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

Laura Lagourgue[a,b], Frederik Leliaert[c] and Claude E. Payri[b]

[a]Sorbonne Universités, UPMC Univ Paris 06, IFD, 4 Place Jussieu, 75252 Paris Cedex 05, France
[b] UMR ENTROPIE (IRD, UR, UNC, CNRS, IFREMER), Institut de Recherche pour le Développement, B.P. A5 Nouméa Cedex, Nouvelle-Calédonie, 98848, France
[c] Meise Botanic Garden, Meise, Belgium

Corresponding author : Lagourgue Laura, UMR ENTROPIE (IRD, UR, UNC, CNRS, IFREMER), Institut de Recherche pour le Développement, B.P. A5 Nouméa Cedex, Nouvelle-Calédonie, 98848, France ; email : laura.lagourgue@ird.fr

Abstract

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

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

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

Highlights:

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

Declarations of conflict of interests: none

1. INTRODUCTION

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

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

The Udoteaceae is a species-rich clade within the Bryopsidales, traditionally recognized as a separate family, but more recently proposed as a tribe (Udoteae) in the family Halimedaceae (Cremen et al., 2019). The group is distributed worldwide, in tropical to warm temperate seas, including the tropical Atlantic, Indian and Pacific Oceans, as well as in the Mediterranean and Red Sea. Some genera are widely distributed, spanning different oceans, while others are more range-restricted, such as *Rhipocephalus*, which only occurs in the tropical western Atlantic (Littler and Littler, 2003) or *Flabellia*, which is only found in the Mediterranean Sea and northeastern Atlantic (Díaz-Tapia et al., 2020b). Next to a high diversity in the Indo-Pacific, species diversity in the Udoteaceae is particularly high in the Greater Caribbean region (Bermuda, Bahamas, Florida, Gulf of Mexico and Caribbean *sensu stricto*). Some remarkably diverse genera, such as *Udotea sensu stricto* (*s.s.*) and those present in the "*Penicillus-Rhipocephalus-Rhipidosiphon-Udotea*" complex, as well as high species endemicity are observed in the Greater Caribbean (Littler and Littler, 1990; Lagourgue et al., 2018 and 2020). Recent taxonomic revision and reassessment of species diversity based on DNA sequence data (Sauvage et al., 2016 and 2020; Wade and Sherwood, 2017; Lagourgue et al., 2018 and 2020; Lagourgue and Payri, 2020) enables the study of its biogeographical history in more detail. In Lagourgue and Payri (2020), the origin of Udoteaceae was estimated in the Late Triassic (ca 216 Ma), with most of the genera originating during the Paleogene (between ca 66 and 23 Ma). This study also highlighted a greater species diversity than traditionally recognized based on morphology, including co-occurring cryptic species. Similar to what has been found in several other seaweed groups (Silberfeld et al., 2013; Vieira et al., 2017; Leliaert et al., 2018; Boo et al., 2018), several species with assumed wide ranges (*i.e.,* pantropical or distributed among several oceans), were found to consist of different species with more restricted geographical ranges (*i.e.,* only found in one ocean or even confined to short stretches of coastline or island groups). Conversely, for a few other species (e.g., *Rhipidodesmis caespitosa*, *Tydemania expeditionis*, *Chlorodesmis fastigiata*), wide ranges have been identified or confirmed, highlighting long-distance dispersal capacity in some species. Large differences in geographical ranges between species is commonly seen in bryopsidalean genera, such as *Caulerpa* (Belton et al., 2020), *Halimeda* (Verbruggen et al., 2005), *Codium* (Verbruggen et al., 2007) and *Bryopsis* (Hollands et al., 2013).

The striking biogeographical pattern of the Udoteaceae, with high species diversity in the Greater Caribbean and Indo-Pacific, and high endemism between the two regions, along with the well documented diversity and distribution of species based on DNA sequence data, makes this family an interesting group to investigate biogeographical patterns of species diversity and their underlying drivers. This study aims to combine the geographical and genetic data of the different Udoteaceae species in order to: (1) analyze the diversification of the family based on a time-calibrated phylogeny and (2) estimate the biogeographical history of the family to identify the role of different marine barriers, dispersal, and different speciation mechanisms in the evolution of the family.

