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Historical biogeography of the highly diverse brown seaweed *Lobophora* (Dictyotales, Phaeophyceae) ☆

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ABSTRACT

The tropical to warm-temperate marine brown macroalgal genus *Lobophora* (Dictyotales, Phaeophyceae) recently drew attention because of its striking regional diversity. In this study we reassess *Lobophora* global species diversity, and species distributions, and explore how historical factors have shaped current diversity patterns. We applied a series of algorithmic species delineation techniques on a global mitochondrial *cox*3 dataset of 598 specimens, resulting in an estimation of 98–121 species. This diversity by far exceeds traditional diversity estimates based on morphological data. A multi-locus time-calibrated species phylogeny using a relaxed molecular clock, along with DNA-confirmed species distribution data was used to analyse ancestral area distributions, dispersal-vicariance-founder events, and temporal patterns of diversification under different biogeographical models. The origin of *Lobophora* was estimated in the Upper Cretaceous (−75 to −60 MY), followed by gradual diversification until present. While most speciation events were inferred within marine realms, founder events also played a non-negligible role in *Lobophora* diversification. The Central Indo-Pacific showed the highest species diversity as a result of higher speciation events in this region. Most *Lobophora* species have small ranges limited to marine realms. *Lobophora* probably originated in the Tethys Sea and dispersed repeatedly in the Atlantic (including the Gulf of Mexico) and Pacific Oceans. The formation of the major historical marine barriers (Terminal Tethyan event, Isthmus of Panama, Benguela upwelling) did not act as important vicariance events. Long-distance dispersal presumably represented an important mode of speciation over evolutionary time-scales. The limited geographical ranges of most *Lobophora* species, however, vouch for the rarity of such events.

1. Introduction

A good understanding of species diversity is essential for addressing biogeographical questions. Recent studies addressing the magnitude of eukaryotic diversity of terrestrial and marine systems (Appeltans et al., 2012; Costello et al., 2013; Mora et al., 2011; Scheffers et al., 2012; Sweetlove, 2011) have highlighted the large uncertainty in global species diversity, with global species diversity estimates ranging between 2 and 50 million species. In addition, the application of DNA markers to delineate species (DNA taxonomy; Blaxter, 2004) disclosed levels of cryptic species diversity, which in many cases outnumber traditionally recognized species by a factor 10 (Adams et al., 2014). Failure to recognize cryptic species not only results in underestimation of species diversity, but may also have significant consequences for the interpretation of macroevolutionary patterns and for species conservation (Agapow et al., 2004; Bickford et al., 2007). Recent estimates of global biodiversity, however, did not take into account the magnitude of cryptic species (but see Appeltans et al., 2012), which is likely to be common in many organismal groups (Adams et al., 2014; Pfenninger and Schwenk, 2007). Algae represent a group for which the magnitude of diversity remains highly uncertain (De Clerck

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et al., 2013; Guiry, 2012). Several regional case studies demonstrated that algal species diversity could be up-scaled with one or two orders of magnitude (e.g. Evans et al., 2007; Leliaert et al., 2014; Payo et al., 2013; Saunders, 2008; Stiller and Waaland, 1993), recognizing the high level of cryptic species in this group (but several studies did not unveil a lot of cryptic species).

Next to the uncertainty on diversity estimates, it is unclear how local diversity estimates translate into global diversity. Estimations of the global diversity of any given group require insights in the geographical structuring of species diversity. High local diversity may not necessarily translate into high global diversity, because of broad geographic ranges and/or the paucity of species diversity in other regions. Conversely, narrow species ranges may result in relatively low species diversity at a local scale, but high global diversity.

While in general diversity is lower in the sea than on land, marine species diversity in some groups and areas can be high (Appeltans et al., 2012; De Vargas et al., 2015; Grosberg et al., 2012; May and Godfrey, 1994; Vermeij and Grosberg, 2010). This high species diversity in the marine environment raises evolutionary questions related to the drivers and mechanisms of evolutionary diversification. Geographic isolation is the traditional explanation for diversification, but there is a growing consensus that sympatric adaptive diversification may be an important source of diversity in the marine environment (Bowen et al., 2013; Schluter, 1996, 2001). Opportunities for allopatric speciation are reduced in the ocean since there are few physical barriers, and dispersal may be extensive (Bowen et al., 2013). Although certainly true for many fishes and invertebrates with pelagic larval stages that have high dispersal potential (Kinlan and Gaines, 2003), long-distance dispersal is rarer in marine macroalgae as propagules have been shown to have limited dispersal capabilities (Kinlan and Gaines, 2003; Norton, 1992; Santelices, 1990). There are, however, exceptions of macroalgal species with high dispersal capacity and wide geographical ranges, including *Macrocystis pyrifera* (Macaya and Zuccarello, 2010), *Boodlea* (Leliaert et al., 2009), *Colpomenia* (Lee et al., 2014, 2013), *Ulva* (Kirkendale et al., 2013), *Adenocystis utricularis* and *Bostrychia intricata* (Fraser et al., 2013). The relative scarcity of cosmopolitan marine macroalgal species, confirmed by molecular methods, is evidence that long-distance dispersal is not as common as in other groups (e.g. with pelagic larval stages). Indeed, many alleged cosmopolitan species have eventually been shown to represent a complex of genetically distinct species with more restricted distributions (De Clerck et al., 2005; Leliaert et al., 2009; Tronholm et al., 2012; Zuccarello and West, 2003). The strength and spatial extent of gene flow is expected to be an important determinant of the spatial scale at which genetic divergence and speciation can occur (Kisel and Barraclough, 2010). Studies of marine tropical fauna (mostly fishes) have highlighted the possible importance of sympatric, ecological speciation in generating diversity (Bowen et al., 2013; Rocha et al., 2005). This could also hold true for marine macroalgae, but speciation modes are only rarely addressed for tropical seaweeds.

In the present study we assess species diversity and distributions on a global scale focusing on the brown macroalga *Lobophora* (Dictyotales, Phaeophyceae). *Lobophora* is a pantropical-temperate genus that has been previously documented in the Atlantic (including the Gulf of Mexico), Indian and Pacific Oceans, across both hemispheres (Vieira et al., 2016) (Fig. 1; this study; Guiry and Guiry, 2015). Before molecular data were available, virtually all specimens, regardless of their origin, had been assigned to *L. variegata* (J.V. Lamour.) Womersley ex E.C. Oliveira, a species that is now hypothesized to be restricted to the Caribbean (Vieira et al., 2016). Recent molecular studies revealed that the biodiversity of this genus has been severely underestimated (Schultz et al., 2015; Sun et al., 2012; Vieira et al., 2016, 2014). This exceptional diversity discovered from limited locations in the Pacific and Atlantic suggests the existence of a much greater diversity on a global level.

