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# Historical biogeographical analysis of the Udoteaceae (Bryopsidales, Chlorophyta) elucidates origins of high species diversity in the Central Indo-Pacific, Western Indian Ocean and Greater Caribbean regions

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► **To cite this version:**

Laura Lagourgue, Frederik Leliaert, Claude E Payri. Historical biogeographical analysis of the Udoteaceae (Bryopsidales, Chlorophyta) elucidates origins of high species diversity in the Central Indo-Pacific, Western Indian Ocean and Greater Caribbean regions. *European Journal of Medicinal Chemistry*, 2022, 230, pp.114104. 10.1016/j.ejmech.2022.114104 . hal-03545559

**HAL Id: hal-03545559**

**<https://hal.sorbonne-universite.fr/hal-03545559>**

Submitted on 27 Jan 2022

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1 **Historical biogeographical analysis of the Udoteaceae (Bryopsidales, Chlorophyta) elucidates**  
2 **origins of high species diversity in the Central Indo-Pacific, Western Indian Ocean and Greater**  
3 **Caribbean regions**

4

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16

17

18 **Abstract**

19 There is a growing interest in elucidating the biogeographical processes underlying biodiversity  
20 patterns of seaweeds, with recent studies largely focusing on red and brown macroalgae. This study  
21 focuses on the siphonous green algal family Udoteaceae, which is diverse and globally distributed in  
22 tropical to warm-temperate seas, and includes species that form important components of tropical  
23 reefs. We explored the historical processes that have shaped current biodiversity patterns in the  
24 family by analyzing a comprehensive dataset of 568 specimens sampled across its geographical  
25 range, and including 45 species, corresponding to 59% of the known diversity. Historical  
26 biogeographical analysis was based on a three-locus time-calibrated phylogeny, and probabilistic  
27 modeling of geographical range evolution. Many species were found to have restricted ranges,  
28 indicative of low dispersal capacity. Our analysis points toward a Western Tethys origin and early  
29 diversification of the Udoteaceae in the Triassic period. Three centers of diversity were identified,  
30 which are, in order of highest species richness, the Central Indo-Pacific, the Western Indian Ocean,  
31 and the Greater Caribbean. Different drivers have likely played a role in shaping these diversity  
32 centres. Species richness in the Central Indo-Pacific likely resulted from speciation within the region,  
33 as well as recolonization from neighbouring regions, and overlap of some wider ranged species,  
34 corroborating the “biodiversity feedback” model. Species richness in the Western Indian Ocean can  
35 be explained by ancient and more recent diversification within the region, and dispersal from the

36 Central Indo-Pacific. The Greater Caribbean region was colonized more recently, followed by  
37 diversification within the region.

38

39

40 **Key words:** historical biogeography, macroalgae, marine biogeography, speciation, vicariance, Pacific  
41 Ocean.

42

43 **Highlights:**

44

- 45 • Most of Udoteaceae species are restricted to a single ocean basin
- 46 • The Udoteaceae likely originated in Western Tethys during the Triassic period
- 47 • The Central Indo-Pacific, Western Indian Ocean, and the Greater Caribbean are the three  
48 centers of species diversity of Udoteaceae
- 49 • Different drivers have likely played a role in shaping these diversity centers
- 50 • The Central Indo-Pacific is a center of origin, accumulation, and overlap

51

52

53 Declarations of conflict of interests: none

54

55

## 56 1. INTRODUCTION

57

58 Marine taxa generally follow a latitudinal diversity gradient, similar to what is found in terrestrial  
59 organisms (Willig et al., 2003; Hillebrand, 2004). In particular, many coastal marine groups reach  
60 greatest species richness in the Indo-Australasian Archipelago (IAA) or Coral Triangle, with diversity  
61 decreasing when moving away from this biodiversity hotspot both latitudinally and longitudinally  
62 (Renema et al., 2008, Connolly et al. 2003, Hoeksema, 2007). This pattern has been observed for  
63 various taxa, including reef fishes (Bellwood and Hughes, 2001; Carpenter and Springer, 2005;  
64 Cowman, 2014; Cowman and Bellwood, 2013a), corals (Hughes et al., 2002; Bellwood and Meyer,  
65 2009), gastropods and crustaceans (Hoeksema, 2007). A number of non-exclusive hypotheses have  
66 been proposed to explain the IAA biodiversity hotspot: 1) the center of origin (Ekman, 1953), which  
67 attributes the high diversity to higher speciation rates within the IAA with subsequent dispersal to  
68 peripheral regions (Cowman and Bellwood, 2011; Alfaro et al., 2007; Barber and Bellwood, 2005;  
69 Williams, 2007); 2) the center of accumulation (Ladd, 1960), which proposes that higher species  
70 richness resulted from a combination of species dispersing into the IAA and persisting there over  
71 time due to lower extinction rates; and 3) the center of overlap (Woodland, 1983), which suggests  
72 that high diversity is due to overlap in species ranges. Evidence for all three hypotheses have been  
73 found in different groups of organisms and the relative importance of the different scenarios have  
74 been widely debated (*e.g.*, Hoeksema, 2007; Barber, 2009; Barber and Meyer, 2015; Bellwood and  
75 Meyer, 2009, Jablonsky et al., 2013).

76 For most marine macroalgae, however, the latitudinal diversity gradient does not seem to hold. It has  
77 been assumed that red (Rhodophyta), brown (Phaeophyceae) and green (Chlorophyta) seaweeds  
78 display highest diversity in temperate regions (Lüning 1990; Kerswell, 2006), in particular the  
79 temperate northern Pacific, northern Atlantic, and Australasia (Kerswell, 2006; Keith et al., 2014).  
80 However, the observed inverse biodiversity gradient in seaweeds may be false due to lack of study in  
81 many tropical areas (Bolton, 1994), or as a result of unrecognized cryptic diversity (Vieira et al., 2017,  
82 2021; Leliaert et al., 2018; Díaz-Tapia et al., 2020a). Unlike many other seaweed groups, siphonous  
83 green seaweeds (Bryopsidales) show a clear pattern of high diversity in the IAA, similar to what is  
84 found in many marine animal groups (Kerwell, 2006). This pattern has been confirmed with  
85 molecular data for the genera *Halimeda* (Verbruggen et al., 2009a) and *Codium* (Verbruggen et al.,  
86 2007), but the biogeography of other groups of Bryopsidales has been less well studied.

87 The Udoteaceae is a species-rich clade within the Bryopsidales, traditionally recognized as a separate  
88 family, but more recently proposed as a tribe (Udoteae) in the family Halimedaceae (Cremen et al.,  
89 2019). The group is distributed worldwide, in tropical to warm temperate seas, including the tropical  
90 Atlantic, Indian and Pacific Oceans, as well as in the Mediterranean and Red Sea. Some genera are

91 widely distributed, spanning different oceans, while others are more range-restricted, such as  
92 *Rhipocephalus*, which only occurs in the tropical western Atlantic (Littler and Littler, 2003) or  
93 *Flabellia*, which is only found in the Mediterranean Sea and northeastern Atlantic (Díaz-Tapia et al.,  
94 2020b). Next to a high diversity in the Indo-Pacific, species diversity in the Udoteaceae is particularly  
95 high in the Greater Caribbean region (Bermuda, Bahamas, Florida, Gulf of Mexico and Caribbean  
96 *sensu stricto*). Some remarkably diverse genera, such as *Udotea sensu stricto* (s.s.) and those present  
97 in the “*Penicillus-Rhipocephalus-Rhipidosiphon-Udotea*” complex, as well as high species endemism  
98 are observed in the Greater Caribbean (Littler and Littler, 1990; Lagourgue et al., 2018 and 2020).  
99 Recent taxonomic revision and reassessment of species diversity based on DNA sequence data  
100 (Sauvage et al., 2016 and 2020; Wade and Sherwood, 2017; Lagourgue et al., 2018 and 2020;  
101 Lagourgue and Payri, 2020) enables the study of its biogeographical history in more detail. In  
102 Lagourgue and Payri (2020), the origin of Udoteaceae was estimated in the Late Triassic (ca 216 Ma),  
103 with most of the genera originating during the Paleogene (between ca 66 and 23 Ma). This study also  
104 highlighted a greater species diversity than traditionally recognized based on morphology, including  
105 co-occurring cryptic species. Similar to what has been found in several other seaweed groups  
106 (Silberfeld et al., 2013; Vieira et al., 2017; Leliaert et al., 2018; Boo et al., 2018), several species with  
107 assumed wide ranges (*i.e.*, pantropical or distributed among several oceans), were found to consist  
108 of different species with more restricted geographical ranges (*i.e.*, only found in one ocean or even  
109 confined to short stretches of coastline or island groups). Conversely, for a few other species (e.g.,  
110 *Rhipidodesmis caespitosa*, *Tydemania expeditionis*, *Chlorodesmis fastigiata*), wide ranges have been  
111 identified or confirmed, highlighting long-distance dispersal capacity in some species. Large  
112 differences in geographical ranges between species is commonly seen in bryopsidalean genera, such  
113 as *Caulerpa* (Belton et al., 2020), *Halimeda* (Verbruggen et al., 2005), *Codium* (Verbruggen et al.,  
114 2007) and *Bryopsis* (Hollands et al., 2013).  
115 The striking biogeographical pattern of the Udoteaceae, with high species diversity in the Greater  
116 Caribbean and Indo-Pacific, and high endemism between the two regions, along with the well  
117 documented diversity and distribution of species based on DNA sequence data, makes this family an  
118 interesting group to investigate biogeographical patterns of species diversity and their underlying  
119 drivers. This study aims to combine the geographical and genetic data of the different Udoteaceae  
120 species in order to: (1) analyze the diversification of the family based on a time-calibrated phylogeny  
121 and (2) estimate the biogeographical history of the family to identify the role of different marine  
122 barriers, dispersal, and different speciation mechanisms in the evolution of the family.