2. MATERIAL & METHODS

2.1. Sampling and data assembly

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

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

2.2. Multilocus time-calibrated species phylogeny

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

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

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

Possible shifts in diversification rates were first evaluated using a lineage-through time (LTT) based on a sub-sampling of 1,000 trees from BEAST analysis with the “ltt95” function of the “phytools” package (Revell, 2012) integrating a 95% confidence range. A "Bayesian analysis of macroevolutionary mixtures" (BAMM; Rabosky, 2014) analysis was also conducted with five million MCMC generations, based directly on the MCCT and on an *a priori* estimation of the parameters by the "setBAMMpriors" function of the "BAMMtools" package on R (R Development Core Team, 2019).

2.3. Geographic data

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

For biogeographical analyses, the following geographical areas are generally defined and used (decreasing scales): regions, realms, provinces and even ecoregions (see Spalding et al., 2007 for definitions of these terms). Three geographical subdivisions were considered for the historical biogeographical analyses: five regions as defined by Vieira et al. (2017), seven realms, and 17 provinces as defined by Spalding et al. (2007). Nevertheless, biogeographical history inference could not be carried out at the province level as the composition of the data (number of provinces and maximum range size) required computing capacity that far exceeded the BioGeoBEARS authors' recommendations (Matzke, 2016; equivalent to > 65,000 states for our study, while a maximum of 500-600 states is recommended by the authors). An alternative analysis, subdividing the Central Indo-Pacific into four different sub-realms (Coral Triangle, Micronesia, Southern Japan, and Melanesia) was carried out in order to refine the information concerning this geographical area. This analysis is given as additional information, as it presents a bias in the division of areas (*i.e.,* other geographical areas remaining the same as for the realms level). The different geographical areas are listed in Table 1 and the realms division is presented in Figure 1. Details of the areas occupied by each species included in this study are available in Table A.4 (Supplementary material; see also Table A.5 for the distribution ranges based on literature of species not included in the analyses).

2.4. Inference of biogeographical history

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

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

3. RESULTS

3.1 Time-calibrated phylogeny of the Udoteaceae

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

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

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

3.2. Geographical patterns of species richness

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

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

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

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

3.3. Biogeographical history

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

Biogeographical inference at the realm level (Figure 3) estimated the ancestral geographical range of the Udoteaceae as the area comprising the Western and Central Indo-Pacific and the Mediterranean Sea in their current configuration, corresponding to the Tethys Sea of the Late Triassic (similar results were obtained at the region level, Figure A.4 in Supplementary material). Most of the diversification events occurred within the Central Indo-Pacific which is also the area that contains most of the current diversity as well as a high number of endemic species. From the Central Indo-Pacific, dispersal occurred to other geographical areas. The Western Indian Ocean, also included in the area of origin, represents an area occupied by species that diverged early in the history of the Udoteaceae (*Tydemania* spp.). The Western Indian Ocean has since experienced at least seven colonization events from the Central Indo-Pacific. The Mediterranean Sea only contains a single species and was not subsequently colonized. Another species of Udoteaceae, *Poropsis subunalis*, has its type locality in the Mediterranean but for the time being, no DNA sequence is reliably associated with the species. The Greater Caribbean was colonized twice independently during the Cretaceous (~80 Ma) and Paleogene (~50 Ma) periods, probably from the Central Indo-Pacific. The Eastern Indo-Pacific was colonized five times independently between the Cretaceous and Paleogene (80-40 Ma), mainly from the Central Indo-Pacific. Finally, colonization of the Eastern Pacific occurred more recently from the Miocene (ca. 19 Ma) onward. Our analysis inferred the Western Indian Ocean as the area of origin of *Tydemania* (40 Ma; dates based on sampling of extant species), and the Central Indo-Pacific for *Udotea s.s.* (85 Ma), *Ventalia* (32 Ma), the PPR complex (35 Ma), *Rhipidosiphon s.s.* (27 Ma) and *Chlorodesmis* (26 Ma). As for the genus *Glaukea* (35 Ma), its geographical origin includes the Western Indian Ocean and the Central Indo-Pacific and finally, the MRCA of the PRRU complex appeared in the Atlantic (53 Ma) from a Central Indo-Pacific ancestor.

