supported (bs: 100; PP: 1) and includes taxa morphologically assigned to *P. capitatus* (type species of the genus *Penicillus*), *Udotea cyathiformis*, *U. conglutinata*, *U.* sp9 and the two species of *Rhipocephalus (R. phoenix* and *R. oblongus*). It is interesting to note that *Rhipocephalus* species used to belong to *Penicillus* until Kützing (1843a and b) described the former. Various authors also highlighted the soft morphological boundaries between the genera *Penicillus, Rhipocephalus* and *Udotea* (Farghaly, 1980; Kooistra, 2002). Morphologically, species in this subclade are relatively coherent and differ only by the type of siphons' arrangement (forming a coherent blade or free) and the organization of the frond (unique or composed). In light of this information, we believe that the most likely genus hypothesis for this clade is *Penicillus*.

Genus hypothesis 2) The second highly supported subclade (bs*:* 100; PP:1, Fig. S5) of the "PRRU complex" includes species assigned to *Penicillus dumetosus, P. pyriformis* and *P. lamourouxii* (the latter was not included in the multilocus analysis since only one *rbcL* sequence was available, but see Figure S2). All species in this subclade are morphologically similar with a capitate (brush-shaped) frond, large siphon diameters, wide and prominent stipe appendages, with pointed (*P. dumetosus, P.*

pyriformis) or finger like (*P. lamourouxii*) apices. Interestingly, Kützing (1849) already had proposed to consider these species, among others, as part of a distinct genus, *Corallocephalus*, but this latter was considered as a synonym of *Penicillus.*

Genus hypothesis 3) The third subclade is represented by the species *Rhipidosiphon floridensis* only (Fig. S5 SI). However, based on the results of Lagourgue et al. (2018) and Figures S1 & S2, it is possible that *Udotea spinulosa* and *U. looensis* belong to same subclade. The situation would be similar for other *Udotea* species such as *U. luna* or *U. verticillosa,* which have never been sequenced but are morphologically close to *Udotea spinulosa* and *U. looensis*. All these species have a flabellate frond (mono or pluristromatic) composed of naked siphons or with protuberances (only on the outer face of the external siphons or at the base of the frond) and of large diameter (≈ 50-100 µm). Additional work, particularly sequencing, is needed to confirm this clade as a genus and the species that should be included in it.

Finally, the "PRRU complex" shows strong morphological discontinuities in this study, and more data are needed (specimens per species, genetic data; some species are still not genetically represented) in order to better identify the species diversity, as well as the number, composition, and phylogenetic position of the different genera included in this complex. Therefore, we choose to postpone any taxonomic decisions about the “PRRU complex” until more data is available.

4.3.8 The “*Poropsis Penicillus Rhipidodesmis* complex” (PPR complex- Clade I)

This clade includes three taxa: an unknown *Poropsi*s sp., *Penicillus nodulosus* and *Chlorodesmis caespitosa* (Figure S6).

Poropsis sp. - Our results point out to several entities from various localities (Hawai‘i, Israel, Mexico; see Figures S1 & S2), which could be considered under the name *Poropsis*, a genus previously thought to be monospecific. However, because of missing data, only one taxon was included in the

multilocus analyses and is represented in Figure S6 as *Poropsis* sp. Our trait inference analysis highlighted numerous symplesiomorphies and synapomorphies, which could be useful for describing the genus. The symplesiomorphic characters include calcification, an unique tufted frond, a creeping and upright axis, a non-ramified and multisiphonous stipe, continuous stipe-frond junction, dichotomous siphon ramifications, primary siphons arranged in one plane, isomorphic dichotomies and supra-dichotomial constrictions. Synapomorphies include a reduced rhizoidal system, absence of secondary structures in frond and stipe siphons, aligned dichotomies, symmetrical constrictions and absence of frond and stipe cortication.

Penicillus nodulosus - Following our proposed revision of the genus *Penicillus* above, *P. nodulosus* needs to be reassigned to a different genus. However, at this stage, we are missing sufficient data to make this taxonomic revision. We need genetic information about other presumed Indo-Pacific *Penicillus* species and their phylogenetic relationships among the Udoteaceae, particularly, their position within or outside this complex. Additional data is needed about the complex itself as well as the closely related species, to assess whether this species should be transferred to a particular genus or whether it should be grouped together with the other two in a same genus.

Chlorodesmis caespitosa - Our redefinition of the genus *Chlorodesmis* s.s. above, led us to reconsider the species *Chlorodesmis caespitosa.* Interestingly, Gepp & Gepp (1911) proposed the genus *Rhipidodesmis* to accommodate the species, because it differs from other *Chlorodesmis* species by their apical branching, thicker upper filaments and the absence of moniliform and radicelliferous basal filaments. However, this was never validated taxonomically. We propose to validate the combination proposed by Gepp & Gepp (1911), including their original diagnosis, and to rename *Chlorodesmis caespitosa* (J. Agardh) as *Rhipidodesmis caespitosa* (J. Agardh) A. Gepp & E.S. Gepp. Also, our ancestral reconstructions of character states identified several symplesiomorphies and synapomorphies supporting and documenting the description of the genus *Rhipidodesmis*: the genus has a unique tufted frond, with dichotomous siphon ramifications and constrictions above the

dichotomies. These three character states are symplesiomorphic. Also, the genus has several synapomorphic character states: it is not calcified, has a discoid holdfast and an upright axis but no stipe; The primary siphons are arranged in one plane, interwoven, with anisomorphic and aligned dichotomies, above which the constrictions are symmetric, but do not have secondary structures, and the frond is uncorticated.

Rhipidodesmis A. Gepp & E.S. Gepp

Diagnosis: Gepp A, Gepp ES. 1911. The codiaceae of the Siboga Expedition, including a monograph of Flabellarieae and Udoteaceae. Siboga-Expeditie 62: 1–150.

Type species: *Rhipidodesmis caespitosa* (J. Agardh) Gepp & Gepp **comb. nov**.

Morphological description emended from Gepp & Gepp (1911): Plant filamentous, gregarious, laxly caespitose, uncalcified, composed of a discoid holdfast, and an upright axis consisting of an unique uncorticated tufted frond but no stipe; Base decubent, colourless and irregularly ramified, very laxly entangled (never densely felted so as to form a spurious stipes); Ascending above, viridescent, fastigiately or flabellately ramified towards the apex; Siphons with dichotomous ramifications (anisomorphic) and evenly (symmetrically) constricted above the dichotomies; Upper dichotomies approximated. Siphons lacking secondary structures.

Geographical distribution (confirmed using DNA sequencing): Pacific Ocean: New Caledonia (Grande Terre, Surprises Is.) (This study), Papua New Guinea (This study), Hawai'i (Wade & Sherwood, 2017), Clipperton (This study). See Guiry & Guiry (2020) for a more detailed distribution in the Indo-Pacific.

Rhipidodesmis caespitosa (J. Agardh) Gepp & Gepp

Type: Ferguson, n° 110

Type locality: Ceylon, Colombo, Sri Lanka

Etymology: Latin adjective for growing in patches or tufts, caespitose (Stearn 1973)

Basionym: *Chlorodesmis caespitosa* J.Agardh (Agardh JG. 1887. Till Algernes Systematik.Nya bidrag. Acta Universitatis Lundensis 23: 1–174, 5 plates)

Synonymes: *Avrainvillea caespitosa* (J.Agardh) G.Murray & Boodle; *Chlorodesmis formosana* Yamada

Description: see Gepp & Gepp (1911).

Geographical distribution (confirmed using DNA sequencing): Pacific Ocean (confirmed with DNA sequencing): New Caledonia (Grande Terre, Surprises Is.) (This study), Papua New Guinea (This study), Hawai'i (Wade & Sherwood, 2017), Clipperton (This study). See Guiry & Guiry (2020) for a more detailed distribution in the Indo-Pacific.

List of vouchers from this study (limited to 2 per locality): New Caledonia, Grande Terre, 2017: NOU203812; New Caledonia, Surprises Is., 2017: NOU203898; Papua New Guinea, Kavieng, 2014: NOU203345; Hawai'i, O'ahu, 2013 :HADL01229; Clipperton, 2010: NOU203464, NOU203470.

The phylogenetic relationships between the three taxa in this clade are strongly supported (bs: 100; PP: 1), and it would also be acceptable to group them under the same genus (Figure S6). The three taxa share several morphological characters including the shape of their monoliform siphons, with deep constrictions at the dichotomies or between them. Within this clade*, P. nodulosus* has a brush-like gross morphology, and differs from the two other taxa which are delicate and filamentous. However, *P. nodulosus* also has a filamentous form in its life cycle, as described by Harvey (1858) – monoliformous and ramified filaments arising directly from the matted-root fibres (*i.e.*, lack of stipe) –, such as the form *P. capitatus* f. *mediterraneus* (Decaisne) Huve & Huve (*i.e., "*ex-Espera"). This filamentous form was found in our specimens of *P. nodulosus,* was confirmed genetically as belonging to the species, and could correspond to that observed by Harvey (1858). Therefore, we could hypothesize that the filamentous forms of *Poropsis* sp. and *Rhipidodesmis caespitosa* are life-stages of a more complex morphological species and considering these three taxa as part of the same genus could make sense. Conversely, numerous species hypotheses were identified in the species delimitation analyses (Fig S1 & S2) but could not be included in our multilocus phylogeny due to

1161 missing genetic data. Thus, it is likely that clade I is more diverse than currently observed in our
1162 analyses, and could be composed of several genera. Larger sampling is therefore essential to
1163 correctly delineate the species and their geographical distributions before taxonomic decisions are
1164 made for the “PPR complex”.