123

## 124 **2. MATERIAL & METHODS**

### 125 **2.1. Sampling and data assembly**

126 537 specimens of Udoteaceae were included in this study, sampled from various localities in Indian  
127 Ocean (*e.g.*, Madagascar, Mayotte, Scattered Islands, Maldives), Pacific Ocean (*e.g.*, Papua New  
128 Guinea, Solomon Is., New Caledonia, Vanuatu, Fiji, French Polynesia), Atlantic Ocean (Caribbean  
129 Islands) and Red Sea (Egypt, Sudan) (Fig. 1; Table A.1 in Supplementary material). Three genes were  
130 sequenced, including two chloroplast genes (*tufA* and *rbcL*) and the nuclear 18S rDNA following  
131 Lagourgue and Payri (2020). The dataset was completed with *tufA* and *rbcL* sequences of missing  
132 species, available on GenBank (Table A.1 & A.2). Sequences were aligned using MUSCLE (Edgar, 2004)  
133 in Geneious v.7.1.9 (<http://www.geneious.com>, Kearse et al., 2012), and 18S rDNA sequences were  
134 aligned using CLUSTALW.

135 From this comprehensive sample and based on the species delimitation results of Lagourgue and  
136 Payri (2020), a dataset including a single specimen per species was assembled for phylogenetic  
137 inference of the species tree (Table A.2 in Supplementary). Only species for which at least sequences  
138 of two of the three markers were available were included in the concatenated alignment to reduce  
139 bias in phylogenetic tree reconciliation (Roure et al., 2013). This has led to a compromise in the  
140 number of species included, but those presented in this study are considered to have  
141 phylogenetically more reliable positions. We refer to the Supplementary Figures S1 and S2 in  
142 Lagourgue & Payri (2020) for a phylogenetic visualization of the molecular species and sequences not  
143 included in this present study. A total of 45 species out of the 76 taxonomically accepted (named)  
144 Udoteaceae species (*i.e.*, 59%) were considered in this study (*cf.* AlgaeBase, Guiry and Guiry, 2021;  
145 excluding fossil species (*e.g.*, *Coralliodendron* and *Pseudopenicillus*) or species and genera transferred  
146 to other families, *e.g.*, *Pseudochlorodesmis* and *Siphonogramen* (Curtis et al., 2008), *Boodleopsis* and  
147 *Callipsygma* (Cremen et al., 2019), *Chlorodesmis baculifera* and *Rhipiliella* (Lagourgue and Payri, 2020  
148 and 2021), and including *Udoteopsis maiottensis* and the 12 undescribed species delimited in  
149 Lagourgue and Payri (2020)). Sequences of ten outgroup species allowing rooting and calibration of  
150 the phylogeny in time were added to the alignment: *Codium duthieae*, *C. platylobium*, *Caulerpa*  
151 *sertularioides*, *C. taxifolia*, *C. verticillata*, *Avrainvillea lacerata*, *A. nigricans*, *Halimeda discoidea*, *H.*  
152 *incrassata*, *H. opuntia*, *Pseudocodium floridanum* and *P. natalense*.

153

## 154 **2.2. Multilocus time-calibrated species phylogeny**

155 A species phylogeny was inferred from the concatenated alignment of the tree genes (*tufA*, *rbcL* and  
156 18S rDNA). PartitionFinder v1.1.1.0 (Lanfear et al., 2012) was used to identify a suitable partitioning  
157 scheme and accompanying evolutionary models. According to the BIC criterion, seven partitions  
158 were favored, *i.e.*, by gene and, for the two chloroplast markers, also by codon position. The  
159 evolutionary models were associated in the order of codon positions as follows: GTR+G, GTR+I+G,  
160 GTR+I+G for *tufA*, GTR+I, K80+I, GTR+I+G for *rbcL*, and TrN+I+G for 18S rDNA.

161 Maximum likelihood analyses were performed using RAXML (Stamatakis, 2014) through the CIPRES  
162 1.5 server (Miller et al., 2010) on the partitioned matrix, under the GTR+I+G model, with the "rapid  
163 bootstrapping and search for best-scoring ML tree" algorithm and node supports were estimated  
164 from 1000 bootstrap iterations (Stamatakis et al., 2008).

165 A time-calibrated phylogeny was reconstructed using BEAST v2.5.0 (Bouckaert et al., 2014) through  
166 the CIPRES server on the partitioned alignment with the corresponding evolutionary models. The  
167 phylogeny was estimated with a relaxed, uncorrelated, lognormal molecular clock (Drummond et al.,  
168 2006) and under the "Calibrated Yule" model (Heled and Drummond, 2012). Two independent  
169 analyses of 75 M generations were run with sampling every 10,000 generations. The first 7.5 M  
170 generations were discarded as burn-in. Verification of convergence and effective sampling size  
171 (greater than 200 for posterior distributions of each parameter) for each run was performed with  
172 Tracer 1.5 (Rambaut and Drummond, 2007). The runs were then assembled using LogCombiner  
173 v.2.6.3 and the "Maximum Clade Credibility Tree" (MCCT) was reconstructed with TreeAnnotator.  
174 FigTree v.1.4.3 (Rambaut, 2014) was used to visualize the phylogenetic trees. Different calibration  
175 points were used to estimate node ages based on Lagourgue and Payri (2020) and detailed in Table  
176 A.3.

177 Possible shifts in diversification rates were first evaluated using a lineage-through time (LTT) based  
178 on a sub-sampling of 1,000 trees from BEAST analysis with the "litt95" function of the "phytools"  
179 package (Revell, 2012) integrating a 95% confidence range. A "Bayesian analysis of  
180 macroevolutionary mixtures" (BAMM; Rabosky, 2014) analysis was also conducted with five million  
181 MCMC generations, based directly on the MCCT and on an *a priori* estimation of the parameters by  
182 the "setBAMMpriors" function of the "BAMMtools" package on R (R Development Core Team, 2019).  
183

### 184 **2.3. Geographic data**

185 Distribution data were extracted from the metadata associated with the sequenced specimens,  
186 including our collection and GenBank sequences (Supplementary material, Table A.1). When DNA-  
187 based species clusters could be linked to species names, the type locality of that species was  
188 integrated to the geographic distribution data. Among the distribution data available on AlgaeBase  
189 (Guiry and Guiry, 2021) many of them were not integrated due to potential errors in species  
190 identification, as highlighted in Lagourgue and Payri (2020).

191 For biogeographical analyses, the following geographical areas are generally defined and used  
192 (decreasing scales): regions, realms, provinces and even ecoregions (see Spalding et al., 2007 for  
193 definitions of these terms). Three geographical subdivisions were considered for the historical  
194 biogeographical analyses: five regions as defined by Vieira et al. (2017), seven realms, and 17  
195 provinces as defined by Spalding et al. (2007). Nevertheless, biogeographical history inference could

196 not be carried out at the province level as the composition of the data (number of provinces and  
197 maximum range size) required computing capacity that far exceeded the BioGeoBEARS authors'  
198 recommendations (Matzke, 2016; equivalent to > 65,000 states for our study, while a maximum of  
199 500-600 states is recommended by the authors). An alternative analysis, subdividing the Central  
200 Indo-Pacific into four different sub-realms (Coral Triangle, Micronesia, Southern Japan, and  
201 Melanesia) was carried out in order to refine the information concerning this geographical area. This  
202 analysis is given as additional information, as it presents a bias in the division of areas (*i.e.*, other  
203 geographical areas remaining the same as for the realms level). The different geographical areas are  
204 listed in Table 1 and the realms division is presented in Figure 1. Details of the areas occupied by  
205 each species included in this study are available in Table A.4 (Supplementary material; see also Table  
206 A.5 for the distribution ranges based on literature of species not included in the analyses).

207

#### 208 **2.4. Inference of biogeographical history**

209 Historical biogeographical analysis was based on the time-calibrated species tree combined with  
210 species distribution data. Ancestral areas were estimated using the "BioGeoBEARS" package (Matzke,  
211 2013) implemented in R, by considering the three available models: the "Dispersal-Extinction  
212 Cladogenesis" (DEC), the "Dispersal Vicariance Analysis" (DIVALIKE) and the "Bayesian Inference of  
213 Historical Biogeography for Discrete Areas" (BAYEAREALIKE). Each of these models includes  
214 speciation events within a geographical area, vicariance events (except the DEC model) and range  
215 expansions or contractions, *i.e.*, respectively dispersal to a new area or extinction within the current  
216 area. In addition, the +J parameter can be added to each of these models to integrate founder-event  
217 speciation. The latter corresponds to the change of area occurring during a division of a lineage, after  
218 which a new area is occupied by one of the daughter lineages, while the other remains in the  
219 ancestral area (Matzke, 2014). A likelihood ratio test can be performed to test whether or not  
220 addition of the +J parameter significantly better fits the data than the simpler model without the +J  
221 parameter. We have carefully compared results with and without the parameter +J as the DEC+J  
222 model has been criticized as a poor model of founder-event speciation (Ree and Sanmartin, 2018).  
223 The appropriate models for analyses at the different geographical subdivisions were statistically  
224 estimated under the Akaike Information Criterion (AIC). The maximum number of ancestral areas for  
225 a single species to occupy was set at four for the region and realm level analyses, and five for the  
226 additional sub-realm analysis.

227 Bayesian Stochastic Mapping (BSM; Matzke, 2016) was carried out using the biogeographical model  
228 favored by the AIC criterion, and analyses were repeated 50 times in order to obtain the frequency of  
229 the different events explaining the biogeographical history of the Udoteaceae.