The present study aims to (1) assess species diversity on a global scale using molecular data, (2) define current species distributional ranges, (3) determine the role of dispersal barriers, and (4) examine spatial and temporal patterns of diversification and dispersal of the genus *Lobophora*.

2. Material and methods

2.1. Taxon sampling

Taxon sampling consisted of 598 *Lobophora* specimens. Sampling was carried out from the intertidal down to 90 m deep by scuba diving, snorkeling, or box-dredging (e.g. Gulf of Mexico). Specimens were sampled in more than 40 countries, spanning the entire range of the genus (Fig. 1, Vieira et al., 2016 appendix). Voucher specimens were preserved in silica gel and mounted on herbarium sheets. Collection information and voucher/herbarium numbers are detailed in Vieira et al. (2016).

2.2. DNA extraction, amplification and sequencing

Total genomic DNA was extracted from tissue samples dried in silica gel, or in some cases from herbarium specimens, using a cetyl-trimethyl ammonium bromide (CTAB) extraction method following De Clerck et al. (2006) or using a DNeasy Plant mini Kit (Qiagen, Hilden, Germany). Sequences were generated from the mitochondrial encoded cytochrome *c* oxidase III gene (*cox*3), the chloroplast encoded ribulose-1,5-biphosphate carboxylase (*rbc*L) and the photosystem II protein D1 (*psbA*) genes. The datasets were complemented with sequences from GenBank (cf. Vieira et al., 2016 appendix). Sequences were aligned using MUSCLE (Edgar, 2004) implemented in eBioX 1.6 beta (Lagercrantz, 2008; available at: http://www.ebioinformatics.org).

2.3. Species delimitation

Since traditional morphology-based species delimitation often yields inaccurate estimates of seaweed diversity (Leliaert et al., 2014), we defined species exclusively based on DNA sequence data. We applied different species delimitation methods i.e., the Maximum Likelihood implementation of the GMYC model (Pons et al., 2006; Reid and Carstens, 2012), the Automatic Barcode Gap Discovery (ABGD; Puillandre et al., 2012) and the Poisson Tree Processes model (PTP; Zhang et al., 2013) on the *cox*3 dataset. The use of *cox*3 alone is enough for delineating species in *Lobophora* (Vieira et al., 2014). GMYC and ABGD approaches were previously applied to define *Lobophora* species from New Caledonia (Vieira et al., 2014) and the Western Atlantic (Schultz et al., 2015). Application of the ML-GMYC on *cox*3 yielded highly similar results (1) with other delimitation methods such as the Bayesian implementation of the GMYC model and the Automatic Barcode Gap Discovery (Puillandre et al., 2012) for the same marker, and (2) with analysis of the other markers, *rbc*L and *psb*A. GMYC analyses under a single-threshold were conducted in R (R Core Team, 2014) using the package "Splits" (Fujisawa and Barraclough, 2013; Monaghan et al., 2009). The *cox*3 ultrametric tree, used to conduct the GMYC species delineation, was constructed using Bayesian analyses in BEAST v1.8.2 (Drummond et al., 2012). A GTR + I + Γ substitution model was identified as the best-fitting model for *cox*3, based on the Akaike Information Criterion (AIC) using jModelTest 2 (Darriba et al., 2012). BEAST analyses were run under a relaxed

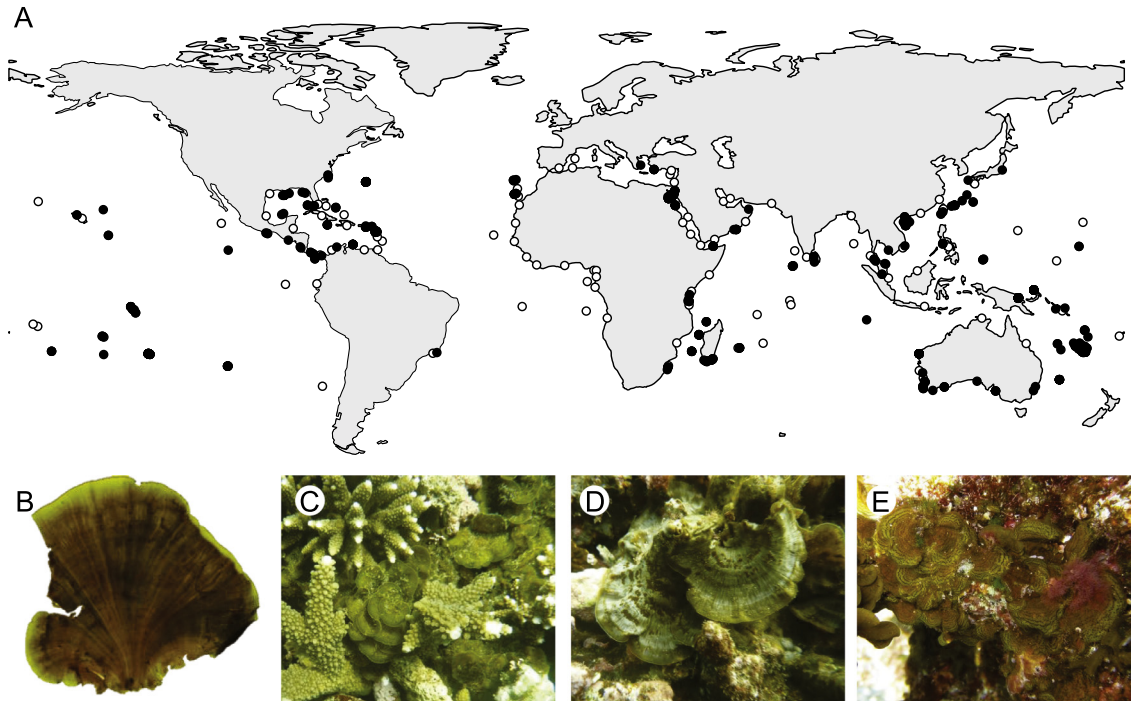

Fig. 1. (A) *Lobophora* global distribution range based on DNA confirmed samples (black circles) and literature records (white circles). Pictures of (B) *L. undulata* thallus, (C) *L. rosacea* growing at the basis of branching *Acropora* corals in New Caledonia, (D) *L. obscura* growing on dead corals in New Caledonia, and (E) *L. canariensis* growing on bedrock in the Canary Islands.

molecular clock in combination with a Yule tree prior. Other priors were set to default. In order to check for convergence of the MCMC chains, we performed two independent runs for 10^7 generations each, starting from random trees and sampling every 10^4 generations. MCMC output files of the independent runs were inspected in Tracer v1.6 (Rambaut et al., 2014) for acceptable effective sample sizes (ESS > 200). A burn-in of 25% was applied once log-likelihood values had stabilized. Maximum clade credibility trees and posterior probability for the nodes were calculated using the postburnin trees using TreeAnnotator 1.8.2 (included in the BEAST package).