1165 .

CONCLUSION

Based on a total of 43 delimited species, our multilocus phylogeny revealed the monophyly of the family Udoteaceae, whereas most of its genera were polyphyletic. We propose to 1) revise the genera *Udotea* s.s., *Rhipidosiphon* s.s. and *Chlorodesmis* s.s.; 2) describe three new genera: *Glaukea* gen. nov., *Ventalia* gen. nov., and *Udoteopsis* gen. nov.; and 3) validate Gepp & Gepp's genus *Rhipidodesmis*. None of these delimited genera or their species appeared pantropical. For the first time, we produced a time-calibrated phylogeny of the family Udoteaceae. We inferred the evolution of its morpho-anatomical trait, and the taxonomic relevance of each morpho-anatomical character, for the diagnosis of the revised genera was reassessed. Numerous homoplasies were identified that remain useful for delimitating the different genera if combined with other characters. They also represent evidence of particular patterns of evolution during the diversification of Udoteaceae, such as parallel or convergent morphological evolutions or adaptations. Additionally, numerous symplesiomorphies and synapomorphies were identified and their relevance for genus-level identification was confirmed. Further study focusing on Core Halimedineae or Bryopsidales would provide information about the evolutionary patterns and taxonomic relevance of the various character states at a wider scale. Finally, considering the Udoteaceae species and genus richness, as well as their molecular and morphological diversity highlighted in this study, we believe that the taxonomic changes proposed by Cremen et al. (2019), particularly the proposal of downgrading family Udoteaceae to tribe is not justified.

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1456

1457 **Tables**

1458 **Table 1:** Number of delimited PSHs, for each of the five methods applied to *tufA* and *rbcL*, including

1459 the number of singletons.

1460

Methods		GMYC	bGMYC	hPTP	mPTP	ABGD
Number of delimited PSHs | number of singletons	*tufA*	39|5	43|8	53|17	50|14	51|10
	rbcL	49|13	48|13	56|27	53|20	55|17

1461

1462 **Table 2:** Main results of the trait evolution mapping for the discrete morpho-anatomical characters having a phylogenetical signal and for which the
1463 ancestral state could be estimated for the Udoteaceae ancestor. Status of each character state (homoplasy, synapomophy or symplesiomorphy) is also
1464 reported.

1465

CHARACTERS	STATUS AND TAXONOMIC RELEVANCE	STATE ESTIMATION FOR THE UDOTEACEAE ANCESTOR
Stipe (presence/absence)	**Presence:** symplesiomorphy; **Absence**: homoplasy/synapomorphy	Presence of stipe
Calcification (presence/absence)	**Presence**: symplesiomorphy; **Absence**: homoplasy/synapomorphy	Calcified
Calcified siphons surface porous or non-porous	**Non-porous**: symplesiomorphy; **Porous**: homoplasy	Non porous
Stipe type	**Multisiphonous**: symplesiomorphy; **Monosiphonous**: homoplasy	Multisiphonous
Primary siphons disposition	**On one plane**: symplesiomorphy; **On several planes**: homoplasy/synapomorphy	On one plane
External habit (Growth)	**Creeping and upright axis**: symplesiomorphy; **Only upright axis**: synapomorphy	Creeping and upright
Thallus cortication	**Total cortication**: symplesiomorphy; **Partial cortication**: homoplasy; **Absence of cortication**: homoplasy/synapomorphy	Total cortication of the thallus
Frond shape	**Flabellate**: symplesiomorphy; **Capitate**: homoplasy; **Caespitose**: homoplasy/synapomorphy; **Axis with different structures**: synapomorphy; **Cyathiform and filiform**: autapomorphies	Flabellate
Frond thickness	**Pluristromatic (or in tuft)**: symplesiomorphy; **Monostromatic**: homoplasy/synapomorphy	Pluristromatic
Secondary structures on the frond siphon	**Appendages**: symplesiomorphy; **Protuberances**: homoplasy; **None**: homoplasy/synapomorphy	Appendages
Frond cortication	**Complete cortication**: symplesiomorphy; **Incomplete cortication**: homoplasy; **Absence of cortication**: homoplasy/synapomorphy	Complete cortication of the frond
Dichotomies alignment	**Not aligned**: symplesiomorphy; **Aligned**: homoplasy; **Aligned only at the basis**: homoplasy/synapomorphy	Not aligned
Type of constrictions	**Asymmetrical**: symplesiomorphy; **Symmetrical**: homoplasy/synapomorphy	Asymmetrical
Secondary structures on the stipe siphon	**Appendages**: symplesiomorphy; **Descending laterals**: homoplasy; **None**: homoplasy/synapomorphy	Appendages
Stipe cortication	**Complete cortication**: symplesiomorphy; **Pseudocortex**: homoplasy; **Absence of cortication**: homoplasy/synapomorphy	Complete cortication of the stipe
Stipe-frond junction	**Continuous**: symplesiomorphy; **Sharp**: homoplasy	Continuous

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1467

Figures Legends

Figure 1. A, ML phylogeny produced using the multi-marker matrix (*tufA*, *rbcL* and 18S rDNA) with bootstraps and posterior probabilities indicated at nodes (bs/PP). Species of the same genus as recognized by Guiry & Guiry (2020, searched on January 2020) are indicated using the same color. (*) indicates type species. **B,** Condensed ML tree showing the nine clades (A-I) proposed for the taxonomic revision of Udoteaceae genera. Clades A, B, D and F represent current genera whose taxonomic boundaries are redefined in this study. Clades C, E, and G represent new genera, while the status of clades H and I remains unclear.

Figure 2. Time-calibrated phylogeny of the Udoteaceae from the BEAST analysis. Estimated divergence times are indicated at the nodes, and grey bars indicate the 95% HPD (highest probability densities). Black asterisks represent nodes supported for both the ML and Bayesian Inference methods (*bs* > 85; PP > 0.95), while grey asterisks represent nodes that are only supported in the BI analysis (PP > 0.95; *bs* < 85). Asterisks after taxon names indicate invalid genus or species requiring taxonomic revision.

Figure 3: Ancestral state reconstruction for **A,** Upright vegetative form; **B,** Thallus cortication; **C,** Presence or absence of calcification; and **D,** Presence or absence of secondary structures on frond siphons. The analyses were carried out using MCCT resulting from the BEAST analysis and 1,000 iterations. Pie charts show the frequency of character states at each node.

Figure 4. ML phylogeny of *Udotea* s.s. Bootstraps and Posterior probabilities (bs/PP) are indicated at nodes. Species hypotheses obtained using the five species delimitation methods on the two markers are shown on the right, along with allocated species names, illustrations and geographical distribution (A= *U. flabellum*; B= *U. dotyi*; C= U. dixonii; D= U. occidentalis; E= U. geppiorum; F= *U.* sp1). The genus symplesiomorphies and synapomorphies, which were identified by inferring morphological characters on the time-calibrated phylogeny, are shown on the left. Image rights: Payri, C.E.; Menou, J.L., Littler & Littler (2000;*).

1493 **Figure 5.** *Glaukea* genus. **A-D,** *Glaukea argentea* 1 (NOU204097; NOU204098). **A,** Herbarium
1494 specimen. **B,** *In situ* specimen. **C,** Siphons with lobed appendages. **D,** Lobed appendages. **E-H,** *G.*
1495 *argentea* 2 (NOU203657, NOU203661). **E,** Herbarium specimen. **F,** *In situ* specimen. **G,** Siphons with
1496 lobed appendages. **H,** Lobed appendages; Scale bars: B= 4 cm; C= 80 µm; D= 57 µm; F= 2.3 cm; G=
1497 120 µm; H= 37.5 µm.

1498 **Figure 6.** ML phylogeny of *Chlorodesmis.* Bootstraps and Posterior probabilities (bs/PP) are indicated
1499 at nodes. Species hypotheses obtained using the five species delimitation methods on the two
1500 markers are shown on the right, along with allocated species names, illustrations and geographical
1501 distribution (B= *C*. cf. *hildebrandtii;* C= *C.* cf. *major;* D= *C*. sp3; F= *C*. sp2). The genus
1502 symplesiomorphies and synapomorphies, which were identified by inferring morphological
1503 characters on the time-calibrated phylogeny, are shown on the left. Abbreviations: PNG, Papua New
1504 Guinea. Image rights: Payri, C.E

1505 **Figure 7.** ML phylogeny of *Ventalia* gen.nov. Bootstraps and Posterior probabilities (bs/PP) are
1506 indicated at nodes. Species hypotheses obtained using the five species delimitation methods on the
1507 two markers are presented on the right, along with allocated species names, illustrations and
1508 geographical distribution (A= *V.* sp1; D= *V. orientalis*; E = *V.* sp2.; H= *V.* sp4). The genus
1509 symplesiomorphies and the synapomorphy, which were identified by inferring morphological
1510 characters on the time-calibrated phylogeny, are indicated on the left. Image rights: Payri, C.E.;
1511 Lasne, G.