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

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

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

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

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

4. DISCUSSION

4.1. Biogeographical patterns

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

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

Our biogeographical inferences are strongly dependent on the phylogeny and taxon sampling. It is therefore possible, with the inclusion of additional species (notably likely cryptic diversity in understudied groups of diminutive species like the PPR complex and *Rhipidosiphon*), supplementary geographical sampling, and variation in phylogenetic relationships, that the patterns reported here and the evolutionary history of the Udoteaceae will change. However, based on our extensive sampling, we are confident that our main conclusion (*e.g.*, the importance of the Central Indo-Pacific as center of origin, the three centers of Udoteaceae diversity) will hold as new data become available.

4.2. Origin and diversification of the Udoteaceae

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

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

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

time scales have also been found in the evolution of other seaweeds (*e.g., Portieria* (Leliaert et al., 2018) or *Padina* (Vieira et al., 2021)) and some tropical marine animals, with one or a few shifts in the Late Cretaceous (Leprieur et al., 2016; for corals, fishes, and foraminifera) or the Oligo/Miocene (Williams and Duda, 2008; for gastropods; Wilson and Rosen,1998; for corals).
The most recent cladogenesis (speciation) events in our phylogeny were in the Paleogene period, but others were inferred during the Cretaceous period or even the Jurassic. However, these speciation age estimates have to be carefully interpreted due to potential incomplete sampling bias as well as extinction. The terminal period of the Tethys Sea (from ca 18 Ma) and its closure (ca 12-15 Ma) can be related to the beginning of multiple speciation events in the Western Indian Ocean for the genera *Ventalia* and *Chlorodesmis*, and to the origin of the two vicariant species pairs (*Udotea* sp1/*U. occidentalis* and *Glaukea argentea* 1/*G. argentea* 2).

4.3 Origins of the centers of diversity

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

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

In the Western Indian Ocean, which is part of the estimated area of origin of the Udoteaceae, early diversification was inferred (*e.g.*, *Tydemania* lineages). The region was subsequently colonized several times independently (by founder-event speciation) mainly from the Central Indo-Pacific, and this was followed by diversification within the region, explaining its current species richness. Only a few dispersal events to other regions and realms were inferred, including from the Western Indian Ocean back to the Central Indo-Pacific. The large number of endemic species in the Western Indian Ocean, and the few species in common with the Central Indo-Pacific is congruent with patterns in fishes (Cowman and Bellwood, 2013a; Hodge and Bellwood, 2016) and corals (Keith et al., 2013), and may be explained by the Middle Indian Ocean barrier. However, given the large number of inferred dispersal events between the Western Indian Ocean and the Central Indo-Pacific, this barrier must have been crossed several times independently during the evolutionary history of the Udoteaceae. The high diversification inferred in the region can be partly explained by the upwelling system of the northern Indian Ocean, which marks a biogeographic delimitation in the species composition and has been considered as a biodiversity generator (Burt et al., 2011; Schils and Wilson, 2006, Leliaert et al., 2018).

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

Thus, for the Udoteaceae, the Central Indo-Pacific can be regarded as a center of origin, accumulation and overlap and can be seen both as a cradle of biodiversity (by housing old species lineages) and a species generator. The Western Indian Ocean can be interpreted as a center of origin and accumulation, as well as a cradle of biodiversity, housing the old lineage leading to *Tydemania* spp. The Greater Caribbean region can be interpreted as a more recent center of origin.

Other geographical areas were found to have a lower diversity of Udoteaceae species. Warm temperate areas such as southern Japan or Micronesia (Guam) were likely colonized from the Central Indo-Pacific several times independently between the Paleogene and Neogene. For the Mediterranean Sea, besides the speciation that led to *Flabellia petiolata,* no subsequent diversification was inferred and the impact of the various paleontological events, such as the Messinian Salinity Crisis (ca 5.9-5.3 Ma) or the Pliocene submersion, are difficult to assess. The islands in the Eastern Indo-Pacific have been colonized several times independently from the Central Indo-Pacific more recently (between 25 and 5 Ma) (Figures 3 and 4). Although founder-event speciation was inferred in our analyses, it is possible that species arrived at these islands by successive short distance dispersal events via intermediate islands that have now disappeared (Neall and Trewick, 2008; Heads, 2018; Leliaert et al., 2018). No subsequent diversification of Udoteaceae in the Pacific islands or dispersal back to the Central Indo-Pacific was deduced in our analysis. This contrasts with some studies on reef fishes that show the Hawaiian archipelago as a center of species diversification and dispersal (Bowen et al., 2013; Eble et al., 2011). The Eastern Pacific also appears to be poor in Udoteaceae species, and the species were found not to be related to those occurring in the Atlantic (Figure 3), indicating that speciation was not correlated with the closure of the Isthmus of Panama.