230



### 231 3. RESULTS

#### 232 3.1 Time-calibrated phylogeny of the Udoteaceae

233 The multilocus concatenated alignment included 3353 positions (*tufA*: 835 bp; *rbcL*: 1306 bp; 18S  
234 rDNA: 1212 bp). The time-calibrated species tree of the Udoteaceae estimated from this alignment is  
235 presented in Figure 2 (see Figure A.1 for ML tree). The topology is similar to the phylogeny of  
236 Lagourgue and Payri (2020), except for the position of *Rhipidosiphon lewmanomontiae*, which was  
237 inferred here outside *Rhipidosiphon s.s.*, and sister to *Ventalia* and *Chlorodesmis*. This may be a  
238 phylogenetic artefact caused by the fact that the species is only represented here by *rbcL* and 18S  
239 sequences from the holotype. The genera revised by Lagourgue and Payri (2020) (*i.e.*, *Chlorodesmis*,  
240 *Udotea s.s.*), as well as the newly described genera (*i.e.*, *Glaukea* and *Ventalia*), are all monophyletic  
241 with high node supports (bs > 90; PP > 98). *Rhipidosiphon* is monophyletic in this study, with the  
242 exclusion of *R. lewmanomontiae* and *R. floridensis* (hereunder referred to as *Rhipidosiphon s.s.*). The  
243 monophyly of the genus *Rhipidosiphon* has already been found unstable depending on analyzed  
244 markers or taxon sets (see Lagourgue and Payri, 2020).

245 Divergence between the Halimedaceae and Pseudocodiaceae + Udoteaceae is estimated at 291 [95%  
246 highest posterior density interval of the estimated divergence times: 279-303] Ma (Permian,  
247 Paleozoic). The divergence between the families Pseudocodiaceae and Udoteaceae is estimated at  
248 247 [220-273] Ma (Triassic, Mesozoic). The origin of the Udoteaceae is estimated at 216 [201-233]  
249 Ma (Late Triassic, Mesozoic), as in Lagourgue and Payri (2020). While the origin of *Udotea s.s.* was  
250 estimated at 85 [53-116] Ma in the Late Cretaceous (Mesozoic), most of the other extant genera was  
251 inferred to be younger with origins in the Paleogene or early Neogene: *Tydemanina* (40 [15-70] Ma),  
252 *Rhipidosiphon s.s.* (27 [14-41] Ma), *Glaukea* (35 [15-59] Ma), *Ventalia* (32 [20-44] Ma) and  
253 *Chlorodesmis* (26 [16-36] Ma). The origin of the two clades containing the “PRRU complex” and “PPR  
254 complex” as defined by Lagourgue and Payri (2020), was estimated at 53 [38-70] and 35 [22-51] Ma,  
255 respectively. Finally, the most recent speciation event, based on our taxa sampling, was dated at 3.8  
256 [1.1-6.9] Ma. Current estimations of the ages of genera and clades ages are also close to previous  
257 findings (Lagourgue and Payri, 2020), only differing by 0.3 to 6 Ma.

258 The lineage-through-time (LTT) plot shows that diversification was relatively constant over time with  
259 slight variations, including a slow-down at the end of the Eocene (42-34 Ma) (Figure 2). The BAMM  
260 analyses estimated one shift in diversification rate but the estimation of the no-shift assumption is  
261 close ( $P(1) = 0.46$  for a shift versus  $P(0) = 0.41$  and  $P(2) = 0.077$ ; Figure A.2, Supplementary material).  
262 The 95% credibility shift is inferred during Late Cretaceous on the branch leading to the most recent  
263 common ancestor (MRCA) of *Ventalia*, *Chlorodesmis*, *Udoteopsis*, *Rhipidosiphon s.s.* and the PPR and  
264 PRRU complexes (Figure 2).

#### 265 3.2. Geographical patterns of species richness

266 Based on the species dataset analyzed, at the realm-level, highest species richness is found in the  
267 Central Indo-Pacific (18 species), in particular in the Melanesian arc (16 species), followed by the  
268 Western Indian Ocean (16 species), and the Tropical Atlantic (14 species). At the province-level, the  
269 Greater Caribbean and the Western Indian Ocean encompass the greatest diversity with 14 species  
270 each, followed by the Tropical Southwestern Pacific (11 species) and the Eastern Coral Triangle (10  
271 species) (Table 2).

272 The Greater Caribbean also shows high endemism (14/14) (Table 2). Other provinces with high  
273 numbers of endemic species are the Western Indian Ocean (7/14), the Eastern Coral Triangle (4/10),  
274 the Tropical Southwestern Pacific (3/11), and the Mediterranean Sea (1/1).

275 At the region and realm levels, 36 out of 45 species are restricted to a single region or realm, nine are  
276 present in only two regions or realms, and one in four regions or realms (Table 2, Figure 3). Of the 10  
277 species that occurred exclusively within the Central Indo-Pacific sub-realm, seven only appeared  
278 within the Melanesian arc (Table 2).

279 Species are most commonly shared between adjacent regions or realms (*e.g.*, Central and Eastern  
280 Indo-Pacific) or in some cases, have a distribution which follows a longitudinal continuum (Western  
281 Indian Ocean, Central Indo-Pacific, Eastern Indo-Pacific and Eastern Pacific), such as *Rhipidodesmis*  
282 *caespitosa*. The largest number of shared species is found between the Central Indo-Pacific and the  
283 Western Indian Ocean (seven species in common), and between the Central Indo-Pacific and the  
284 Eastern Indo-Pacific (four species in common). No common species were found between the Atlantic  
285 and Indo-Pacific, but some occur throughout the Indo-Pacific (*e.g.*, *Rhipidosiphon javensis*, *Ventalia*  
286 *papillosa* and *Tydemanina expeditionis*; Figure 3).

287

### 288 **3.3. Biogeographical history**

289 For the region- and realm-level analyses, the DIVALIKE + J model best explains the biogeographical  
290 history of the Udoteaceae under the AIC criterion (Table 3). Inclusion of the +J parameter resulted in  
291 a significantly better fit according to the likelihood ratio test at the regions and realms levels (Table  
292 A.6, Supplementary material). However, because the +J model has been criticized (Ree and  
293 Sanmartin 2018) we also provide the results of the biogeographical inference based on the DIVALIKE  
294 model in Supplementary material (Figure A.3).

295 Biogeographical inference at the realm level (Figure 3) estimated the ancestral geographical range of  
296 the Udoteaceae as the area comprising the Western and Central Indo-Pacific and the Mediterranean  
297 Sea in their current configuration, corresponding to the Tethys Sea of the Late Triassic (similar results  
298 were obtained at the region level, Figure A.4 in Supplementary material). Most of the diversification  
299 events occurred within the Central Indo-Pacific which is also the area that contains most of the  
300 current diversity as well as a high number of endemic species. From the Central Indo-Pacific,

301 dispersal occurred to other geographical areas. The Western Indian Ocean, also included in the area  
302 of origin, represents an area occupied by species that diverged early in the history of the Udoteaceae  
303 (*Tydemanina* spp.). The Western Indian Ocean has since experienced at least seven colonization  
304 events from the Central Indo-Pacific. The Mediterranean Sea only contains a single species and was  
305 not subsequently colonized. Another species of Udoteaceae, *Poropsis subunalis*, has its type locality  
306 in the Mediterranean but for the time being, no DNA sequence is reliably associated with the species.  
307 The Greater Caribbean was colonized twice independently during the Cretaceous (~80 Ma) and  
308 Paleogene (~50 Ma) periods, probably from the Central Indo-Pacific. The Eastern Indo-Pacific was  
309 colonized five times independently between the Cretaceous and Paleogene (80-40 Ma), mainly from  
310 the Central Indo-Pacific. Finally, colonization of the Eastern Pacific occurred more recently from the  
311 Miocene (ca. 19 Ma) onward. Our analysis inferred the Western Indian Ocean as the area of origin of  
312 *Tydemanina* (40 Ma; dates based on sampling of extant species), and the Central Indo-Pacific for  
313 *Udotea* s.s. (85 Ma), *Ventalia* (32 Ma), the PPR complex (35 Ma), *Rhipidosiphon* s.s. (27 Ma) and  
314 *Chlorodesmis* (26 Ma). As for the genus *Glaukea* (35 Ma), its geographical origin includes the Western  
315 Indian Ocean and the Central Indo-Pacific and finally, the MRCA of the PRRU complex appeared in  
316 the Atlantic (53 Ma) from a Central Indo-Pacific ancestor.

317 Biogeographical Stochastic Mapping (BSM) at both the region and realm levels indicated speciation  
318 within the regions or realms ('sympatric' speciation) as the main type of process in the evolution of  
319 the family (48.6% and 49.2% respectively for the regions and realms levels), followed by dispersal  
320 (28.1% and 27.7%), founder-event speciation (12.6% and 12.7%), and vicariance (10.7% and 10.4%)  
321 (Figure 4). Subset sympatry does not seem to have played a major role, although it appeared in the  
322 additional sub-realm analysis (see Figure A.5 in Supplementary material).

323 From the Central Indo-Pacific westward and eastward dispersal (including founder-event speciation)  
324 was inferred. The Eastern Indo-Pacific was colonized only from the Central Indo-Pacific. The Western  
325 Indian Ocean was colonized from the Central Indo-Pacific by dispersal (followed by vicariance for  
326 *Glaukea* species), and founder-event speciation. This was followed by a number of recolonizations of  
327 the Central Indo-Pacific, notably from the Eastern Indo-Pacific (e.g., *Rhipidosiphon* sp4, *Penicillus*  
328 *nodulosus*) or from the Western Indian Ocean (e.g., *Ventalia papillosa*, *Ventalia orientalis*) but only as  
329 far as the Coral Triangle, thus not reaching Melanesia (see further analyses, Figure A.5 in  
330 Supplementary material). A recolonization event of the Central Indo-Pacific from the Atlantic was  
331 also inferred in *Udotea*.

332 Two founder-events have been inferred to the Greater Caribbean, followed by successive speciation  
333 within that region. Founder-events may also explain the colonization of the Western Indian Ocean  
334 (three times) and of the Eastern Indo-Pacific (twice).

335 Vicariance events may be at the origin of speciation in *Tydemania* (separation of the Western Indian  
336 Ocean from the Central Indo-Pacific + Mediterranean), the presence of *Flabellia* in the  
337 Mediterranean Sea (separation Mediterranean/Central Indo-Pacific), and may also be at the origin of  
338 the sister species *Udotea occidentalis* and *U. sp1* (Atlantic/Central Indo-Pacific) as well as the two  
339 *Glaukea* species (Western Indian Ocean/Central Indo-Pacific).