1512 **Figure 8.** *Ventalia* genus. **A-D**, *Ventalia indica* (NOU203645-8). **A,** Herbarium specimen. **B,** *In situ*
1513 specimen. **C,** Blade siphons with protuberances. **D,** Stipe siphon with dichotomously divided
1514 appendages. **E-H,** *Ventalia orientalis* (NOU203718-722; NOU203680; NOU203683). **E,** Herbarium
1515 specimen. **F,** *In situ* specimen. **G,** Smooth blade siphon. **H,** Stipe siphon with dichotomously divided
1516 appendages. **I-L,** *Ventalia papillosa* (NOU203603; NOU203587). **I,** Herbarium specimen. **J,** *In situ*
1517 specimen. **K,** Blade siphons with protuberances. **L,** Stipe siphon with dichotomously divided

1518 appendages. Scale bars: B= 3 cm; C= 80 µm; D= 65 µm; F= 0.8 cm; G= 80 µm; H= 65 µm; J= 0.7 cm; K=
1519 80 µm; L= 120 µm.

1520 **Figure 9.** ML phylogeny of *Rhipidosiphon*. Bootstraps and Posterior probabilities (bs/PP) are indicated
1521 at nodes. Species hypotheses obtained using the five species delimitation methods on the two
1522 markers are shown on the right, along with allocated species names, illustrations and geographical
1523 distribution (B= *R.* sp4; D= *R. javensis*). The genus symplesiomorphies and synapomorphies, which
1524 were identified by inferring morphological characters on the time-calibrated phylogeny, are shown
1525 on the left. Image rights: Payri, C.E.; Lasne, G, Coppejans et al. (2011;*).

1526 **Figure 10**. *Udoteopsis maiottensis* (NOU203562; NOU203570; PC0171655). **A,** Herbarium specimen.
1527 **B,** Specimen with corticated stipe and growth zone at the margin. **C-E,** Frond. **C,** Smooth siphon;
1528 asymetrical dichotomies with constricitions. **D,** Calcificed siphons sheath with pores or cracks. **E,**
1529 Growth zone with swollen siphons. **F-H,** Corticated stipe with protuberances. Scale bars: B= 0.75 cm;
1530 C= 125 µm; D= 16 µm; E= 120 µm; F= 250 µm; G= 415 µm; H= 250 µm.

Supporting Information

Data S1: Morpho-anatomical characters studied and associated states.

Data S2: Results of the species delimitation analyses on *tufA* and *rbcL* markers.

Data S3: Supports (ML) of hPTP partitions for the *tufA* dataset on Udoteaceae.

Data S4: Supports (ML) of hPTP partitions for the *rbcL* dataset on Udoteaceae.

Data S5: Summary of correlations, ancestral estimations and stochastic mapping results for all the characters studied.

Figure S1: Species delimitation results obtained with the five methods (ABGD, GMYC, bGMYC, PTP and mPTP) on the *tufA* dataset. The tree represented is MCCT tree from the BEAST analysis. Partitions retained as SSHs following the majority rule are indicated by black bars. Blue bars represent the partition retained as SSHs, although not in the majority rule, while grey bars are the different partitions not retained. The defined SSHs (= clades) are indicated in the right column, together with species assignments obtained from morpho-anatomical observations.

Figure S2: Species delimitation results obtained with the five methods (ABGD, GMYC, bGMYC, PTP and mPTP) on the *rbcL* dataset. The tree represented is MCCT tree from the BEAST analysis Partitions retained as SSHs following the majority rule are indicated by black bars. Blue bars represent the partition retained as SSHs, although not in the majority rule while grey bars are the different partition not retained. The defined SSHs (= clades) are indicated in the right column, together with species assignments obtained from morpho-anatomical observations.

Figure S3: ML phylogeny of the Udoteaceae obtained using RAXML on chloroplast genes (*tufA*+*rbcL*). Bootstraps are indicated at nodes.

Figure S4: ML phylogeny of the Udoteaceae obtained using RAXML on the nuclear 18S rDNA gene. Bootstraps are indicated at nodes.

Figure S5: ML phylogeny of the "PRRU complex". Bootstrap and Posterior probabilities (bs/PP) are indicated at nodes. Species hypotheses obtained using the five species delimitation methods on the two markers are presented on the right, along with allocated species names and illustrations. The epithets of the species are left as used in Guiry & Guiry (2020), but are no longer valid after this study. The two alternative proposals for taxonomic treatment are proposed on the right, as well as the symplesiomorphies and synapomorphies of the "single genus" hypothesis, identified by inferring morphological characters on the time-calibrated phylogeny. Image rights: Payri, C.E., Littler & Littler (2000; *).

Figure S6: ML phylogeny of the "PPR complex". Bootstrap and Posterior probabilities (bs/PP) are indicated at nodes. The species hypotheses obtained using the five species delimitation methods on the two markers are shown on the right, along with allocated species names, illustrations and geographical distribution. Image rights: Payri, C.E.

Table S1: List of specimens with sample ID, species identification, location of sampling, Genbank accession numbers (or BOLD sequence ID in grey for those not submitted), the sequences used in the species delimitation approach and the corresponding SSH number, as well as the sequences used in multilocus and time-calibrated phylogenies.

Table S2: Primers used for amplification of the *tuf*A, *rbc*L, and 18S rDNA markers.

Table S3: Details of ML and BI phylogenetic analyses for the different Udoteaceae datasets.

Table S4: Calibration points used for the reconstruction of the Udoteaceae time-calibrated phylogeny. Literature references, age, as well as node position and calibration priors are indicated.

1576 **Table S5:** *A posteriori* probabilities (PP) of the partitions defined by the bGMYC method on the *tufA*
1577 marker for Udoteaceae.

1578 **Table S6:** *A posteriori* probabilities (PP) of the partitions defined by the bGMYC method on the *rbcL*
1579 marker for Udoteaceae.

1580 **Table S7:** Number of common PSHs between the different methods and markers.

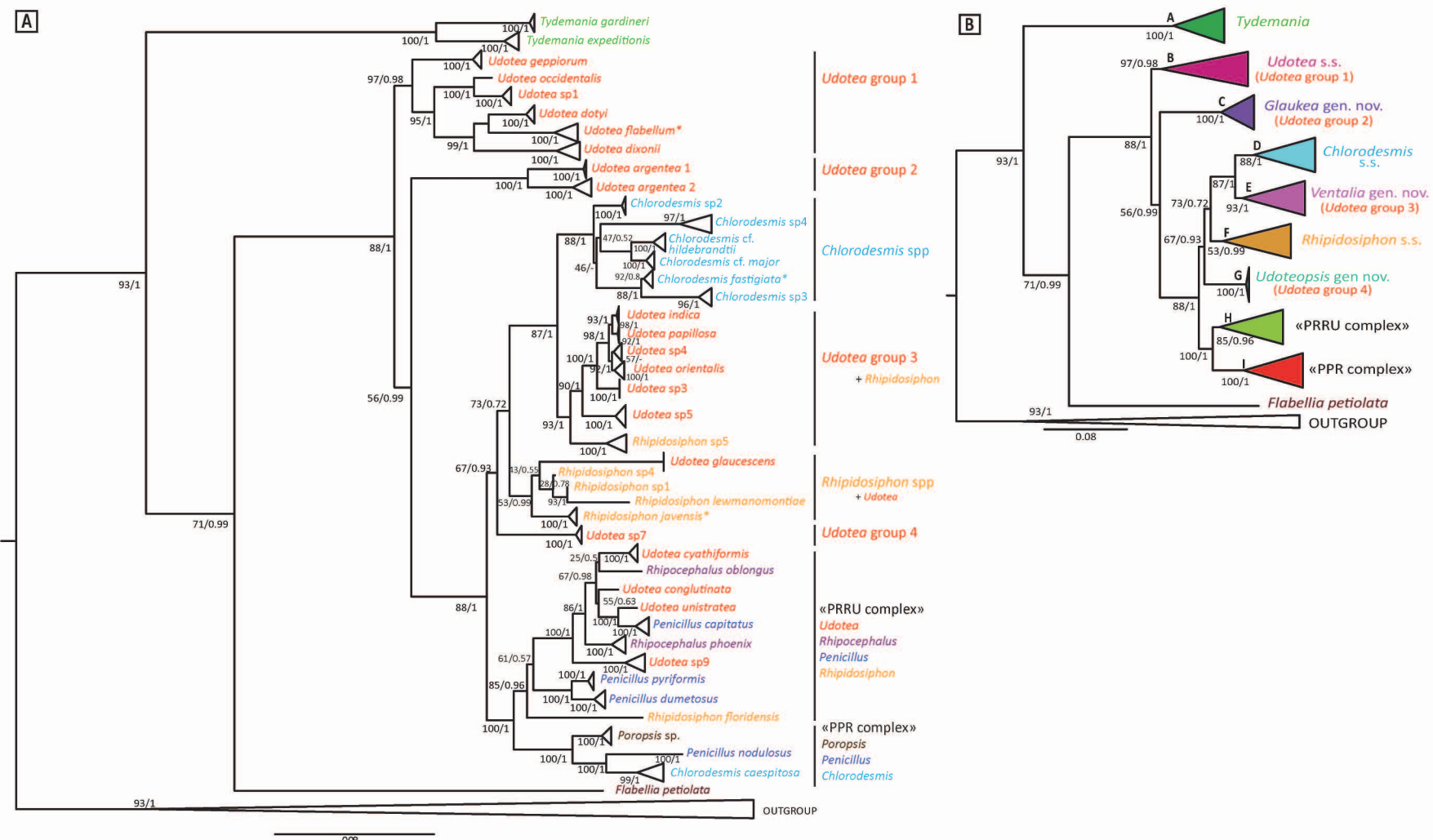
1581 **Table S8:** Details of the incongruence resolution process and species assignment of the SSHs.