2.4. Geographical scales

Different hierarchical geographical scales were considered to assess the patterns of diversity and historical biogeography analyses: (1) two basins: Atlantic and Indo-Pacific; (2) three regions: Indo-Pacific, East Pacific and Atlantic; (3) five sub-regions: Indo-Australian Archipelago (IAA; 'A' in Figs. 5 and 6), West Indo-Pacific ('B' in Figs. 5 and 6), Central Pacific ('C' in Figs. 5 and 6), East Pacific ('D' in Figs.5 and 6) and Atlantic ('E' in Figs. 5 and 6); and (4) 9 realms based on the Marine Ecoregions of the World from Spalding et al. (2007): Temperate Northern Pacific, Central Indo-Pacific, Western Indo-Pacific, Eastern Indo-Pacific, Tropical Eastern Pacific, Tropical Atlantic, Temperate Northern Atlantic, Temperate Southern Africa and Temperate Australasia; and also two climate zones: tropical and temperate.

2.5. Species richness estimation and patterns of diversity

Global species diversity was estimated using non-parametric richness estimators and extrapolation of the rarefaction curve (Shen et al., 2003). We used sample-based rarefaction, rescaled to number of individuals, to interpolate species richness per individual sampled, based on the analytical formulas of Colwell et al. (2004). Additionally, we computed three species richness estimators: the incidence-based coverage estimator (ICE; Chao and Lee, 1992), the Chao 2 richness estimators (Chao 2; Chao, 1987), and the first-order Jackknife richness estimator (Jack 1; Burnham and Overton, 1979). ICE distinguishes between frequent and infrequent species in analysis. Jack 1 does not differentiate the species frequency and relies on the number of species only found once. Chao 2 relies on the number of unique units and duplicates. Extrapolation of the rarefaction curve and species richness estimators were computed with the software EstimateS (Version 9; Colwell, 2013). We compared the observed and Chao 2 estimated species diversity between the marine sub-regions in order to compare the level of diversity in each of these regions. We compared the observed and Chao 2 estimated species diversity between four spatial scales i.e. local, sub-regional, regional and global. We took the most well-sampled locality (New Caledonia), realm (Central Indo-Pacific) and region (Indo-Pacific), in order to get the best idea of what it takes in terms of sampling to properly assess species diversity at a given spatial scale. Finally, to evaluate species range overlap between marine realms, we calculated the similarity matrix between the nine marine realms with respect to their species overlap, applying the Sørensen index (Magurran, 2013).

2.6. Reconstruction of species phylogeny

Based on the results of the species delimitation analyses, a concatenated alignment of the *cox*3 (610 bp) + *psb*A (919 bp) + *rbc*L (1360 bp) dataset was made containing a single representative per species. The matrix was 80% filled at the species × gene level. Species used as outgroup taxa used for the time-calibrated phylogeny are given in Table S1. Maximum Likelihood (ML) and Bayesian Inference (BI) species trees were generated from the concatenated alignment, partitioned by gene and codon position. ML analyses were conducted using RAxML under a GTR + CAT model (Stamatakis, 2006). The robustness of the resulting phylogenies was tested using 1000 replicates of a rapid bootstrap heuristic (Stamatakis, 2006); and for the BI, using MrBayes v3.2.2 (Ronquist

and Huelsenbeck, 2003), initiated with a random starting tree and with four chains of MCMC iterations ran simultaneously for 100 million generations. The first 100,000 (25%) trees sampled were discarded as burn-in, based on the stationarity of ln*L* for all parameters as assessed using Tracer version 1.6 (Rambaut et al., 2014). A consensus topology and posterior probabilities of the nodes were calculated from the remaining trees.

2.7. Time-calibrated species phylogeny

The occurrence of Phaeophyceae as fossils is rare due to their generally soft-bodied nature (Arnold, 1947), and scientists continue to debate the identification of some fossils (Coyer et al., 2001). *Padina* and *Newhousia* are the only two genera of the class Phaeophyceae which deposit calcium carbonate. While no fossils of *Newhousia* are documented to date, the Early Cretaceous (−145.5 to −99.6 Ma) clay shales from the Gangapur formation (Andhra Pradesh state, India) yielded a macroalgal fossil reminiscent of extant species of the genus *Padina* (Rajanikanth, 1989). Babcock et al. (2012) reported a new species of *Padina* from the Drumian Stage (Cambrian) in Hunan, China. From our own observations of the available pictures, their identification of a *Padina* is doubtful, and we decided not to consider this fossil since it is challenging the current view of the time-scale of brown algal evolution (Brown and Sorhannus, 2010). Our *Lobophora* phylogeny was therefore calibrated with (1) a fossil of *Padina*, (2) the Dictyotales node as estimated in Silberfeld et al. (2010), and (3) the Phaeophyceae node as estimated in Brown and Sorhannus (2010). The age of *Padina* was constrained at −95 Ma and tailing off according to a gamma distribution with shape = 3.0 and scale = 5.5 (Silberfeld et al., 2014). The split between the Dictyotales and the outgroup *Syringoderma*, i.e. the crown group Dictyotales-*Syringoderma*, was constrained between −130 and −195 Ma using a uniform prior (Silberfeld et al., 2014). The age of the split between Phaeophyceae and Schizocladiophyceae lineages, i.e. the crown group Phaeophyceae-Schizocladiophyceae, was constrained in the Lower Jurassic between −125 and −253 Ma using a uniform prior (Brown and Sorhannus, 2010). The time-calibrated *Lobophora* phylogeny (i.e. chronogram) was inferred using Bayesian analyses in BEAST 1.8.2 (Drummond et al., 2012), for the concatenated (*cox*3 + *rbc*L + *psb*A) alignment partitioned by gene and codon position, using a lognormal relaxed molecular clock method, with autocorrelated rates in combination with a Yule model tree prior, and the GTR + I + Γ substitution model for the three unlinked markers. The GTR + I + Γ substitution model was identified as the best-fitting model for each gene, based on the Akaike Information Criterion (AIC) using jModelTest 2 (Darriba et al., 2012). Other priors were set to default. In order to check for convergence of the MCMC chains, we performed two independent runs for 10^7 generations each, starting from random trees and sampling every 10^4 generations. MCMC output files of the independent runs were inspected in Tracer v1.6 (Miller et al., 2010) for acceptable effective sample sizes (ESS > 200). A burn-in was applied once log-likelihood values for all parameters had stabilized. Maximum clade credibility trees and posterior probabilities for the nodes were calculated using the postburnin trees using TreeAnnotator 1.8.2 (included in the BEAST package). All phylogenetic analyses were conducted on the Cipres web portal (Miller et al., 2010).

2.8. Historical biogeography

To infer the evolution of geographical ranges, we used the R package BioGeoBEARS (Matzke, 2013). This package implements the most common biogeographical history reconstruction methods in a likelihood framework: dispersal-extinction-cladogenesis model (DEC; Ree et al., 2005; Ree and Smith, 2008), dispersal-vicariance analysis (DIVA; Ronquist, 1997) and the BayArea model (Landis et al., 2013). Moreover, it also incorporates a model of founder-event speciation ('+J') and allows the fit of models to be compared using a model choice procedure (Matzke, 2013).