4.4. Speciation processes

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

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

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

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

5. CONCLUSIONS

Our analyses point towards a Late Triassic origin of the Udoteaceae with a marked diversification from the Late Cretaceous onward. Based on our historical biogeographical inference, along with the early branching Mediterranean and the Western Indo-Pacific lineages, and fossil data, the ancestral area was likely located in the Western Tethys. Early diversification in this region was likely followed by eastward dispersal to the Central Indo-Pacific. Currently the family has three main centers of species diversity: the Central Indo-Pacific, which was inferred as a center of origin, accumulation and overlap; the Western Indian Ocean, which was inferred as a center of origin and accumulation; and the Greater Caribbean, constituting a more recent center of origin. Contrary to previous understanding, most species have restricted ranges, and none of them appear pantropical. This is similar to many other species of Bryopsidales, although a number of families also contain species that are truly pantropical, including several species of *Caulerpa*, *Codium* and *Halimeda*. Furthermore, the family is distinct in its high endemicity between the Greater Caribbean and the Indo-Pacific, a pattern that has also been observed in *Halimeda* (Verbruggen et al., 2009b). The main process in the diversification of the Udoteaceae is speciation within regions, followed by dispersal, the two often acting in an interrelated way. Species in Udoteaceae appear to have the capacity to disperse and colonize new regions (founder events). However, and although range-switching, subset speciation and range contractions were not inferred in our analyses, further study, including the missing species or more sampled localities, would better confirm these patterns in the Udoteaceae biogeographical history.

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

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) *sensu* Vieira et al. (2017)	E: Central Indo-Pacific	South Kuroshio
		Tropical Northwestern Pacific
	Sub-realms:	Western Coral Triangle
	1: Southern Japan	Eastern Coral Triangle
	2. Micronesia	Northeast Australian Shelf
	3: Coral Triangle	Tropical Southwestern Pacific
	4: Melanesia	Sunda Shelf
Central Pacific	C: Eastern Indo-Pacific	Central Polynesia
		Hawaii
		Southeast Polynesia
Eastern Pacific	F: Tropical Eastern Pacific	Tropical East Pacific

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

REALMS	TOTAL NUMBER OF SPECIES; ENDEMIC SPECIES

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

Table 3: Comparison of the likelihood (LnL) and AICc values of the different models for the study of Udoteaceae at the regions and realm levels. The model with the highest score is indicated in green.