340 The inferred biogeographical events at the realm level are summarized in Figure 5.

341

## 342 **4. DISCUSSION**

### 343 **4.1. Biogeographical patterns**

344 Most species in the Udoteaceae are restricted to a single region, realm or even province. A few  
345 species have wider ranges throughout the Indo-West Pacific, but none are shared between the  
346 Atlantic and Indo-Pacific, contrary to what has been suggested based on morphology-based species  
347 circumscriptions (AlgaeBase; Guiry and Guiry, 2021). Although restricted ranges could be explained in  
348 part by incomplete geographical sampling, there are numerous cases where geographical ranges  
349 have been overestimated. For example, the allegedly globally distributed species *Udotea flabellum*  
350 (*e.g.*, Western Indian Ocean (Silva et al., 1996), Australia (Kraft, 2007; Huisman, 2019), Pacific Islands  
351 (Payri, 2007)) is likely restricted to the Western Tropical Atlantic (Sauvage et al., 2020; Lagourgue and  
352 Payri, 2020). Similarly, *Ventalia orientalis* reported from Papua New Guinea (Coppejans et al., 2001),  
353 Australia (Kraft, 2007; Huisman, 2019) and Pacific Islands (Littler and Littler, 2003; Payri, 2007) is  
354 likely restricted to Indonesia and the Indian Ocean (Lagourgue and Payri, 2020).

355 The Central Indo-Pacific, Western Indian Ocean and Greater Caribbean represent the areas with the  
356 highest species richness of Udoteaceae. While Greater Caribbean species are endemic to the region,  
357 the Central Indo-Pacific includes endemic as well as shared species, mainly with the Western Indian  
358 Ocean. The lack of species spanning the Atlantic and the Indo-Pacific can be explained by strong  
359 geographical barriers represented by the Isthmus of Panama and the Benguela upwelling (Cowman  
360 and Bellwood, 2013a; Hodge et al., 2013; Vieira et al., 2017). Within the Bryopsidales, a similar  
361 pattern has been found in *Halimeda* (Verbruggen et al., 2009b), and using a niche modelling  
362 approach, this Atlantic/Indo-Pacific division has been attributed to dispersal limitation rather than  
363 habitat unsustainability. High species endemism is also found in *Codium* (Verbruggen et al., 2007)  
364 and *Lobophora* (Vieira et al., 2020). However, the absence of species occurring on both sides of the  
365 Panama isthmus, or the low number of species observed in the Eastern Pacific, should be considered  
366 with caution, as they may result from a low sampling effort in the Eastern Pacific.

367 Our biogeographical inferences are strongly dependent on the phylogeny and taxon sampling. It is  
368 therefore possible, with the inclusion of additional species (notably likely cryptic diversity in  
369 understudied groups of diminutive species like the PPR complex and *Rhipidosiphon*), supplementary

370 geographical sampling, and variation in phylogenetic relationships, that the patterns reported here  
371 and the evolutionary history of the Udoteaceae will change. However, based on our extensive  
372 sampling, we are confident that our main conclusion (*e.g.*, the importance of the Central Indo-Pacific  
373 as center of origin, the three centers of Udoteaceae diversity) will hold as new data become  
374 available.

375

#### 376 **4.2. Origin and diversification of the Udoteaceae**

377 Our time-calibrated phylogeny points toward a Tethys origin of the Udoteaceae. The Tethyan origin  
378 of the Udoteaceae is similar to the Halimedaceae (*Halimeda*, ca 250 Ma) and Caulerpaceae  
379 (*Caulerpa*, ca 280 Ma) for which fossil data also indicates a Tethyan origin (Gustavson and  
380 Delevoryas, 1992, Poncet, 1989; Draisma et al., 2014). This corroborates with the pantropical  
381 distribution of the families or genera, which has been assumed to result from their Tethyan origin,  
382 when east and westwards tropical exchanges were free (Hillis-Collinvaux, 1986). Similar historical  
383 biogeographical patterns have been observed in the red algae (*e.g.*, Portieria, Leliaert et al. 2018),  
384 and brown algae (*e.g.*, Dictyotales, Vieira et al. 2021). Within the latter group, the historical  
385 biogeography is more complex with some clades retaining a tropical niche, while others have  
386 expanded their distribution into temperate regions. The origin of the Udoteaceae was estimated at  
387 the end of the Triassic, between 201 and 233 Ma. The inclusion of the fossil *Pseudopenicillus*  
388 *aegaeicus* from Hydra Island (Greece, Mediterranean) dated at Late Triassic (Dragastan et al., 1997)  
389 allowed a more precise time-calibration, corroborates results of previous studies (Verbruggen et al.  
390 2009b, Lagourgue and Payri 2020), and is compatible in terms of geography since the Mediterranean  
391 Sea was part of the Western Tethys Sea at the time. Based on the ranges of the early diverging  
392 lineages (*Tydemania*, *Flabellia*) and fossils, we think it is plausible that the family originated in the  
393 Western Tethys and only later shifted its center of diversity to the Central Indo-Pacific, when  
394 archipelagos in this region were formed. This is in line with the “hopping hotspots” scenario of  
395 Renema et al. (2008).

396 The Triassic is generally recognized as a period of diversification and spreading of warm water marine  
397 organisms across the Tethys Sea after the End Permian mass extinction (Scotese, 1998), and ended  
398 with the Triassic/Jurassic crisis during which the oceans experienced another significant extinction of  
399 biodiversity. The later event is not evident in our diversification analysis, which instead shows a  
400 relatively constant diversification rate of the Udoteaceae over time. A phylogenetic analysis at the  
401 order level would be needed to investigate these early diversification patterns.

402 Only one diversification-rate shift in the history of the Udoteaceae has been estimated by the BAMM  
403 analysis during Late Cretaceous (Figure 2), although these results have to be interpreted with care  
404 (Moore et al., 2016; Meyer and Wiens, 2018). Relatively constant diversification rates over similar

405 time scales have also been found in the evolution of other seaweeds (*e.g.*, *Portieria* (Leliaert et al.,  
406 2018) or *Padina* (Vieira et al., 2021)) and some tropical marine animals, with one or a few shifts in  
407 the Late Cretaceous (Leprieur et al., 2016; for corals, fishes, and foraminifera) or the Oligo/Miocene  
408 (Williams and Duda, 2008; for gastropods; Wilson and Rosen, 1998; for corals).

409 The most recent cladogenesis (speciation) events in our phylogeny were in the Paleogene period, but  
410 others were inferred during the Cretaceous period or even the Jurassic. However, these speciation  
411 age estimates have to be carefully interpreted due to potential incomplete sampling bias as well as  
412 extinction. The terminal period of the Tethys Sea (from ca 18 Ma) and its closure (ca 12-15 Ma) can  
413 be related to the beginning of multiple speciation events in the Western Indian Ocean for the genera  
414 *Ventalia* and *Chlorodesmis*, and to the origin of the two vicariant species pairs (*Udotea* sp1/*U.*  
415 *occidentalis* and *Glaukea argentea* 1/*G. argentea* 2).

416

#### 417 **4.3 Origins of the centers of diversity**

418 Different drivers have likely shaped the three main centers of diversity of the Udoteaceae. Our  
419 analyses indicate that the highest species diversity in the Central Indo-Pacific likely resulted from  
420 high speciation within this region, in addition to recolonizations from neighboring regions, and  
421 overlap of some wider ranged species (Figure 5). The dating of these events (between 50 and 10 Ma),  
422 and the ages of the clades in this area (*i.e.*, *Rhipidosiphon* s.s., *Chlorodesmis*, *Ventalia*, the PPR  
423 complex) are consistent with the timing of the formation of the Central Indo-Pacific. This area, which  
424 was once a mosaic of coral reefs and deeper waters, was gradually transformed into an area of high  
425 geographical complexity by tectonic movements during the Late Cretaceous or Oligo/Miocene (Hall,  
426 2002). This resulted in the emergence of high species diversity for various marine organismal groups,  
427 including corals (Wilson and Rosen, 1998; Leprieur et al, 2016; Halas and Winterbottom, 2009),  
428 gastropods (Williams and Duda, 2008), stomatopods (Barber and Boyce, 2006), fishes (Drew and  
429 Barber, 2009; Leprieur et al, 2016), and macroalgae (Vieira et al., 2017; Leliaert et al., 2018). Given  
430 the diversity of the traits specific to each group, this high diversity is probably the result of multiple  
431 processes (Barber, 2009; Halas and Winterbottom, 2009; Leliaert et al., 2018). Nevertheless, our  
432 findings corroborate the hypothesis that coral reefs act as a driving force for cladogenesis,  
433 particularly by offering new habitats to colonize and opportunities for ecological diversification, and  
434 thus promote the diversification of associated marine organisms (Cowman and Bellwood, 2011).  
435 Coral environments are often associated with high herbivore pressures, and the role of herbivores in  
436 macroalgae diversification has been highlighted in some groups, such as the brown seaweed  
437 *Lobophora* (Vieira et al., 2017). Ecological speciation may also be a driver in the evolution of  
438 Udoteaceae (Littler and Littler, 1990).

439 Our results are in line with the "biodiversity feedback" model in which diversity hotspots act as both  
440 exporter (by speciation and dispersal) and importer of species (by recolonization from the initially  
441 colonized areas) (Bowen et al. 2013). In addition, it is interesting to note that the clades of Central  
442 Indo-Pacific regions north (*e.g.*, Indonesia, Philippines) and south (*e.g.*, Papua New Guinea, New  
443 Caledonia) of the Wallace line are somewhat distinct (*e.g.*, *Rhipidosiphon lewmanomontiae* vs. *R. sp1*  
444 and *R. sp4*, or *Ventalia papillosa* and *V. orientalis* vs. *V. sp1*; cf. Figure A.5). Similar observations have  
445 been reported in the red alga *Portieria* (Leliaert et al., 2018) and marine fishes and invertebrates  
446 (Carpenter and Springer, 2005; Rosen and Smith, 1988). This separation may reflect a geological  
447 footprint, prevailing over dispersal capacity, left by the tectonic movement of the plates (over 50  
448 million years) and the integration of new biota from the South (Australia) or the Philippines (Barber  
449 et al., 2000, Renema et al., 2008; Santini and Winterbottom, 2002; Leliaert et al., 2018).