3. Results

3.1. Lobophora global species diversity

The GMYC analysis based on the mitochondrial *cox*3 marker, significantly rejected the null model (single coalescence model for the entire tree), resulting in delimitation of 109 evolutionary significant units (ESUs) (Fig. 2), with a confidence interval of 98–121. ABGD and PTP resulted in the delineation of 100 and 141 ESUs, respectiveley. ABGD lineages were subdivided 5 and 26 times by GMYC and PTP, respectively. Subdivisions of GMYC and ABGD lineages in the PTP delineation, generally reflected the biogeography of the lineages, i.e. sibling lineages in PTP are geographically distinct. For example *L.* sp.35 split into two lineages in the PTP analysis, which correspond to two regions, namely South Africa and Juan de Nova. For this study, we considered the GMYC delineation results since the geographic distances between these additional species delineated by PTP generally did not extend further than within a marine region.

Extrapolation of the rarefaction curve indicates a mean value of ~190 *Lobophora* species, with a confidence interval of 140–235 species (Fig. S1). The species diversity value reaches a plateau at ca. 3000 samples. Species richness estimators projected a diversity of 179 (Jack 1) to 209 (ICE) species (Table 1). Taking the mean and the confidence interval of the GMYC results into consideration, and estimators and extrapolation values, we estimate having discovered 42–86% of the *Lobophora* extant species diversity (Table 1).

3.2. Regional diversity

Substantial differences in species diversity were observed between some marine sub-regions. The Indo-Pacific stands out with the highest diversity with 95 species and an estimate of 150 species based on the Chao2 species richness estimator (Fig. 3A, S2A). The level of diversity drops to 18 species in the Atlantic with an estimate of 20 species based on Chao2 (Fig. 3A, S2A). The least speciose regions are Temperate Australasia and the Tropical Eastern Pacific with six and four species, respectively, and with similar Chao 2 based-estimates (Fig. 3A, S2A). We also examined species diversity along a multiscale gradient from a local (i.e. New Caledonia) to a global scale (Fig. 3B, S2B). Fig. 3 displays the cumulative number of species observed as a function of sampling effort in different marine regions (Fig. 3A, S2A) and at different scales (Fig. 3B, S2B). The shape of the curves is not the same for all regions, with three out of four approximately reaching an asymptote shape, implying that the Indo-Pacific region reserves a greater diversity yet to be explored, while the diversity of the other regions was mostly revealed by our sampling.

3.3. Inter-regional species overlap

Twenty-five percent of all *Lobophora* species span more than one sub-region (Fig. 6). With 16 species shared with neighbouring sub-regions (nine with the Western Indo-Pacific and seven with the Eastern Indo-Pacific) the Indo-Australian Archipelago is the sub-region that shares the most species with its adjacent sub-regions (Fig. 6). The tropical Eastern Pacific, which shares no species with the Eastern Indo-Pacific and only one species with the Atlantic (Fig. 6), is the most 'isolated' region followed by the Atlantic (Fig. 6). A Sørensen similarity matrix shows an overall

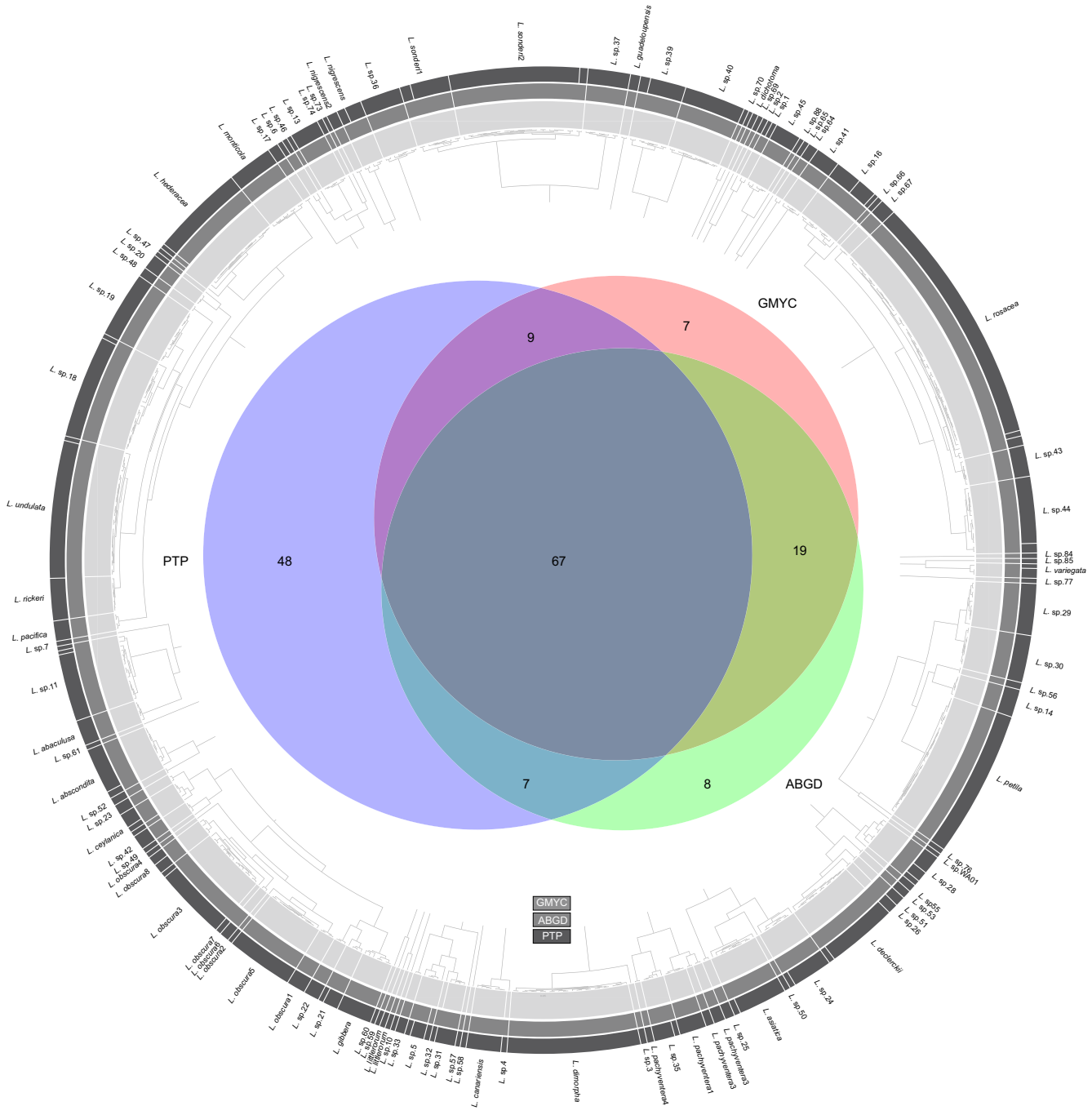

Fig. 2. Results of the three species delimitation methods based on the *cox*3 data set. Species delimitation results of GMYC (inner), ABGD (middle), and PTP (outer) are represented by three concentric circles. The tree is the maximum clade credibility tree obtained from BEAST. Only the terminal part of the tree, used for species delineation, is represented. In the center, a Venn diagram illustrating overlap (consensus) between the PTP, GMYC and ABGD species delimitation results.

low similarity (<0.20) between the nine marine realms in terms of species overlap (Table S2), meaning that a limited number of species span more than one realm. The highest level of similarity (0.92) is observed between the Tropical Atlantic and Temperate Northern Atlantic, which have four species in common. Despite the high diversity in the Indo-Pacific, provinces display low species overlap.