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

BAYAREALIKE+J	-94.16	194.9	-99.75	206.1

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

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

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

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

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

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

Appendix A: Supplementary material

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

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

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

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

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

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

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

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

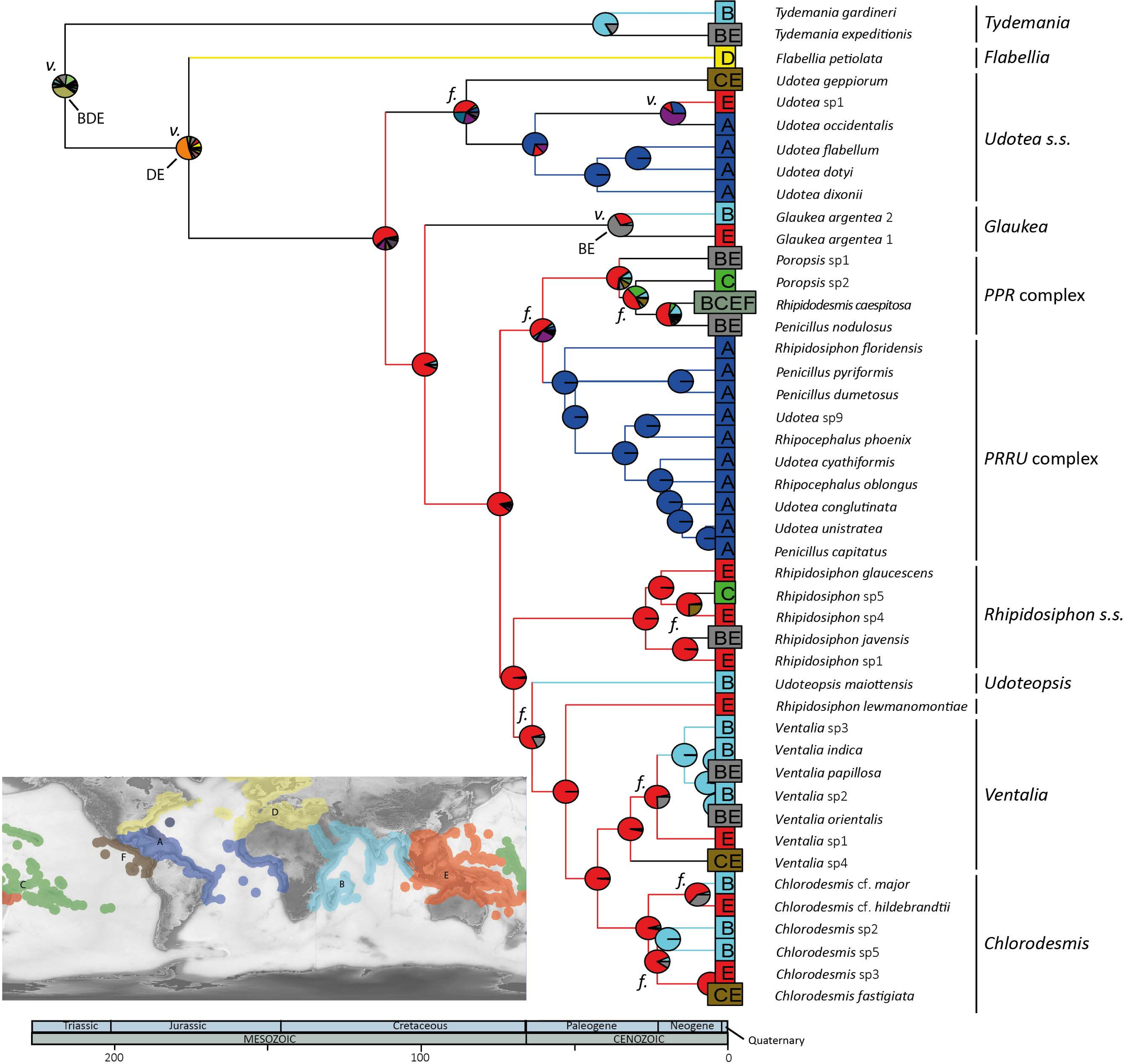
Figure A.3: Realm-level analysis results of the biogeographical history of Udoteaceae under the DIVALIKE model

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

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


A
B
C
D
E
F


B
Lineages
50
20
10
5
2
1
Time (Ma)
200
150
100
50
0
A
Chlorodesmis fastigiata
Chlorodesmis sp3
Chlorodesmis sp2
Chlorodesmis sp5
Chlorodesmis cf. hildebrandtii
Chlorodesmis cf. major
Ventalia sp4
Ventalia sp1
Ventalia orientalis
Ventalia sp2
Ventalia papillosa
Ventalia indica
Ventalia sp3
Rhipidosiphon lewmanomontiae
Udoteopsis maiottensis
Rhipidosiphon sp1
Rhipidosiphon javensis
Rhipidosiphon sp4
Rhipidosiphon sp5
Rhipidosiphon glaucescens
Penicillus capitatus
Udotea unistratea
Udotea conglutinata
Rhipocephalus oblongus
Udotea cyathiformis
Rhipocephalus phoenix
Udotea sp9
Penicillus dumetosus
Penicillus pyriformis
Rhipidosiphon floridensis
Penicillus nodulosus
Rhipidodesmis caespitosa
Poropsis sp2
Poropsis sp1
Glaukea argentea 1
Glaukea argentea 2
Udotea dixonii
Udotea dotyi
Udotea flabellum
Udotea occidentalis
Udotea sp1
Udotea geppiorum
Flabellia petiolata
Tydemania expeditionis
Tydemania gardineri
Pseudocodium spp
Halimeda spp
Chlorodesmis
Ventalia
Udoteopsis
Rhipidosiphon s.s.
PRRU complex
PPR complex
Glaukea
Udotea s.s.
Flabellia
Tydemania
5.7
23
20
26
10
43
32
3.8
23
6.7
4
14
53
64
70
14
27
13
22
7.3
15
19
22
34
26
50
74
53
15
99
60
19
30
35
112
35
43
29
63
18
85
176
40
216
247
291
Permian
Triassic
Jurassic
Cretaceous
Paleogene
Neogene
Quaternary
PALEOZOIC
MESOZOIC
CENOZOIC
300
200
100
0