450 In the Western Indian Ocean, which is part of the estimated area of origin of the Udoteaceae, early  
451 diversification was inferred (*e.g.*, *Tydemania* lineages). The region was subsequently colonized  
452 several times independently (by founder-event speciation) mainly from the Central Indo-Pacific, and  
453 this was followed by diversification within the region, explaining its current species richness. Only a  
454 few dispersal events to other regions and realms were inferred, including from the Western Indian  
455 Ocean back to the Central Indo-Pacific. The large number of endemic species in the Western Indian  
456 Ocean, and the few species in common with the Central Indo-Pacific is congruent with patterns in  
457 fishes (Cowman and Bellwood, 2013a; Hodge and Bellwood, 2016) and corals (Keith et al., 2013), and  
458 may be explained by the Middle Indian Ocean barrier. However, given the large number of inferred  
459 dispersal events between the Western Indian Ocean and the Central Indo-Pacific, this barrier must  
460 have been crossed several times independently during the evolutionary history of the Udoteaceae.

461 The high diversification inferred in the region can be partly explained by the upwelling system of the  
462 northern Indian Ocean, which marks a biogeographic delimitation in the species composition and has  
463 been considered as a biodiversity generator (Burt et al., 2011; Schils and Wilson, 2006, Leliaert et al.,  
464 2018).

465 The Greater Caribbean region was only colonized much later, from the Late Cretaceous to Eocene (ca  
466 83-50 Ma), likely by founder-event speciation from the Central Indo-Pacific, possibly through crossing  
467 of the Eastern Pacific barrier, before the closure of the Isthmus of Panama. Two independent  
468 dispersal events to the Greater Caribbean were inferred (for PRRU complex and within *Udotea*), and  
469 this was followed by diversification within the region, explaining the high diversity of the region. No  
470 dispersal to other areas was inferred, which can be explained by various barriers including the  
471 closure of the Tethys Sea and Panama Isthmus, and the Benguela upwelling.

472 Thus, for the Udoteaceae, the Central Indo-Pacific can be regarded as a center of origin,  
473 accumulation and overlap and can be seen both as a cradle of biodiversity (by housing old species

474 lineages) and a species generator. The Western Indian Ocean can be interpreted as a center of origin  
475 and accumulation, as well as a cradle of biodiversity, housing the old lineage leading to *Tydemania*  
476 spp. The Greater Caribbean region can be interpreted as a more recent center of origin.  
477 Other geographical areas were found to have a lower diversity of Udoteaceae species. Warm  
478 temperate areas such as southern Japan or Micronesia (Guam) were likely colonized from the Central  
479 Indo-Pacific several times independently between the Paleogene and Neogene. For the  
480 Mediterranean Sea, besides the speciation that led to *Flabellia petiolata*, no subsequent  
481 diversification was inferred and the impact of the various paleontological events, such as the  
482 Messinian Salinity Crisis (ca 5.9-5.3 Ma) or the Pliocene submersion, are difficult to assess. The  
483 islands in the Eastern Indo-Pacific have been colonized several times independently from the Central  
484 Indo-Pacific more recently (between 25 and 5 Ma) (Figures 3 and 4). Although founder-event  
485 speciation was inferred in our analyses, it is possible that species arrived at these islands by  
486 successive short distance dispersal events via intermediate islands that have now disappeared (Neall  
487 and Trewick, 2008; Heads, 2018; Leliaert et al., 2018). No subsequent diversification of Udoteaceae  
488 in the Pacific islands or dispersal back to the Central Indo-Pacific was deduced in our analysis. This  
489 contrasts with some studies on reef fishes that show the Hawaiian archipelago as a center of species  
490 diversification and dispersal (Bowen et al., 2013; Eble et al., 2011). The Eastern Pacific also appears to  
491 be poor in Udoteaceae species, and the species were found not to be related to those occurring in  
492 the Atlantic (Figure 3), indicating that speciation was not correlated with the closure of the Isthmus  
493 of Panama.

494

#### 495 **4.4. Speciation processes**

496 Our historical biogeographical analysis along with analysis of ranges of sister species allowed us to  
497 put forward some hypotheses on modes of speciation. Speciation of *Udotea* sp1 (Indo-Pacific) and *U.*  
498 *occidentalis* (Greater Caribbean) may be explained by vicariance during the Miocene and could  
499 correspond to the closure of the Tethys Sea (ca 18-12 Ma), but before the closure of the Isthmus of  
500 Panama (irrespective of the middle-Miocene model (Montes et al., 2015) or the Pliocene model  
501 (Keigwin, 1978).

502 Similarly, speciation within the *Glaukea argentea* complex may have occurred by vicariance  
503 separating the Central Indo-Pacific and the Western Indian Ocean during the Late Paleogene (ca. 56-  
504 23 Ma), when Australia stood out and the Indo-Australasian archipelagos (IAA) were formed. These  
505 events may have created a barrier within the Indo-Pacific realm (see Cowman and Bellwood, 2013b),  
506 allowing allopatric speciation.

507 *Chlorodesmis* cf. *hildebrandtii* (Central Indo-Pacific) and *C.* cf. *major* (Western Indian Ocean) have a  
508 much more recent evolutionary history, with an inferred founder-event speciation that has occurred



509 less than 10 Ma ago from the Central Indo-Pacific to the Western Indian Ocean, indicating that in  
510 some instances the IAA barrier could have been crossed, as has also been shown in *Lobophora* (Vieira  
511 et al., 2017). Further surveys should be carried out in the Eastern Indian Ocean to verify whether this  
512 represents truly a founder-event speciation, or rather gradual and successive dispersal events, which  
513 could indicate the role of the Coral Triangle as a dispersal relay. The literature reports these species  
514 throughout the Indo-Pacific (Guiry and Guiry, 2021), but their identity should be verified by DNA  
515 sequence data.

516 A number of lineages of Udoteaceae can be regarded as relic species. One such lineage, represented  
517 by *Tydemanina gardineri* and *T. expeditionis*, diverged early in the phylogeny and possibly originated  
518 in the Western Tethys Sea. *Tydemanina expeditionis* would then have dispersed eastward to the  
519 Central Indo-Pacific, while *T. gardineri* remained confined to the Western Indian Ocean. The other  
520 lineage includes *Flabellia petiolata*, whose origin was inferred from the Tethys Sea and which is  
521 currently restricted to the Mediterranean Sea. *Flabellia* represents, together with *Tydemanina*, an  
522 ancient lineage, further supporting a Western Tethys origin of the family. Our study adds to the  
523 number of Western Indian Ocean relict taxa that have been found in other groups such as corals,  
524 fish, and mangroves, and which have been related to high past diversity in the Western Tethys Sea  
525 (Cowman, 2014; Leprieur et al., 2016; Obura, 2016; Renema et al., 2008).

526

## 527 **5. CONCLUSIONS**

528

529 Our analyses point towards a Late Triassic origin of the Udoteaceae with a marked diversification  
530 from the Late Cretaceous onward. Based on our historical biogeographical inference, along with the  
531 early branching Mediterranean and the Western Indo-Pacific lineages, and fossil data, the ancestral  
532 area was likely located in the Western Tethys. Early diversification in this region was likely followed  
533 by eastward dispersal to the Central Indo-Pacific. Currently the family has three main centers of  
534 species diversity: the Central Indo-Pacific, which was inferred as a center of origin, accumulation and  
535 overlap; the Western Indian Ocean, which was inferred as a center of origin and accumulation; and  
536 the Greater Caribbean, constituting a more recent center of origin. Contrary to previous  
537 understanding, most species have restricted ranges, and none of them appear pantropical. This is  
538 similar to many other species of Bryopsidales, although a number of families also contain species  
539 that are truly pantropical, including several species of *Caulerpa*, *Codium* and *Halimeda*. Furthermore,  
540 the family is distinct in its high endemism between the Greater Caribbean and the Indo-Pacific, a  
541 pattern that has also been observed in *Halimeda* (Verbruggen et al., 2009b). The main process in the  
542 diversification of the Udoteaceae is speciation within regions, followed by dispersal, the two often  
543 acting in an interrelated way. Species in Udoteaceae appear to have the capacity to disperse and

544 colonize new regions (founder events). However, and although range-switching, subset speciation  
545 and range contractions were not inferred in our analyses, further study, including the missing species  
546 or more sampled localities, would better confirm these patterns in the Udoteaceae biogeographical  
547 history.