3.4. Geographical diversity patterns

The Central Indo-Pacific is the richest realm with at least 57 species, followed by the Western Indo-Pacific with 35 species, the Eastern Indo-Pacific with 19 species and the Tropical Atlantic with 14 species. The remaining realms contain between one to 6 species (Table 2). Only three species are occurring across both hemispheres (*L. asiatica*, *L.* sp.18 and *L.* sp44). Ninety-nine *Lobophora* species (87%) are strictly tropical, 5 species (4%) are strictly temperate and 10 species (9%) are tropico-temperate (present in warm temperate and tropical regions). Nearly all *Lobophora* species (109 species = 97%) are restricted to one ocean basin (Table 2), and 86 species (75%) are restricted to one marine realm (Table 2). Twenty-three (20%) and five (3.5%) species are spanning two and three realms, respectively. In the Indo-Pacific, only four species are distributed across the centro-western part (*L.* sp28

Table 1
Number of estimated species and resultant percentage of species discovered. The number of species is estimated with the species-richness estimators (ICE, Chao 2 and Jack 1) and with the extrapolation (mean and lower and upper 95% confidence interval). The percentage of species discovered based on the number of estimated species and the number of discovered species identified.

	Richness estimators			Extrapolation		
	ICE	Chao 2	Jack 1	Lower 95%	Mean	Upper 95%
No. of species[a]	209	185	179	140	188	235
Low DS (%)[b]	47	53	55	70	52	42
Mean DS (%)[c]	52	59	61	78	58	46
Upper DS (%)[c]	58	65	68	86	64	51

(1) Number of estimated species. Percentage of discovered species considering the mean and the lower ([(2)] 98) and upper ([(4)] 121) 95% confidence interval number of species identified with the GMYC model based on *cox*3. DS: described species.
[a] Number of estimated species.
[b] Percentage of discovered species considering the mean and the lower (98) 95% confidence interval number of species identified with the GMYC model based on *cox*3.
[c] Number of estimated species. Percentage of discovered species considering the mean and upper (121) 95% confidence interval number of species identified with the GMYC model based on *cox*3.

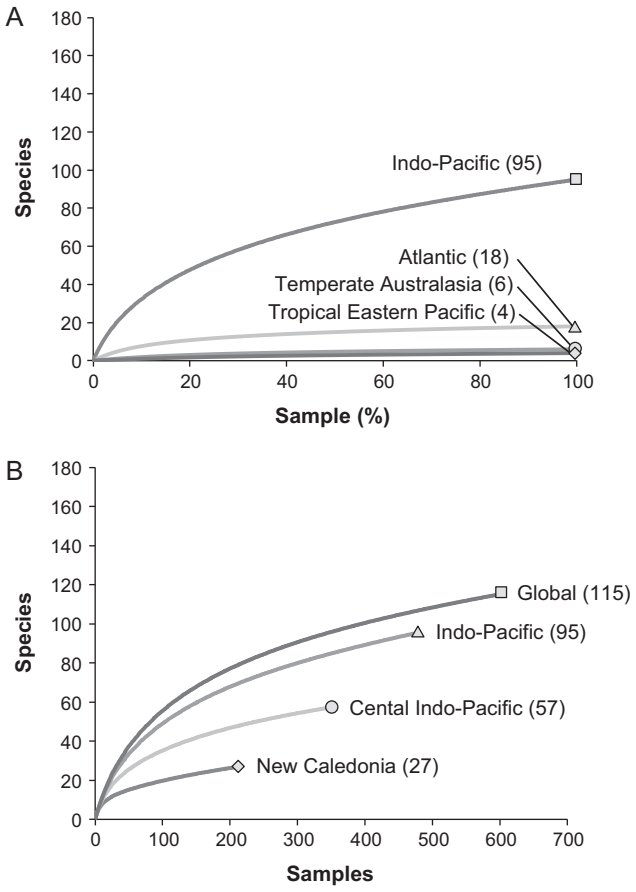

Fig. 3. Observed richness (S_{obs}) in *Lobophora* species. (A) Comparison between four marine regions: Indo-Pacific (square), Atlantic (triangle), Temperate Australasia (circle), Tropical Eastern Pacific (diamond). (B) Comparison between multiple spatial scales: local (New Caledonia, diamond), sub-regional (Central Indo-Pacific, circle), regional (Indo-Pacific, triangle), and global (square).

(8 specimens), *L. rosacea* (67 specimens), *L. gibbera* (7 specimens), *L. ceylanica* (5 specimens)) and only three in the centro-eastern part (*L. pacifica* (11 specimens), *L. undulata* (31 specimens), *L.* sp19 (20 specimens)), but in our dataset no species are found across the entire the Indo-Pacific.

3.5. Dated molecular phylogeny of Lobophora

A *Lobophora* species tree, inferred from a concatenated alignment of *rbc*L, *cox*3 and *psb*A sequences, presented with maximum-likelihood bootstrap and Bayesian posterior probability values, is given in Fig. S3. Our time-calibrated phylogeny indicates that *Lobophora* originated in the Upper Cretaceous between 65 and 90 MY (Fig. 4). From the beginning of the Cenozoic onward, *Lobophora* diversification occurred rather steadily through its evolutionary history (Fig. 4). None of the major marine vicariance events (e.g. closure of the Tethys Sea, Benguela upwelling, Panama Isthmus closure; indicated as vertical lines in Fig. 4) nor sea level variations (indicated as a blue line in Fig. 4) seem to have caused major shifts in diversification rates of *Lobophora*. On the other hand, the East Pacific barrier represents a clear dispersal barrier since the East Pacific has a lower number of *Lobophora* species, and only three that span the central and eastern Pacific.

Table 2
Lobophora species diversity per marine region.