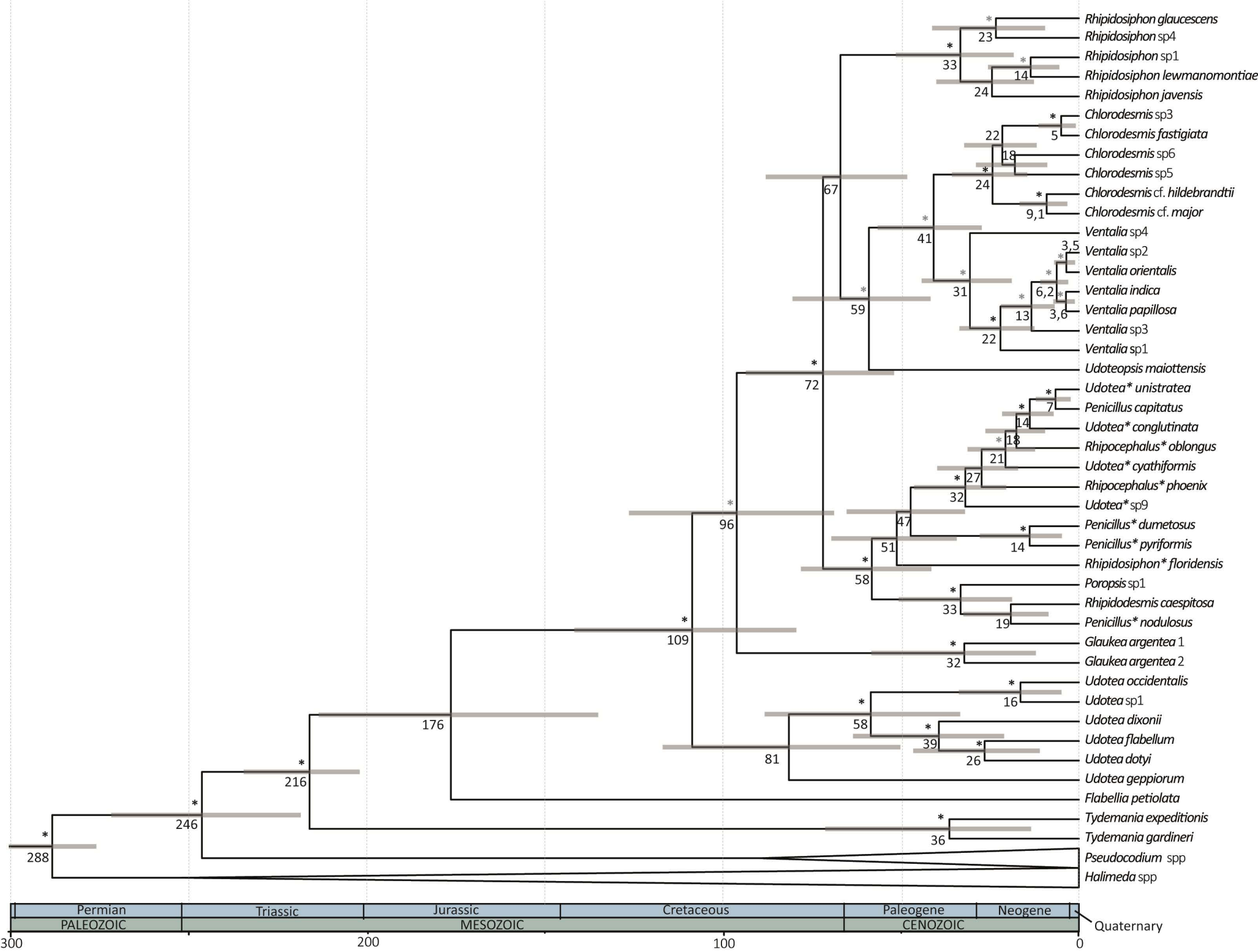
1582 **Table S9:** Analysis of the phylogenetic signal (PS) for continuous traits using the Bloomberg (K) and
1583 Pagel statistics (λ). The PS is considered strong if $K > 1$ or $\lambda \geq 1$ and weak if $0 < K < 1$. If $0 < \lambda < 1$, the PS
1584 does not follow the BM model.

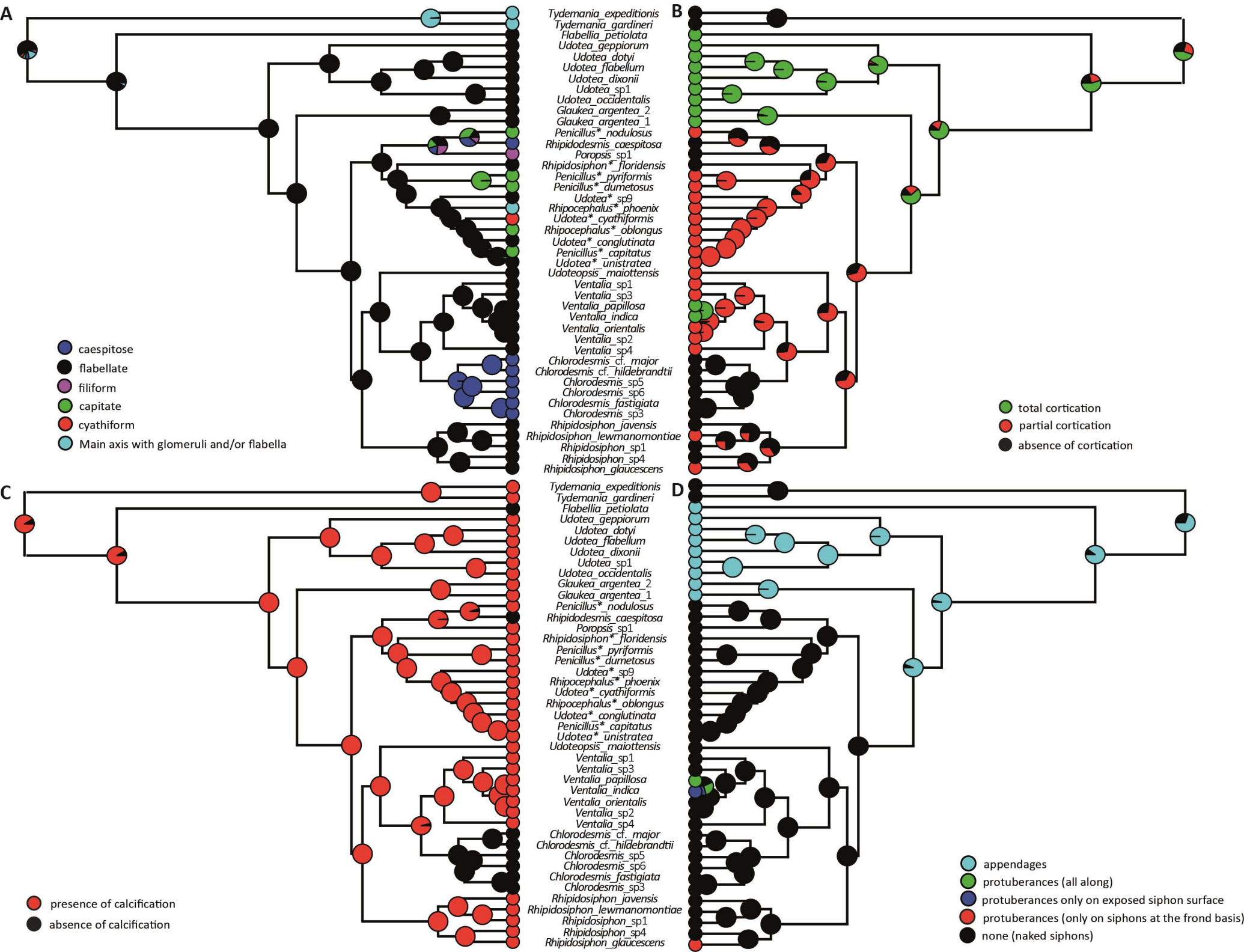
1585 **Table S10:** Results of phylogenetic signal analyses on discrete characters. Traits with strong
1586 phylogenetic signal ($D < 0$) are indicated in bold with D values in green.