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## Acknowledgments

This work was supported by the DUNE Labex-CORAIL project and UMR ENTROPIE (IRD) funds. Samples were collected by various collectors whom authors would like to acknowledge here. In particular, the authors are grateful to Mayalen Zubia, Florence Rousseau, Line Le Gall, Serge Andréfouët, Elvan Ampou, Heroen Verbruggen, and Chiela Cremen for providing additional samples or sequences. Samples were collected during the following campaigns. Bunaken, 2014 : INDES0 project (research permit 133/SIP/FRP/SM/V/2015 and 918/BLITBANKKP/II/2016 issued by the Indonesian government and under a material transfer agreement between BALITBANG KP (now BRSDM KP, Ministry of Maritime Affairs and Fisheries) and the IRD); Clipperton, 2010 : "Passion 2015" project financed by the « Agence française de Développement » and the Pacific Fund; Fiji, 2007: R/V Alis, BSM-Fidji, doi: [10.17600/7100030](https://doi.org/10.17600/7100030); French Polynesia, 2013 : LOF ; Kavieng, 2014: doi:[10.17600/14004400](https://doi.org/10.17600/14004400); Madagascar, 2010 : Atimo Vatae, doi:[10.17600/10110040](https://doi.org/10.17600/10110040) ; 2016: R/V Antea, MAD, doi: [10.17600/16004700](https://doi.org/10.17600/16004700); Madang, 2012: R/V Alis, NUIGUINI campaign, doi:[10.17600/12100070](https://doi.org/10.17600/12100070); Maldive Is., 2009 : Sampling during the 2009 Baa Atoll expedition, with the Marine Research Center of Maldives, which did not require collection permits; Mayotte, 2010 : TARA; 2016: SIREME; New Caledonia, 2005 : R/V Alis, BSM-LOYAUTE, doi:[10.17600/5100030](https://doi.org/10.17600/5100030); 2008 : CORALCAL2, doi:[10.17600/8100050](https://doi.org/10.17600/8100050); 2012: CORALCAL4, doi:[10.17600/12100060](https://doi.org/10.17600/12100060); 2013: LOF ; 2015: R/V Alis, CHEST, doi:[10.17600/15004500](https://doi.org/10.17600/15004500); 2017: R/V Alis PostBlanco1 & TARA-NC ; Scattered Islands, Glorioso Is. (2012) & Juan de Nova Is. (2013) : BIORECIE; Solomon Islands, 2004: R/V Alis, BSM-Salomon; Tonga, 2013 : PRISTINE ; Vanuatu, 2006: SANTO, doi:[10.17600/6100100](https://doi.org/10.17600/6100100). Materials from PC were collected during the Atimo Vatae expedition to South Madagascar (Principal Investigator, Philippe Bouchet), part of a cluster of Mozambique-Madagascar expeditions funded by the Total Foundation, Prince Albert II of Monaco Foundation, and Stavros Niarchos Foundation under "Our Planet Reviewed", a joint initiative of Muséum national d'histoire naturelle (MNHN) and Pro Natura International (PNI) in partnership with Institut d'Halieutique et des Sciences Marines, University of Toliara (IH.SM) and the Madagascar bureau of Wildlife Conservation Society (WCS). The Institut de Recherche pour le Développement (IRD) deployed its research vessel Antéa.

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879 **List of tables**

880

881 **Table 1:** Three geographical subdivisions (region, realm and provinces) considered for the  
 882 biogeography analyses of Udoteaceae. \*: Within the West Indo-Pacific realm, most observations for  
 883 the species included in this study come from the Western Indian Ocean, and the latter term will thus  
 884 be used preferentially for the following, in order to better situate the statements. Similarly, within  
 885 the Tropical Atlantic, most observations come from the Greater Caribbean, and the latter term will  
 886 thus be used preferentially for the following.

887

888

REGIONS	REALMS	PROVINCES
Atlantic Ocean	A: Tropical Atlantic*	Tropical Northwestern Atlantic (Greater Caribbean)
	D: Temperate Northern Atlantic	Mediterranean Sea
Indian Ocean	B: Western Indo-Pacific*	Western Indian Ocean
		Red Sea
		West and South Indian Shelf
		Central Indian Ocean Islands
Indo-Australasian Archipelago (IAA) <i>sensu</i> Vieira et al. (2017)	E: Central Indo-Pacific  Sub-realms: 1: Southern Japan 2: Micronesia 3: Coral Triangle 4: Melanesia	South Kuroshio
		Tropical Northwestern Pacific
		Western Coral Triangle
		Eastern Coral Triangle
		Northeast Australian Shelf
		Tropical Southwestern Pacific
Central Pacific	C: Eastern Indo-Pacific	Central Polynesia
		Hawaii
		Southeast Polynesia
Eastern Pacific	F: Tropical Eastern Pacific	Tropical East Pacific

889

890 **Table 2:** Species diversity of Udoteaceae (total number of species and number of endemic species)  
 891 within the six realms (detailed of the four sub-realms level for Central Indo-Pacific), as well as at the  
 892 province-level, based on the species dataset included in this study and distribution records confirmed  
 893 with DNA.

REALMS	TOTAL NUMBER OF SPECIES; ENDEMIC SPECIES
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<b>A: Tropical Atlantic</b>	<b>14 ; 14</b>
<b>D: Temperate Northern Atlantic</b>	<b>1 ; 1</b>
<b>B: Western Indo-Pacific/Indian Ocean</b>	<b>16 ; 9</b>
<b>E: Central Indo-Pacific</b>	<b>18 ; 10</b>
E.1: Southern Japan	3 ; 0
E.2: Micronesia	3 ; 0
E.3: Coral Triangle	5 ; 0
E.4: Melanesia	16 ; 7
<b>C: Eastern Indo-Pacific</b>	<b>6 ; 2</b>
<b>F: Eastern Pacific</b>	<b>1 ; 0</b>
<b>PROVINCES</b>	<b>TOTAL NUMBER OF SPECIES; ENDEMIC SPECIES</b>
<b>Greater Caribbean</b>	<b>14 ; 14</b>
<b>Mediterranean Sea</b>	<b>1 ; 1</b>
<b>Western Indian Ocean</b>	<b>14 ; 7</b>
<b>Red Sea</b>	<b>1 ; 0</b>
<b>West and South Indian Shelf</b>	<b>2 ; 0</b>
<b>Central Indian Ocean Islands (Maldives)</b>	<b>4 ; 0</b>
<b>South Kuroshio</b>	<b>3 ; 0</b>
<b>Tropical Northwestern Pacific (Micronesia)</b>	<b>3 ; 0</b>
<b>Western Coral Triangle</b>	<b>4 ; 0</b>
<b>Eastern Coral Triangle</b>	<b>10 ; 4</b>
<b>Northeast Australian Shelf</b>	<b>2 ; 0</b>
<b>Tropical Southwestern Pacific</b>	<b>11 ; 3</b>
<b>Sunda Shelf</b>	<b>1 ; 0</b>
<b>Central Polynesia</b>	<b>1 ; 0</b>
<b>Hawaii</b>	<b>3 ; 0</b>
<b>Southeast Polynesia</b>	<b>1 ; 0</b>
<b>Tropical East Pacific</b>	<b>1 ; 0</b>

894

895 **Table 3:** Comparison of the likelihood (LnL) and AICc values of the different models for the study of

896 Udoteaceae at the regions and realm levels. The model with the highest score is indicated in green.

897

Models	Region		Realms	
	LnL	AICc	LnL	AICc
<b>DEC</b>	-98.27	200.8	-103.8	211.8
<b>DEC+J</b>	-98.19	200.7	-103.7	211.6
<b>DIVALIKE</b>	-98.05	200.4	-103.9	212.1
<b>DIVALIKE+J</b>	-93.67	193.9	-99.45	205.5
<b>BAYAREALIKE</b>	-107.4	219.1	-110.6	225.5

898

<b>BAYAREALIKE+J</b>	-94.16	194.9	-99.75	206.1
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899 **List of Figures**

900

901 **Figure 1:** Geographical areas considered at the realm level. The six realms (A-F) refer to those  
902 indicated in Table 1. Blue and red circles represent our sampling and sequences from GenBank,  
903 respectively.

904

905 **Figure 2:** A. Multilocus time-calibrated phylogeny (*tufA*, *rbcl* and 18S rDNA) of Udoteaceae from  
906 BEAST analysis. The estimated divergence times are indicated at the nodes and the grey bars indicate  
907 the 95% HPD (highest probability densities). Black asterisks represent highly supported nodes for  
908 both methods ( $bs > 85$ ;  $PP > 0.95$ ) while grey asterisks represent well-supported nodes only in  
909 Bayesian inference ( $bs < 85$ ;  $PP > 0.95$ ). The grey circle represents the 95% credibility shift inferred  
910 with BAMM. B. LTT plot with a 95% confidence interval based on 1,000 BEAST trees. Major  
911 paleontological events or barriers are represented by the red lines: K-T crisis (66 Ma), E/O cooling (34  
912 Ma), terminal Tethyan Event (18 Ma), closure of the Isthmus of Panama (3 Ma) and Benguela  
913 upwelling (1-2 Ma).

914

915 **Figure 3:** Biogeographical history of the Udoteaceae at the level of the six realms, under the  
916 DIVALIKE+J model. The estimation of the most likely ancestral areas is represented at the nodes, as  
917 well as the position of the founder-event speciation (f.) and vicariance (v.) events. The colored  
918 branches represent occupied ancestral areas with probability  $> 50$ . The species' current ranges are  
919 indicated at the terminal branches and refer to the map (A: Tropical Atlantic; B: Western Indo-Pacific;  
920 C: Eastern Indo-Pacific; D: Temperate Northern Atlantic; E: Central Indo-Pacific; F: Tropical Eastern  
921 Pacific).

922

923 **Figure 4:** Graphical representation of the mean frequencies of the different events occurred at the  
924 region and realm levels (under DIVALIKE+J model) estimated through the 50 BSM analyses (area  
925 change, extinction and subset speciation are not represented as they were null).

926

927 **Figure 5:** Summary of biogeographical events of the Udoteaceae based on the results of the realm-  
928 level analysis. The six realms (A: Tropical Atlantic; B: Western Indo-Pacific; C: Eastern Indo-Pacific; D:  
929 Temperate Northern Atlantic; E: Central Indo-Pacific; F: Tropical Eastern Pacific) are represented by  
930 colored circles with indication of species diversity/number of endemic species (bottom), and the  
931 number of speciation events within the realm (in the arrow circles, at the top). The number of shared



932 species between realms is indicated at the intersections of the colored circles. The numbers  
933 associated with the arrows indicate the number of founder-event speciation/dispersal.

934 **Appendix A: Supplementary material**

935

936 **Table A.1:** List of specimens included in the geographical and biogeographical analyses, detailing  
937 voucher name, molecular identity, collect locality with GPS coordinates, corresponding biogeographic  
938 areas, GenBank accession numbers (or BOLD ID in grey) and reference studies.

939 **Table A.2:** List of our specimens included in the time-calibrated phylogeny with GenBank accession  
940 numbers (or Bold ID), as well as the GenBank sequences added to the dataset.

941 **Table A.3:** Calibration points used for the reconstruction of the time-calibrated phylogeny. Literature  
942 references, age, as well as node position and calibration priors are provided.