	Species # (%)
Tropical	109 (81)
Temperate	15 (11)
Tropico-temperate	10 (7)
Pacific	102 (87)
Atlantic	15 (10)
Pacific-Atlantic	4 (3)
Indo-Australian Archipelago	60 (39)
Western Indo-Pacific	36 (23)
Central Pacific	19 (12)
Eastern Pacific	4 (3)
Atlantic	15 (10)
Central Indo-Pacific	57 (31)
Western Indo-Pacific	35 (19)
Eastern Indo-Pacific	19 (10)
Temperate Australasia	6 (3)
Temperate Northern Pacific	2 (1)
Tropical Eastern Pacific	4 (2)
Temperate Southern Africa	1 (1)
Tropical Atlantic	14 (8)
Temperate Northern Atlantic	7 (4)

3.6. Historical biogeographical inference

The Dispersal-Extinction-Cladogenesis with founder-event speciation model (DEC + J) was identified as the best model in the BioGeoBEARS analyses when considering nine marine realms or five marine sub-regions (Table 3). These results highlight the importance of founder-event speciation ($j = 0.0254 > d = 0.0019 > e = 0$). When the number of regions was reduced to three (Atlantic, Indo-Pacific and Eastern Pacific) or two (Atlantic and Indo-Pacific), DIVA + J was identified as the best model. Based on the historical biogeographical inference based on the basins level (Atlantic and Indo-Pacific), the DEC + J model informs us that the *Lobophora* ancestor (LA) originated from the Indo-Pacific which corresponded to the Upper Cretaceous Tethys Sea (Figs. 4 and 5).

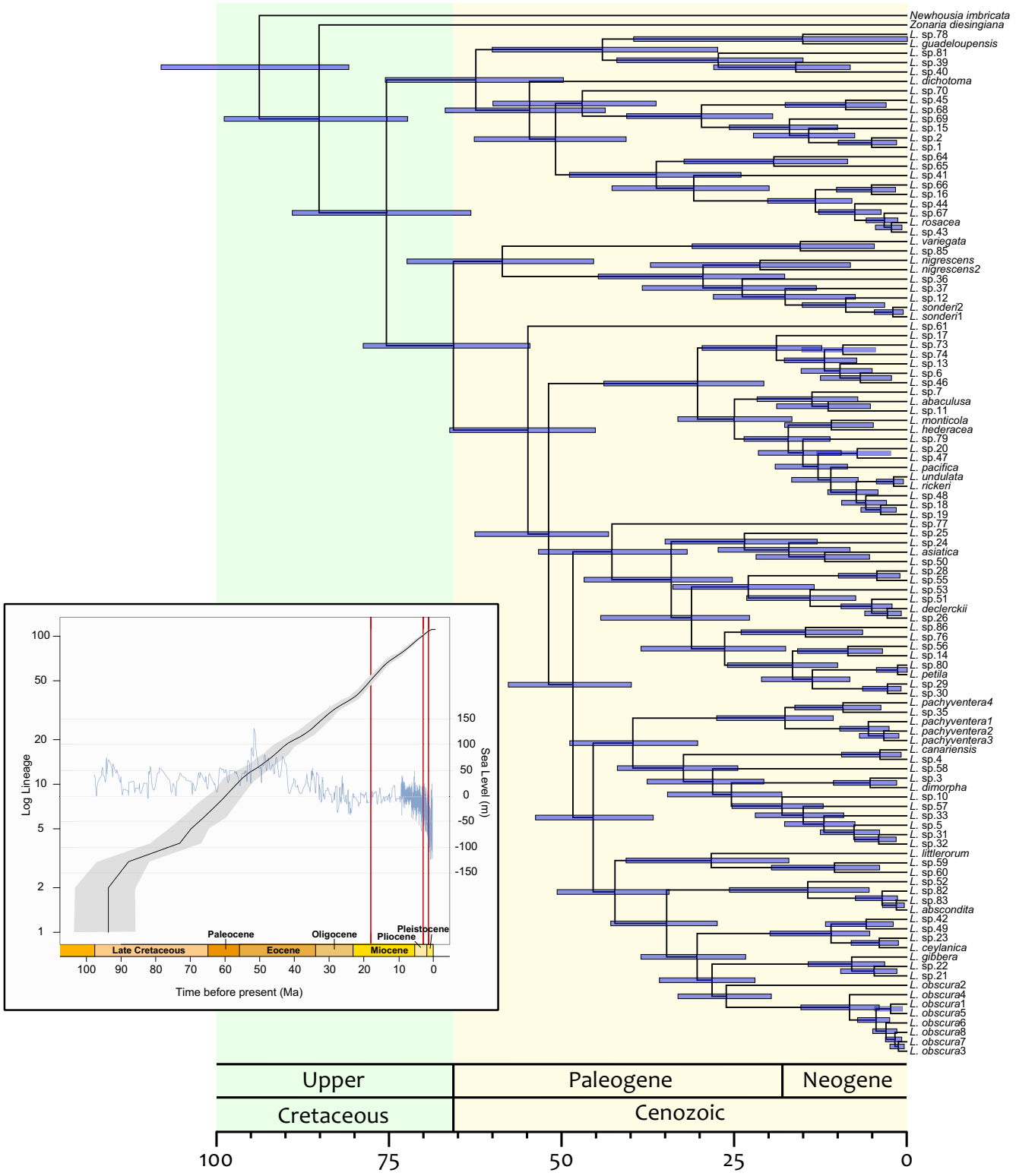

Fig. 4. Chronogram resulting from the Bayesian relaxed clock analysis with BEAST 1.8.2. The purple bars display the 95% HDP (highest probability density). Lineage-through-time (LTT) plot of *Lobophora* based on the chronogram presented in Fig. 4, with the 95% confidence intervals. The red vertical lines display the emergence of major marine barriers: Terminal Tethyan event (ca. −18 Ma), the Isthmus of Panama (ca. 3 Ma), Benguela upwelling formation (ca. 1–2 Ma). The blue line displays sea-level variation based on Miller et al. (2005). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.7. Relative contribution of sympatry, vicariance and founder events

"Biogeographical Stochastic Mapping" (BSM), implemented in BioGeoBEARS, allows to quantify speciation events. 'Sympatric' speciation, i.e. speciation within a predefined region, comes as the most important speciation mode (90%) at the basin level, with the remaining 10% being founder events, e.g. dispersal from one basin on to another. At a finer scale, i.e. marine realms level, speci-

Table 3
Comparison of the fit of the dispersal-extinction-cladogenesis (DEC), dispersal-vicariance analysis (DIVA) and BayArea biogeographical reconstruction models, all with the possibility of founder-event speciation ('+J'). The log-likelihood (ln*L*) of each model is given for the analyses. For each geographical subdivision, the best model is indicated in bold.