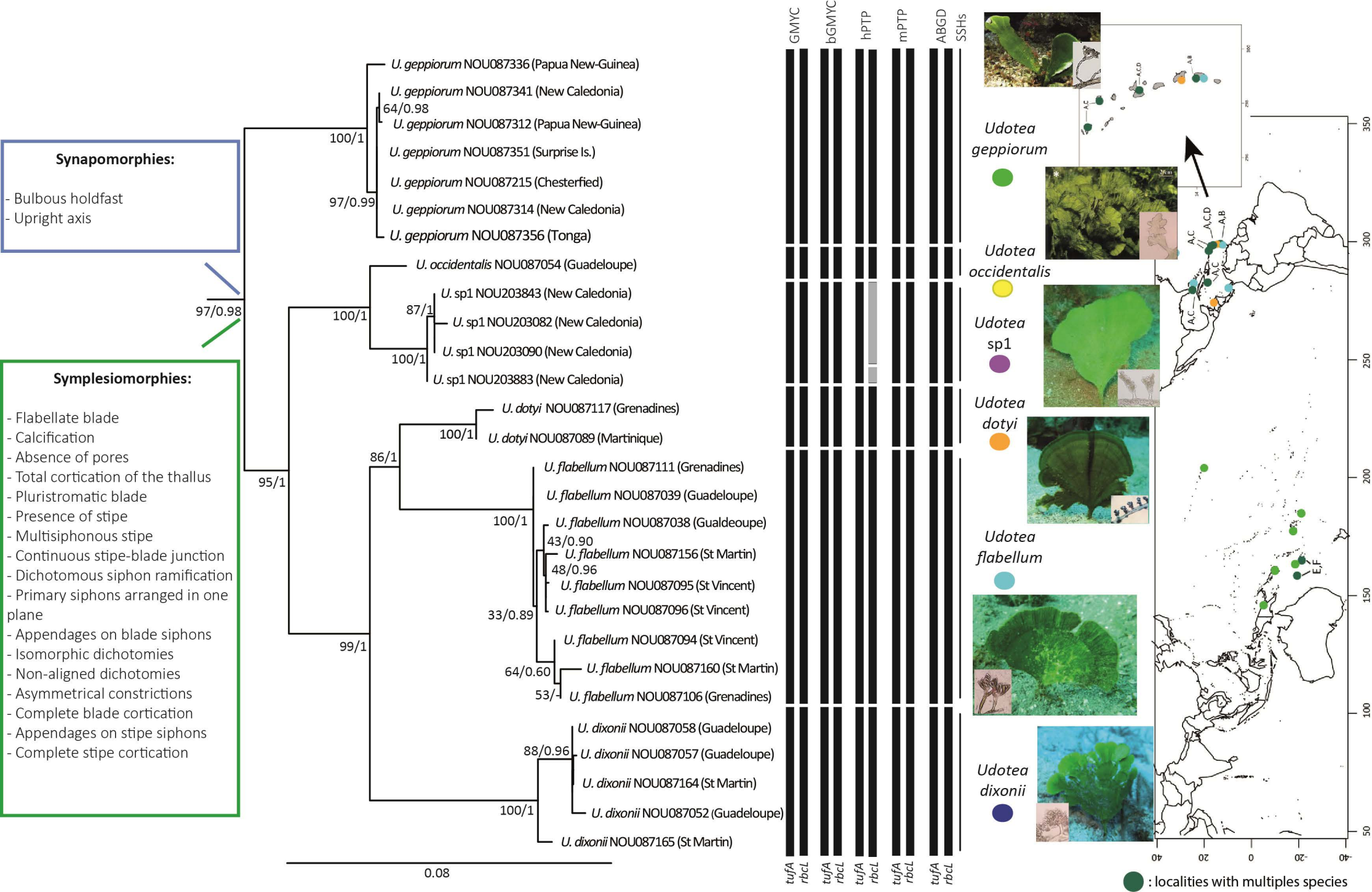
1587 **Table S11**: Results of the discrete character correlation test. Acronyms refer to those used in Data S1.

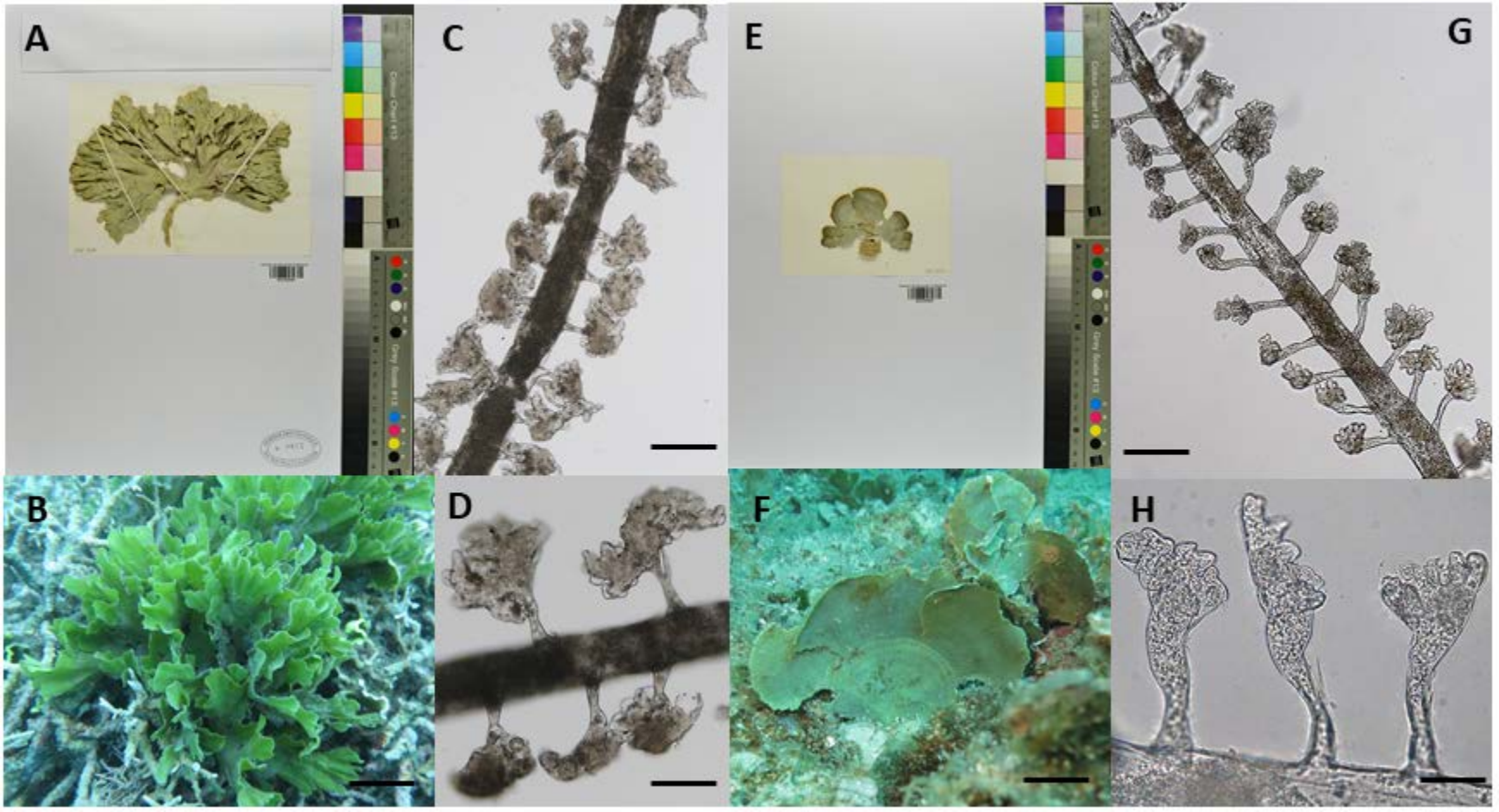
1588 **Table S12:** Summary of phylogenetic signal, taxonomic relevance and ancestral state estimation for
1589 each trait studied. The absence of convincing results for a given character is indicated by a “X”.