943 **Table A.4:** Details of the areas occupied by each species

944 **Table A.5.** Geographical distribution of the Udoteaceae species based on literature cited in AlgaeBase  
945 that were excluded in our time-calibrated tree and the biogeographical analyses (see Material and  
946 methods for rationale), and the corresponding regions, realms and sub-realms. These distributions  
947 have not been verified by molecular analyses. Region-level: IAA = Indian-Australasian Archipelago; OI  
948 = Indian Ocean; A = Atlantic; PC = Central Pacific; PE = Eastern Pacific. Realm-level: CIP = Central Indo-  
949 Pacific; WIP = Western Indo-Pacific; TA = Tropical Atlantic; TNA= Temperate Northern Atlantic; EIP =  
950 Eastern Indo-Pacific; TEP = Temperate Eastern Pacific. Sub-realm-level: acronyms identical to those of  
951 realm-level, with the addition of Mi = Micronesia; Me= Melanesia; SJ = South Japan; TC = Coral  
952 Triangle.

953 **Table A.6:** Results of the likelihood test for +J parameter integration.

954

955

956 **Figure A.1:** ML tree of Udoteaceae based on the concatenated multilocus matrix (*tufA*, *rbcl* and 18S  
957 rDNA). Black asterisks represent highly supported nodes ( $bs > 85$ ) while grey asterisks represent  
958 moderately supported nodes ( $70 < bs < 85$ ).

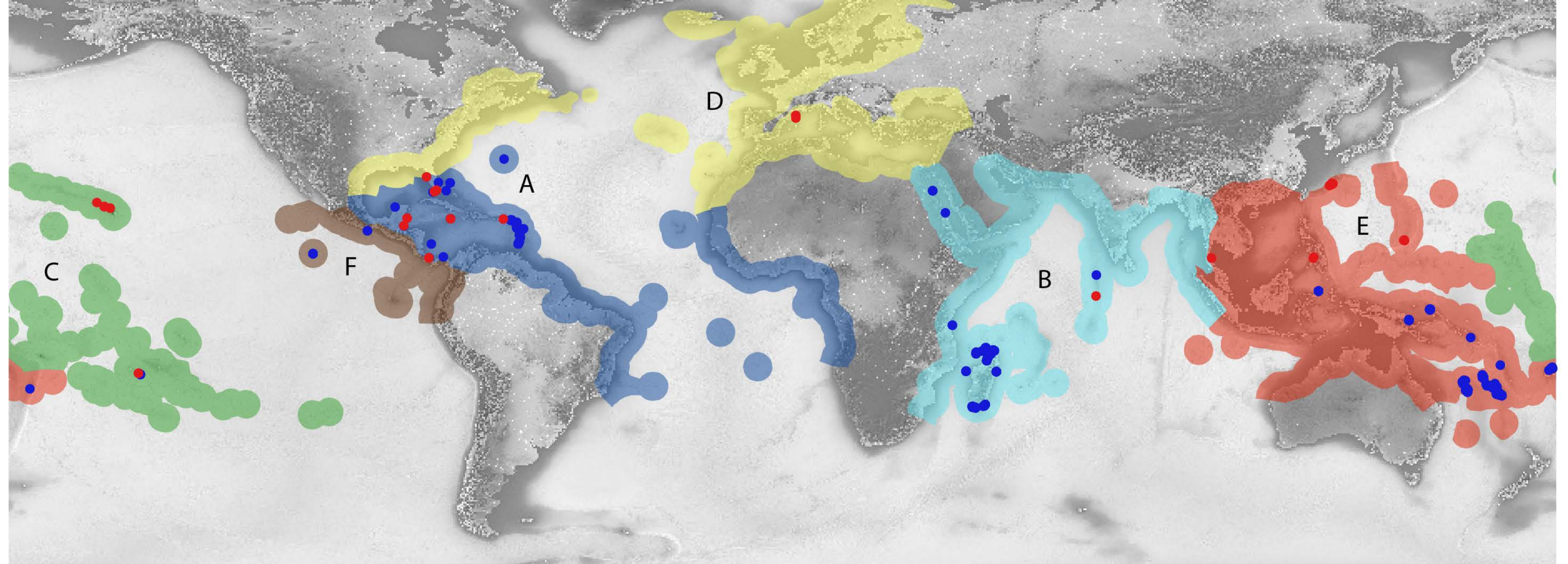
959 **Figure A.2:** Results of the BAMM analysis: Probabilities of changes (0-4) in the diversification rate for  
960 Udoteaceae.

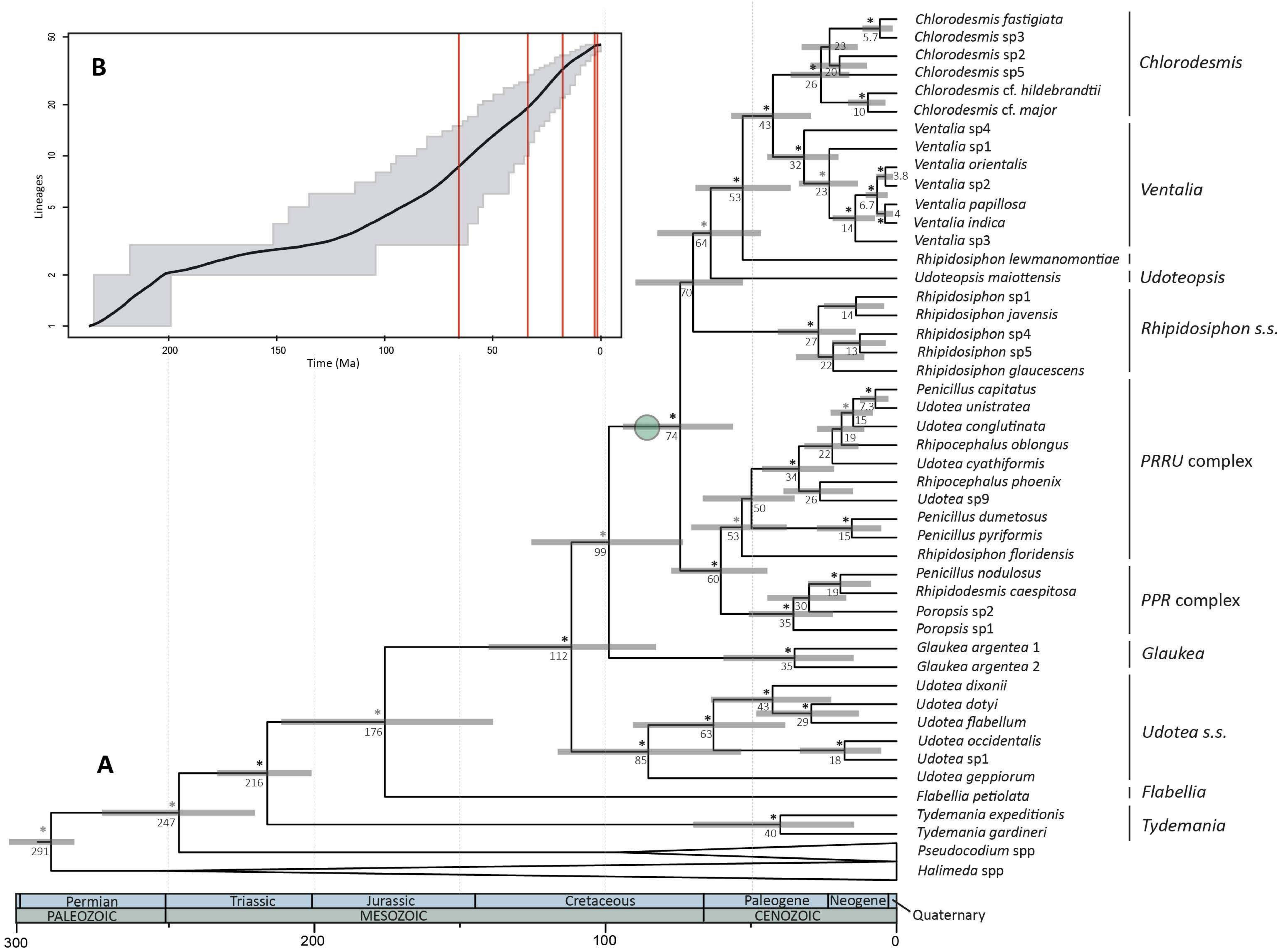
961 **Figure A.3:** Realm-level analysis results of the biogeographical history of Udoteaceae under the  
962 DIVALIKE model