	9 realms[a]	5 regions[b]	3 regions[c]	2 basins[d]	Temp-Trop
DEC	−316.5	−248.0	−69.8	−50.2	**−46.3**
DEC + J	**−298.1**	**−219.9**	−63.3	−46.4	−46.3
DIVA Like	−324.8	−248.3	−64.4	−46.7	−51.1
DIVA Like + J	−309.1	−226.8	**−62.6**	**−45.9**	−51.1
BayArea Like	−339.9	−280.6	−97.9	−72.8	−53.5
BayArea Like + J	−313.8	−231.3	−66.6	−50.1	−53.3

[a] 9 realms: Central Indo-Pacific, Western Indo-Pacific, Eastern Indo-Pacific, Temperate Australasia, Temperate Northern Pacific, Tropical Eastern Pacific, Temperate Southern Africa, Tropical Atlantic, Temperate Northern Atlantic.
[b] 5 regions: Indo-Australian Archipelago, Western Indo-Pacific, Central Pacific, Eastern Pacific, Atlantic.
[c] 3 regions: Atlantic, Pacific, Indian Ocean.
[d] 2 basins: Atlantic, Indo-Pacific.

ation within marine regions remains the most important mode of speciation (71%), followed by founder events (19%) and vicariance (9%). The relative contribution of each of these modes of speciation varies between the different realms (Figs. 6 and S5). For instance, while most of *Lobophora* diversity within the Central Indo-Pacific and the Western Indo-Pacific result from 'sympatric' speciation, *Lobophora* diversity within the Temperate Northern Pacific and Temperate Southern Africa exclusively results from founder events (Figs. 6 and S5).

4. Discussion

4.1. Species diversity

We assessed species diversity of the marine brown algal genus *Lobophora* on a global scale. The level of *Lobophora* diversity unveiled from local studies in the Pacific Ocean (Sun et al., 2012; Vieira et al., 2014) already predicted a richer global biodiversity for this genus than previously recognized. Our DNA sequence data indicate an increase of the species diversity of the genus *Lobophora* by five to six folds, from 20 to 30 species to more than 100 species, which makes *Lobophora* a hyperdiverse genus of marine macroalgae. Our results once again show how morphology-based taxonomy fails to accurately estimate species diversity in some algal groups (De Clerck et al., 2013; Leliaert et al., 2014; Packer et al., 2009).

4.2. Geographic distributions

While sister species may be geographically widely separated (Fig. S4), the distribution of single species are mostly restricted to one ocean basin and usually do not expand beyond marine realms as defined by Spalding et al. (2007), but there are exceptions, namely *L.* sp37, *L.* sp44 and *L.* sp77, which are spanning beyond the Atlantic. Not a single *Lobophora* species was found to be pantropical, i.e. cosmopolitan. Several other algal taxa with allegedly broad distribution have been shown to correspond to complexes of species with restricted distributions. A study conducted on the genus *Padina* (Silberfeld et al., 2014) (a member of the same family as *Lobophora*, Dictyotaceae) resolved that globally distributed morphospecies segregated into evolutionary lineages with more restricted ranges. Working on two supposedly circumtropical *Dictyota* species (also Dictyotaceae), *D. ciliolata* and *D. crenulata*, Tronholm et al. (2012) concluded that the former consisted of several pseudocryptic species with restricted distributions in the Atlantic Ocean and Pacific Central America, while the pantropic distribution of the latter was confirmed. Other examples can be given, such as *Colpomenia sinuosa* which consist of several species with more or less wide distribution (Lee et al., 2013). Although red algae may have a different evolutionary history, at a finer geographical scale, Zuccarello and West (2003) study on the *Bostrychia radicans*/*B. moritziana* complex resulted in the identification of distinct evolutionary lineages with defined areas along the eastern North American coast.

4.3. Patterns of diversity

The majority of the *Lobophora* species are restricted to tropical regions, and have small ranges limited to marine realms. *Lobophora* species diversity is highest in the Indo-Australian Archipelago (IAA). In contrast to the general patterns of most macroalgal genera (e.g. Santelices and Marquet, 1998), the center of diversity for the genus *Lobophora* is located in the tropics. Similar patterns are observed among several other macroalgal groups such as siphonous green algae (Kerswell, 2006), but also genera belonging to the same order as *Lobophora*, i.e. *Dictyota* (Guiry and Guiry, 2015) and *Padina* (Silberfeld et al., 2014). In the Atlantic Ocean, the center of diversity is located in the central Caribbean. However, diversity in the Atlantic (14 species) is much lower compared to the Indo-Pacific (102 species). Several possible explanations have been discussed in the literature, e.g. greater diversity and extent of shallow water habitats in the central Indo-Pacific compared to the Atlantic (both historically and today); bigger size of the tropical Indo-Pacific, and higher number of islands, relative to the Atlantic, providing more opportunities for isolation and speciation; greater age of the Indo-Pacific; increased diversification in Oligo-Miocene related to tectonic activity in central IWP (e.g. collision of Australia-New Guinea plate with SE Eurasia) increasing shallow water habitats (Williams and Duda, 2008); increased speciation by isolation and reconnection of Indo-Pacific populations as sea levels drop and rise (e.g. during Pleistocene glaciation events); ecological speciation (e.g. Bowen et al., 2013, see discussion below). Then, there is the classical discussion whether the high diversity in the central Indo-Pacific is the result of high speciation rates within the region (center of origin), speciation in peripheral regions and dispersal and survival in the central IP (center of accumulation), or the result of overlapping ranges (center of overlap) (Barber and Meyer, 2015).

4.4. Tethyan diaspora: origin and early diversification

The time-calibrated phylogeny and historical biogeographical analysis suggest that *Lobophora* originated in the Upper Cretaceous in the remains of the Tethys Sea. Origination in the Tethys Sea is inferred, yet with a high level of uncertainty, as possible/putative ancestral area a region common to the current Atlantic and Indo-Pacific Oceans. On the other hand the ancestral range of the large clade encompassing *L.* sp61 as outgroup, that originated −55 My, is inferred to be the Central Indo-Pacific with high certainty. From the Tethys Sea, *Lobophora* species experienced multiple, more