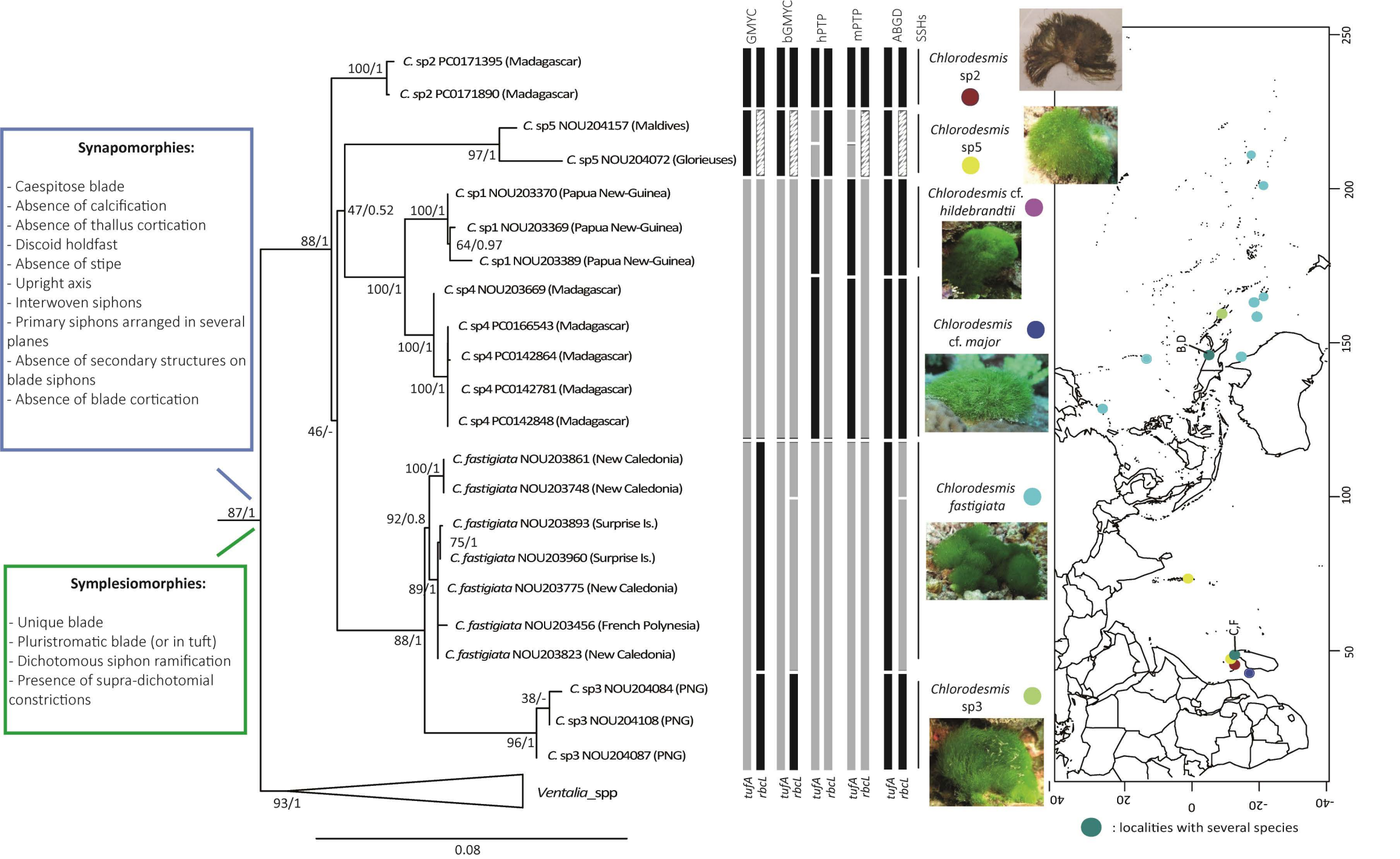

A
Tydemania gardineri
Tydemania expeditionis
Udotea geppiorum
Udotea occidentalis
Udotea sp1
Udotea dotyi
Udotea flabellum*
Udotea dixonii
Udotea argentea 1
Udotea argentea 2
Chlorodesmis sp2
Chlorodesmis sp4
Chlorodesmis cf. hildebrandtii
Chlorodesmis cf. major
Chlorodesmis fastigiata*
Chlorodesmis sp3
Udotea indica
Udotea papillosa
Udotea sp4
Udotea orientalis
Udotea sp3
Udotea sp5
Rhipidosiphon sp5
Udotea glaucescens
Rhipidosiphon sp4
Rhipidosiphon sp1
Rhipidosiphon lewmanomontiae
Rhipidosiphon javensis*
Udotea sp7
Udotea cyathiformis
Rhipocephalus oblongus
Udotea conglutinata
Udotea unistratea
Penicillus capitatus
Rhipocephalus phoenix
Udotea sp9
Penicillus pyriformis
Penicillus dumetosus
Rhipidosiphon floridensis
Poropsis sp.
Penicillus nodulosus
Chlorodesmis caespitosa
Flabellia petiolata
OUTGROUP
Udotea group 1
Udotea group 2
Chlorodesmis spp
Udotea group 3
+ Rhipidosiphon
Rhipidosiphon spp
+ Udotea
Udotea group 4
«PRRU complex»
Udotea
Rhipocephalus
Penicillus
Rhipidosiphon
«PPR complex»
Poropsis
Penicillus
Chlorodesmis
B
Tydemania
Udotea s.s.
(Udotea group 1)
Glaukea gen. nov.
(Udotea group 2)
Chlorodesmis s.s.
Ventalia gen. nov.
(Udotea group 3)
Rhipidosiphon s.s.
Udoteopsis gen nov.
(Udotea group 4)
«PRRU complex»
«PPR complex»
Flabellia petiolata
OUTGROUP
0.08

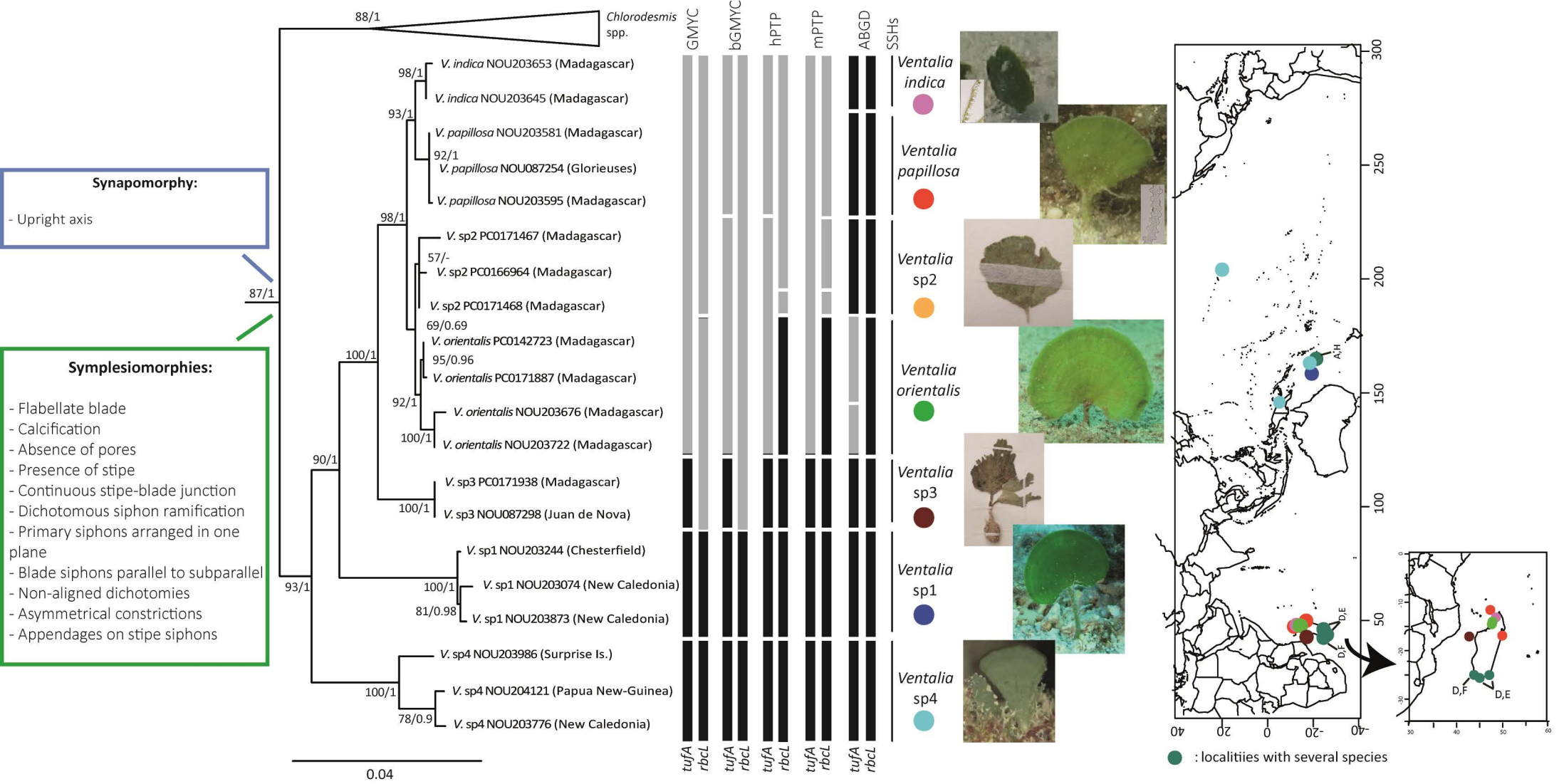

Rhipidosiphon glaucescens
Rhipidosiphon sp4
Rhipidosiphon sp1
Rhipidosiphon lewmanomontiae
Rhipidosiphon javensis
Chlorodesmis sp3
Chlorodesmis fastigiata
Chlorodesmis sp6
Chlorodesmis sp5
Chlorodesmis cf. hildebrandtii
Chlorodesmis cf. major
Ventalia sp4
Ventalia sp2
Ventalia orientalis
Ventalia indica
Ventalia papillosa
Ventalia sp3
Ventalia sp1
Udoteopsis maiottensis
Udotea* unistratea
Penicillus capitatus
Udotea* conglutinata
Rhipocephalus* oblongus
Udotea* cyathiformis
Rhipocephalus* phoenix
Udotea* sp9
Penicillus* dumetosus
Penicillus* pyriformis
Rhipidosiphon* floridensis
Poropsis sp1
Rhipidodesmis caespitosa
Penicillus* nodulosus
Glaukea argentea 1
Glaukea argentea 2
Udotea occidentalis
Udotea sp1
Udotea dixonii
Udotea flabellum
Udotea dotyi
Udotea geppiorum
Flabellia petiolata
Tydemania expeditionis
Tydemania gardineri
Pseudocodium spp
Halimeda spp
Permian
Triassic
Jurassic
Cretaceous
Paleogene
Neogene
PALEOZOIC
MESOZOIC
CENOZOIC
Quaternary
300
200
100
0