B Tydemania gardineri
BE Tydemania expeditionis
Tydemania
D Flabellia petiolata
Flabellia
CE Udotea geppiorum
E Udotea sp1
A Udotea occidentalis
A Udotea flabellum
A Udotea dotyi
A Udotea dixonii
Udotea s.s.
B Glaukea argentea 2
E Glaukea argentea 1
Glaukea
BE Poropsis sp1
C Poropsis sp2
BCEF Rhipidodesmis caespitosa
BE Penicillus nodulosus
PPR complex
A Rhipidosiphon floridensis
A Penicillus pyriformis
A Penicillus dumetosus
A Udotea sp9
A Rhipocephalus phoenix
A Udotea cyathiformis
A Rhipocephalus oblongus
A Udotea conglutinata
A Udotea unistratea
A Penicillus capitatus
PRRU complex
E Rhipidosiphon glaucescens
C Rhipidosiphon sp5
E Rhipidosiphon sp4
BE Rhipidosiphon javensis
E Rhipidosiphon sp1
Rhipidosiphon s.s.
B Udoteopsis maiottensis
Udoteopsis
E Rhipidosiphon lewmanomontiae
B Ventalia sp3
B Ventalia indica
BE Ventalia papillosa
B Ventalia sp2
BE Ventalia orientalis
E Ventalia sp1
CE Ventalia sp4
Ventalia
B Chlorodesmis cf. major
E Chlorodesmis cf. hildebrandtii
B Chlorodesmis sp2
B Chlorodesmis sp5
E Chlorodesmis sp3
CE Chlorodesmis fastigiata
Chlorodesmis
v.
BDE
v.
DE
f.
v.
v.
BE
f.
f.
f.
f.
f.
f.
f.
D
A
F
C
B
E
Triassic
Jurassic
Cretaceous
Paleogene
Neogene
MESOZOIC
CENOZOIC
Quaternary
200
100
0

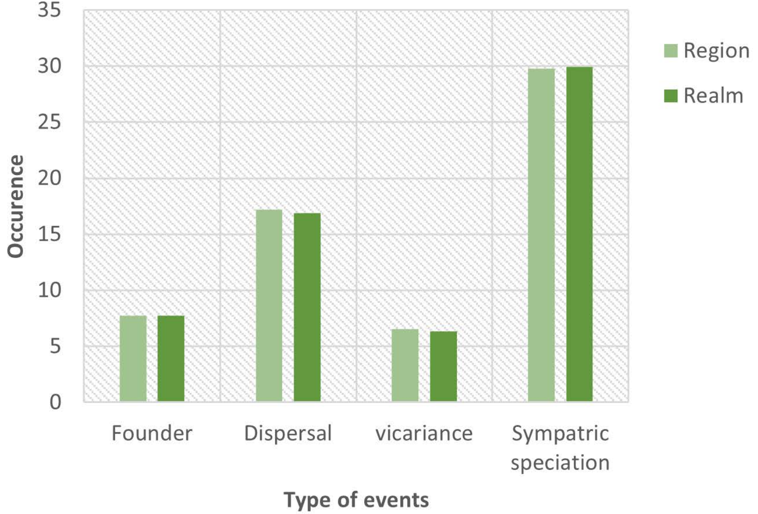

35
30
25
20
15
10
5
0
Occurence
Founder
Dispersal
vicariance
Sympatric speciation
Type of events
Region
Realm

Table 1 :

Calibration points	Type; Source	Dating (Ma); Period	Position	Distribution law and setting up
Bryopsidales root (except *Ostreobium*)	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 ; Denovian	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
Caulerpa sp.	Fossil; Gustavson & Delevoryas (1992)	280; Permian	Caulerpaceae crown	Uniform Min: 280 Max: 298
Halimeda soltanensis	Fossil; Poncet (1989)	250; Upper Trias	*Halimeda* crown	Uniform Min: 250 Max: 272
Pseudopenicillus aegaeicus	Fossil; Dragastan et al. (1997)	Lower Trias	Udoteaceae crown	Uniform Min: 201 Max: 237

Table 2

REGIONS	REALMS	PROVINCES
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) *sensu* 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 Pacific	C : Eastern Indo-Pacific	Central Polynesia
		Hawaii
		Southeast Polynesia
Pacifique Est	F : Tropical Eastern Pacific	Tropical East Pacific

Table 3 :

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

Table 4 :

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