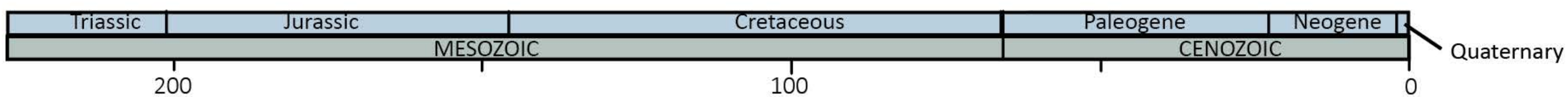
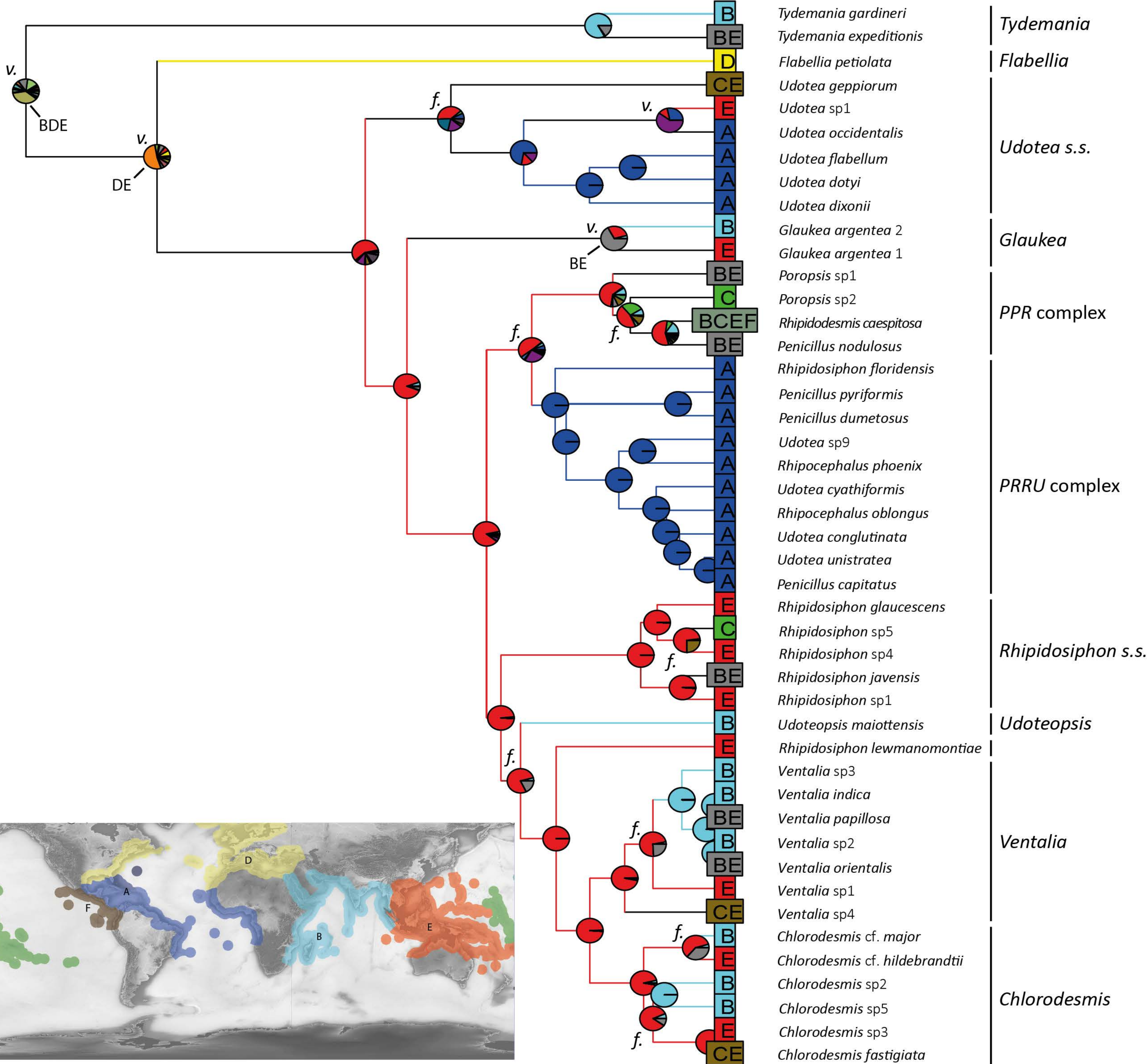
963 **Figure A.4:** Region-level analysis results of the biogeographical history of the Udoteaceae under the  
964 DIVALIKE+J model

965 **Figure A.5:** Subrealm-level analysis results of the biogeographical history of the Udoteaceae under  
966 the DIVALIKE+J model

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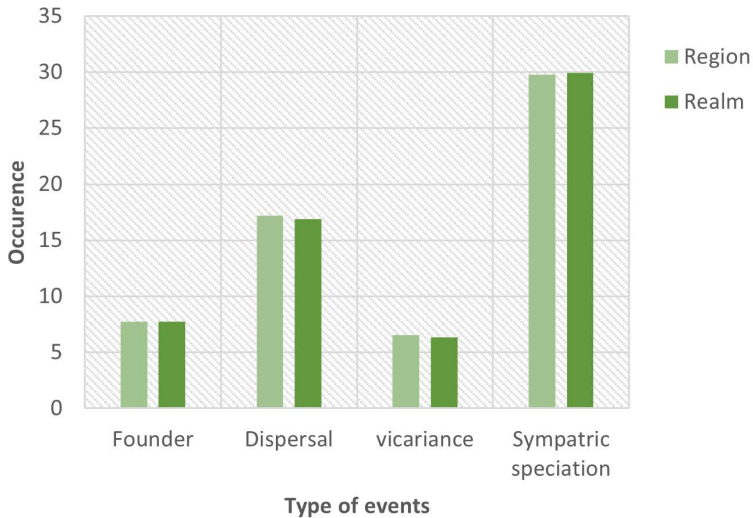


Table 1 :

Calibration points	Type; Source	Dating (Ma); Period	Position	Distribution law and setting up
Bryopsidales root (except <i>Ostreobium</i> )	Estimation; Verbruggen et al. (2009a)	456 ; Ordovician	Root of the tree	Normal Mean: 456 Sigma: 0.09
Halimedinaeae suborder	Estimation; Verbruggen et al. (2009a)	391 ; Devonian	Crown of Halimedinaeae suborder	Normal Mean: 391 Sigma: 0.09
Divergence of the families Udoteaceae and Pseudocodiaceae from the Halimedaceae	Estimation; Verbruggen et al. (2009a)	273 ; Permian	Crown of Halimedaceae + Udoteaceae + Pseudocodiaceae	Normal Mean: 273 Sigma: 0.09
<i>Caulerpa</i> sp.	Fossil; Gustavson & Delevoryas (1992)	280; Permian	Caulerpanceae crown	Uniform Min: 280 Max: 298
<i>Halimeda soltanensis</i>	Fossil; Poncet (1989)	250; Upper Trias	<i>Halimeda</i> crown	Uniform Min: 250 Max: 272
<i>Pseudopenicillus aegaeicus</i>	Fossil; Dragastan et al. (1997)	Lower Trias	Udoteaceae crown	Uniform Min: 201 Max: 237

Table 2

<b>REGIONS</b>	<b>REALMS</b>	<b>PROVINCES</b>
Atlantic Ocean	A : Tropical Atlantic	Tropical Northwestern Atlantic (Caribbean)
	D : Temperate Northern Atlantic	Mediterranean Sea
Indian Ocean	B : Western Indo-Pacific*	Western Indian Ocean
		Red Sea
		West and South Indian Shelf
		Central Indian Ocean Islands (Maldives)
Indo-Australasian Archipelago (IAA) <i>sensu</i> Vieira et al. (2017)	E : Central Indo-Pacific	South Kuroshio
		Tropical Northwestern Pacific (Micronesia)
		Western Coral Triangle
		Eastern Coral Triangle
		Northeast Australian Shelf
		Tropical Southwestern Pacific (Melanesia)
		Sunda Shelf
		Central Polynesia
Central Pacific	C : Eastern Indo-Pacific	Hawaii
		Southeast Polynesia
		Tropical East Pacific
Pacifique Est	F : Tropical Eastern Pacific	Tropical East Pacific



Table 3 :

<b>REALMS</b>	<b>TOTAL NUMBER OF SPECIES ; EXCLUSIVE SPECIES</b>
<b>A : TROPICAL ATLANTIC</b>	<b>14 ; 14</b>
<b>D : TEMPERATE NORTHERN ATLANTIC</b>	<b>1 ; 1</b>
<b>B : WESTERN INDO-PACIFIC/INDIAN OCEAN</b>	<b>16 ; 9</b>
<b>C: CENTRAL INDO-PACIFIC</b>	<b>18 ; 10</b>
C.1 : SOUTH KUROSHIO	3 ; 0
C.2 : MICRONESIA (TROPICAL NORTHWESTERN)	3 ; 0
C.3 : CORAL TRIANGLE	5 ; 0
C.4 : MELANESIA (TROPICAL SOUTHWESTERN)	16 ; 7
<b>D : EASTERN INDO-PACIFIC</b>	<b>6 ; 2</b>
<b>E : EASTERN PACIFIC</b>	<b>1 ; 0</b>
<b>PROVINCES</b>	<b>TOTAL NUMBER OF SPECIES ; EXCLUSIVE SPECIES</b>
<b>CARIBBEAN</b>	<b>14 ; 14</b>
<b>MEDITERRANEAN SEA</b>	<b>1 ; 1</b>
<b>WESTERN INDIAN OCEAN</b>	<b>14 ; 7</b>
<b>RED SEA</b>	<b>1 ; 0</b>
<b>WEST AND SOUTH INDIAN SHELF</b>	<b>2 ; 0</b>
<b>CENTRAL INDIAN OCEAN ISLANDS (MALDIVES)</b>	<b>4 ; 0</b>
<b>SOUTH KUROSHIO</b>	<b>3 ; 0</b>
<b>TROPICAL NORTHWESTERN PACIFIC (MICRONESIA)</b>	<b>3 ; 0</b>
<b>WESTERN CORAL TRIANGLE</b>	<b>4 ; 0</b>
<b>EASTERN CORAL TRIANGLE</b>	<b>10 ; 4</b>
<b>NORTHEAST AUSTRALIAN SHELF</b>	<b>2 ; 0</b>
<b>TROPICAL SOUTHWESTERN PACIFIC</b>	<b>11 ; 3</b>
<b>SUNDA SHELF</b>	<b>1 ; 0</b>
<b>CENTRAL POLYNESIA</b>	<b>1 ; 0</b>
<b>HAWAII</b>	<b>3 ; 0</b>
<b>SOUTHEAST POLYNESIA</b>	<b>1 ; 0</b>
<b>TROPICAL EAST PACIFIC</b>	<b>1 ; 0</b>

Table 4 :

Models	Region		Realms	
	LnL	AICc	LnL	AICc
<b>DEC</b>	-98.27	200.8	-103.8	211.8
<b>DEC+J</b>	-98.19	200.7	-103.7	211.6
<b>DIVALIKE</b>	-98.05	200.4	-103.9	212.1
<b>DIVALIKE+J</b>	-93.67	193.9	-99.45	205.5
<b>BAYAREALIKE</b>	-107.4	219.1	-110.6	225.5
<b>BAYAREALIKE+J</b>	-94.16	194.9	-99.75	206.1