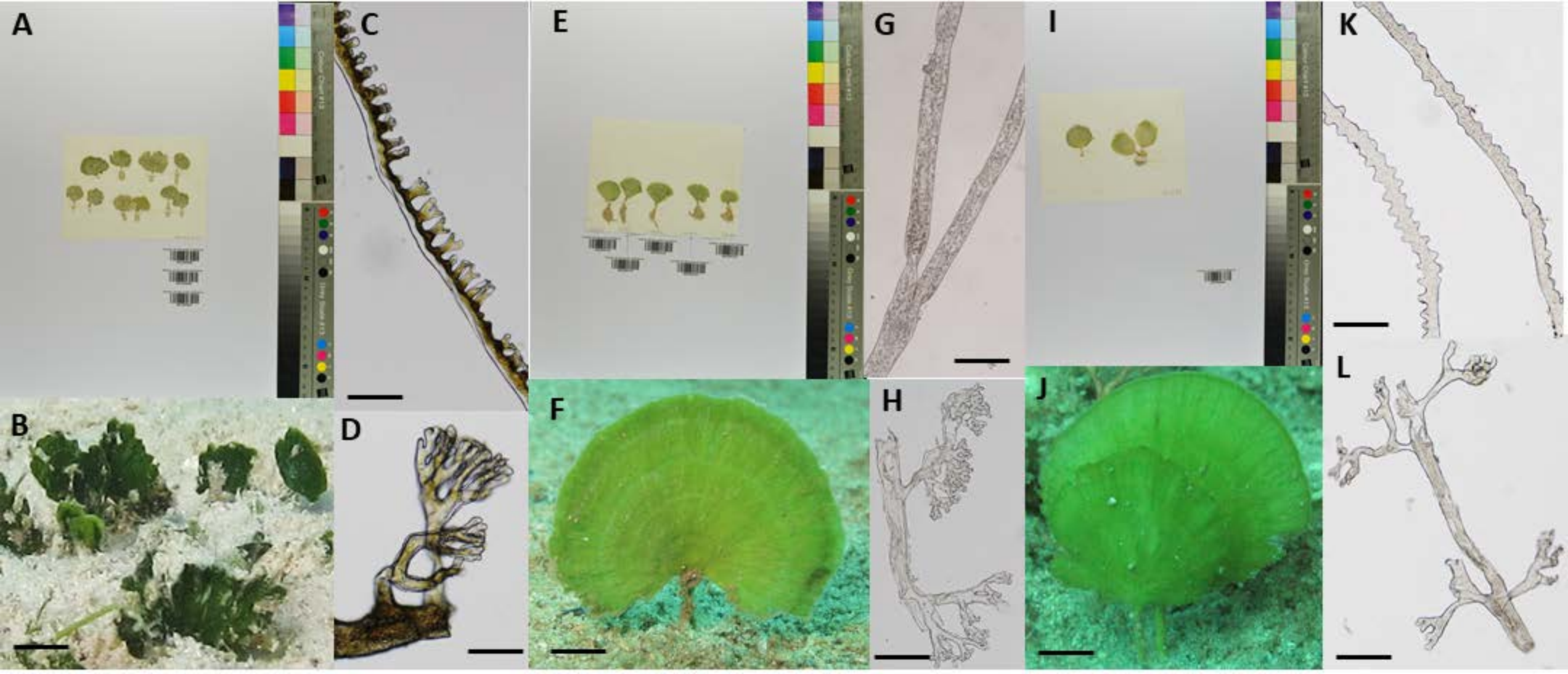

A
B
C
D
Tydemania_expeditionis
Tydemania_gardineri
Flabellia_petiolata
Udotea_geppiorum
Udotea_dotyi
Udotea_flabellum
Udotea_dixonii
Udotea_sp1
Udotea_occidentalis
Glaukea_argentea_2
Glaukea_argentea_1
Penicillus*_nodulosus
Rhipidodesmis_caespitosa
Poropsis_sp1
Rhipidosiphon*_floridensis
Penicillus*_pyriformis
Penicillus*_dumetosus
Udotea*_sp9
Rhipocephalus*_phoenix
Udotea*_cyathiformis
Rhipocephalus*_oblongus
Udotea*_conglutinata
Penicillus*_capitatus
Udotea*_unistratea
Udoteopsis_maiottensis
Ventalia_sp1
Ventalia_sp3
Ventalia_papillosa
Ventalia_indica
Ventalia_orientalis
Ventalia_sp2
Ventalia_sp4
Chlorodesmis_cf._major
Chlorodesmis_cf._hildebrandtii
Chlorodesmis_sp5
Chlorodesmis_sp6
Chlorodesmis_fastigiata
Chlorodesmis_sp3
Rhipidosiphon_javensis
Rhipidosiphon_lewmanomontiae
Rhipidosiphon_sp1
Rhipidosiphon_sp4
Rhipidosiphon_glaucescens
caespitose
flabellate
filiform
capitate
cyathiform
Main axis with glomeruli and/or flabella
total cortication
partial cortication
absence of cortication
presence of calcification
absence of calcification
appendages
protuberances (all along)
protuberances only on exposed siphon surface
protuberances (only on siphons at the frond basis)
none (naked siphons)

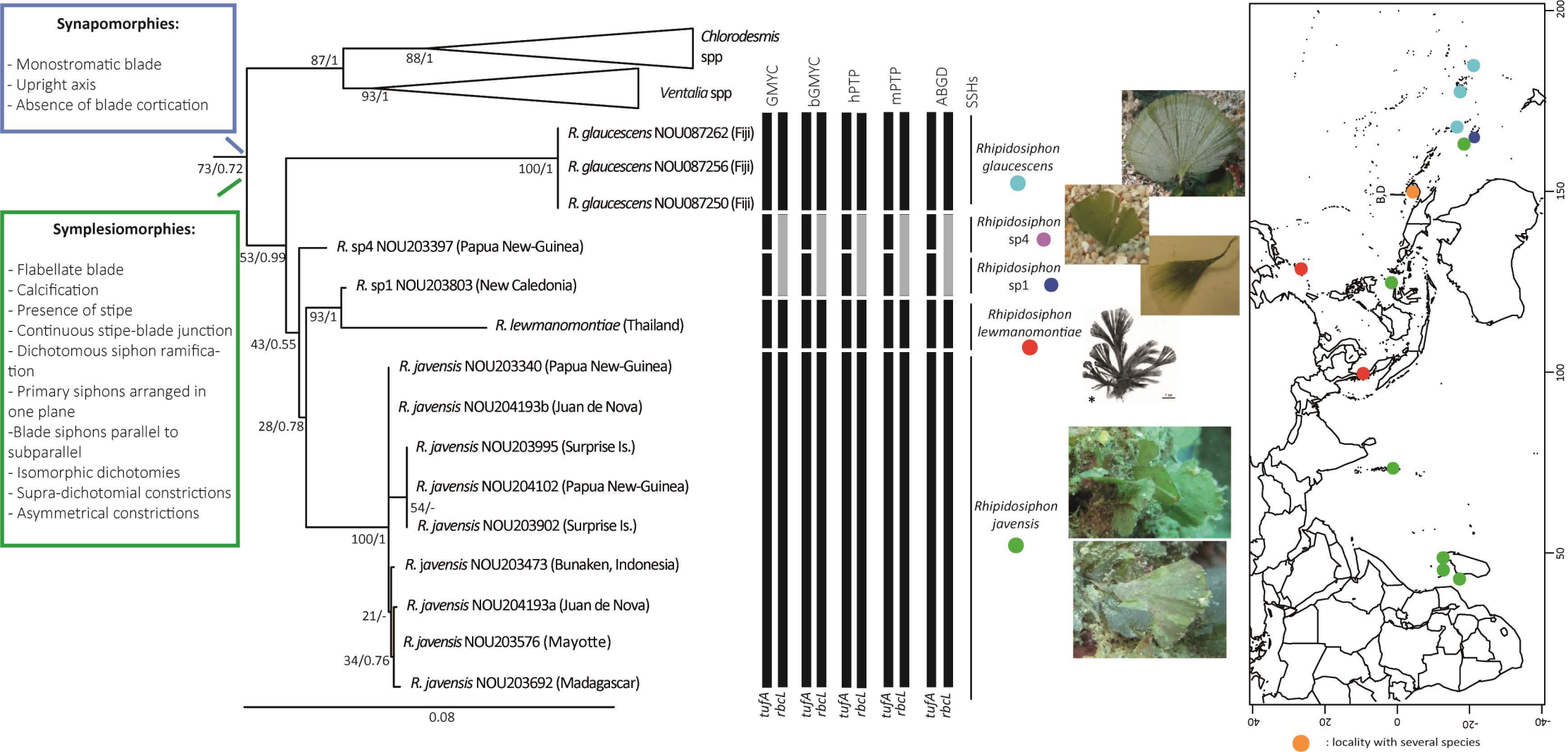

Synapomorphies:
- Bulbous holdfast
- Upright axis
Symplesiomorphies:
- Flabellate blade
- Calcification
- Absence of pores
- Total cortication of the thallus
- Pluristromatic blade
- Presence of stipe
- Multisiphonous stipe
- Continuous stipe-blade junction
- Dichotomous siphon ramification
- Primary siphons arranged in one plane
- Appendages on blade siphons
- Isomorphic dichotomies
- Non-aligned dichotomies
- Asymmetrical constrictions
- Complete blade cortication
- Appendages on stipe siphons
- Complete stipe cortication
U. geppiorum NOU087336 (Papua New-Guinea)
U. geppiorum NOU087341 (New Caledonia)
64/0.98
U. geppiorum NOU087312 (Papua New-Guinea)
100/1
U. geppiorum NOU087351 (Surprise Is.)
U. geppiorum NOU087215 (Chesterfied)
97/0.99
U. geppiorum NOU087314 (New Caledonia)
U. geppiorum NOU087356 (Tonga)
U. occidentalis NOU087054 (Guadeloupe)
U. sp1 NOU203843 (New Caledonia)
87/1
100/1
U. sp1 NOU203082 (New Caledonia)
97/0.98
100/1
U. sp1 NOU203090 (New Caledonia)
U. sp1 NOU203883 (New Caledonia)
U. dotyi NOU087117 (Grenadines)
100/1
U. dotyi NOU087089 (Martinique)
86/1
U. flabellum NOU087111 (Grenadines)
95/1
U. flabellum NOU087039 (Guadeloupe)
100/1
U. flabellum NOU087038 (Gualdeoupe)
43/0.90
U. flabellum NOU087156 (St Martin)
48/0.96
U. flabellum NOU087095 (St Vincent)
33/0.89
U. flabellum NOU087096 (St Vincent)
99/1
U. flabellum NOU087094 (St Vincent)
64/0.60
U. flabellum NOU087160 (St Martin)
53/-
U. flabellum NOU087106 (Grenadines)
U. dixonii NOU087058 (Guadeloupe)
88/0.96
U. dixonii NOU087057 (Guadeloupe)
U. dixonii NOU087164 (St Martin)
100/1
U. dixonii NOU087052 (Guadeloupe)
U. dixonii NOU087165 (St Martin)
0.08
GMYC
bGMYC
hPTP
mPTP
ABGD
SSHs
tufA rbcL
Udotea geppiorum
Udotea occidentalis
Udotea sp1
Udotea dotyi
Udotea flabellum
Udotea dixonii
A,C
A,C,D
A,B
E,F
: localities with multiples species


A
C
E
G
B
D
F
H


Synapomorphies:
- Caespitose blade
- Absence of calcification
- Absence of thallus cortication
- Discoid holdfast
- Absence of stipe
- Upright axis
- Interwoven siphons
- Primary siphons arranged in several planes
- Absence of secondary structures on blade siphons
- Absence of blade cortication
Symplesiomorphies:
- Unique blade
- Pluristromatic blade (or in tuft)
- Dichotomous siphon ramification
- Presence of supra-dichotomial constrictions
87/1
100/1
C. sp2 PC0171395 (Madagascar)
C. sp2 PC0171890 (Madagascar)
97/1
C. sp5 NOU204157 (Maldives)
C. sp5 NOU204072 (Glorieuses)
88/1
47/0.52
100/1
C. sp1 NOU203370 (Papua New-Guinea)
C. sp1 NOU203369 (Papua New-Guinea)
64/0.97
C. sp1 NOU203389 (Papua New-Guinea)
100/1
C. sp4 NOU203669 (Madagascar)
100/1
C. sp4 PC0166543 (Madagascar)
C. sp4 PC0142864 (Madagascar)
100/1
C. sp4 PC0142781 (Madagascar)
C. sp4 PC0142848 (Madagascar)
46/-
100/1
C. fastigiata NOU203861 (New Caledonia)
C. fastigiata NOU203748 (New Caledonia)
92/0.8
C. fastigiata NOU203893 (Surprise Is.)
75/1
C. fastigiata NOU203960 (Surprise Is.)
89/1
C. fastigiata NOU203775 (New Caledonia)
C. fastigiata NOU203456 (French Polynesia)
88/1
C. fastigiata NOU203823 (New Caledonia)
38/-
C. sp3 NOU204084 (PNG)
C. sp3 NOU204108 (PNG)
96/1
C. sp3 NOU204087 (PNG)
Ventalia_spp
93/1
0.08
GMYC
bGMYC
hPTP
mPTP
ABGD
SSHs
tufA rbcL
Chlorodesmis sp2
Chlorodesmis sp5
Chlorodesmis cf. hildebrandtii
Chlorodesmis cf. major
Chlorodesmis fastigiata
Chlorodesmis sp3
B,D
C,F
250
200
150
100
50
40
20
0
-20
-40
: localities with several species


Synapomorphy:
- Upright axis
Symplesiomorphies:
- Flabellate blade
- Calcification
- Absence of pores
- Presence of stipe
- Continuous stipe-blade junction
- Dichotomous siphon ramification
- Primary siphons arranged in one plane
- Blade siphons parallel to subparallel
- Non-aligned dichotomies
- Asymmetrical constrictions
- Appendages on stipe siphons
88/1
Chlorodesmis spp.
98/1
V. indica NOU203653 (Madagascar)
V. indica NOU203645 (Madagascar)
93/1
V. papillosa NOU203581 (Madagascar)
92/1
V. papillosa NOU087254 (Glorieuses)
V. papillosa NOU203595 (Madagascar)
98/1
V. sp2 PC0171467 (Madagascar)
57/-
V. sp2 PC0166964 (Madagascar)
87/1
V. sp2 PC0171468 (Madagascar)
69/0.69
V. orientalis PC0142723 (Madagascar)
100/1
95/0.96
V. orientalis PC0171887 (Madagascar)
92/1
V. orientalis NOU203676 (Madagascar)
100/1
V. orientalis NOU203722 (Madagascar)
90/1
V. sp3 PC0171938 (Madagascar)
100/1
V. sp3 NOU087298 (Juan de Nova)
V. sp1 NOU203244 (Chesterfield)
93/1
100/1
V. sp1 NOU203074 (New Caledonia)
81/0.98
V. sp1 NOU203873 (New Caledonia)
V. sp4 NOU203986 (Surprise Is.)
100/1
V. sp4 NOU204121 (Papua New-Guinea)
78/0.9
V. sp4 NOU203776 (New Caledonia)
0.04
GMYC
bGMYC
hPTP
mPTP
ABGD
SSHs
tufA
rbcL
Ventalia indica
Ventalia papillosa
Ventalia sp2
Ventalia orientalis
Ventalia sp3
Ventalia sp1
Ventalia sp4
A,H
D,E
D,F
: localitiies with several species


A
B
C
D
E
F
G
H
I
J
K
L


Synapomorphies:
- Monostromatic blade
- Upright axis
- Absence of blade cortication
Symplesiomorphies:
- Flabellate blade
- Calcification
- Presence of stipe
- Continuous stipe-blade junction
- Dichotomous siphon ramification
- Primary siphons arranged in one plane
-Blade siphons parallel to subparallel
- Isomorphic dichotomies
- Supra-dichotomial constrictions
- Asymmetrical constrictions
Chlorodesmis spp
Ventalia spp
87/1
88/1
93/1
73/0.72
100/1
R. glaucescens NOU087262 (Fiji)
R. glaucescens NOU087256 (Fiji)
R. glaucescens NOU087250 (Fiji)
53/0.99
R. sp4 NOU203397 (Papua New-Guinea)
R. sp1 NOU203803 (New Caledonia)
93/1
R. lewmanomontiae (Thailand)
43/0.55
R. javensis NOU203340 (Papua New-Guinea)
R. javensis NOU204193b (Juan de Nova)
28/0.78
R. javensis NOU203995 (Surprise Is.)
R. javensis NOU204102 (Papua New-Guinea)
54/-
R. javensis NOU203902 (Surprise Is.)
100/1
R. javensis NOU203473 (Bunaken, Indonesia)
R. javensis NOU204193a (Juan de Nova)
21/-
R. javensis NOU203576 (Mayotte)
34/0.76
R. javensis NOU203692 (Madagascar)
0.08
GMYC
bGMYC
hPTP
mPTP
ABGD
SSHs
tufA
rbcL
Rhipidosiphon glaucescens
Rhipidosiphon sp4
Rhipidosiphon sp1
Rhipidosiphon lewmanomontiae
Rhipidosiphon javensis
*
B,D
40
20
0
-20
-40
200
150
100
50
: locality with several species

A
B
C
D
E
F
G
H
Grey Scale #13