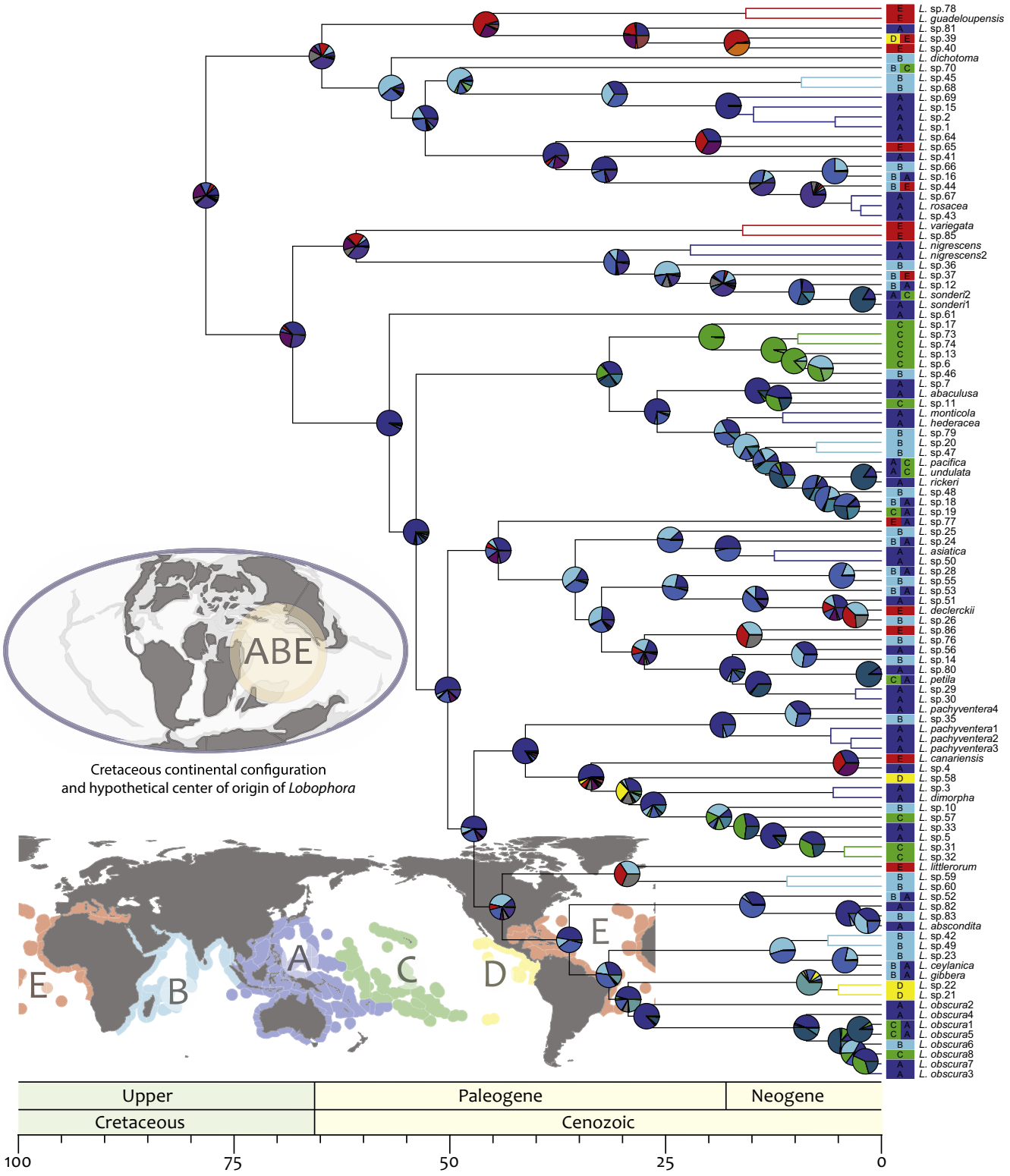

Fig. 5. Ancestral ranges of *Lobophora* species, estimated under a DEC + J model with BioGeoBears based on the BEAST tree (Fig. 4). Boxes at the tips indicate extant *Lobophora* species geographic area(s). Colored branches indicate regions of maximal probability. Ancestral area reconstructions are shown by pie diagrams at each node. World map (inset lower left) shows the 5 marine realms: Central Indo-Pacific (A), Western Indo-Pacific (B), Eastern Indo-Pacific (C), Tropical Eastern Pacific (D), Atlantic (E). World map (inset middle left) depicts Late Cretaceous continental configuration with the hypothetical center of origin of *Lobophora* (ABE). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

recent, dispersal events to the Atlantic, with little diversification within the region. Diversification has been considerably higher in the Indo-West Pacific compared to the Atlantic and Eastern Pacific (see discussion above). Nevertheless, dispersal events in the Atlantic Ocean may have occurred more recently than during the Upper Cretaceous (e.g. Oligocene and Miocene) which could explain why

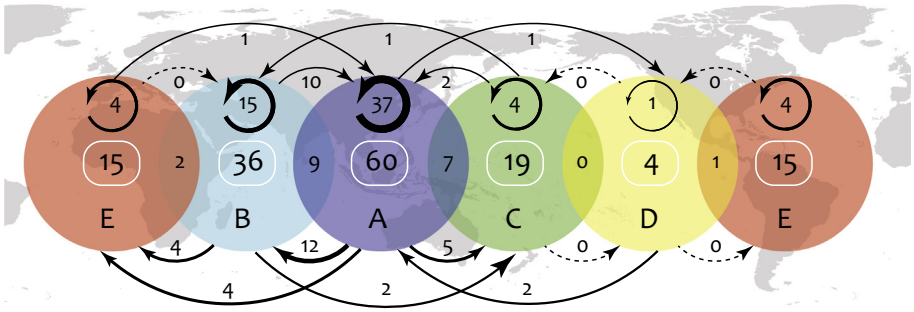

Fig. 6. Sympatry and founder events across the five marine realms. The five marine realms are represented by anotated colored circles: Central Indo-Pacific (A), Western Indo-Pacific (B), Eastern Indo-Pacific (C), Tropical Eastern Pacific (D), Atlantic (E). Numbers within squircles indicate the total number of species per realm. Numbers adjacent to the curved arrows indicate the number of founder events from one realm to another. Numbers within circle arrows indicate the number of sympatric events within a realm. Numbers at the intersection between circles represent the number of species shared between these two realms. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the number of species is lower in the Atlantic. In fact, while Atlantic species branched off early in the tree, dispersal events could have taken place anywhere along these branches (e.g. the actual dispersal event could have taken place close to the nodes of Atlantic clades). Generally, founder speciation occurred several times throughout *Lobophora* evolutionary history thus playing an important role in its diversification. High diversity within the Central Indo-Pacific region may have resulted from a combination of within region speciation and of regular colonization from adjacent regions (West Indo-Pacific and Eastern Indo-Pacific; Fig. 6). Furthermore, 70% of the species distributed within at least two different marine realms are present in the Central Indo-Pacific. These observations suggest that this region acted not only as a region of origination/diversification but also a center of overlap (Barber, 2009; Connolly et al., 2003; Halas and Winterbottom, 2009). Colonization of the Caribbean occurred several times and from different origins, and resulted in very low regional diversification (e.g. Atlantic clades of maximum two species). The presence of only two species (*L.* sp44 and *L.* sp37) distributed in the Western Indo-Pacific and in the Eastern Atlantic also suggests that while the Benguela upwelling may represent an efficient dispersal barrier, dispersal across it occurred at least twice. Finally, colonization of temperate regions occurred at different periods of *Lobophora* evolution history. The earliest dispersal to temperate region occurred during the Paleocene (−60 Ma) in the southern hemisphere. Northern hemisphere temperate regions were colonized more recently. The current global *Lobophora* taxonomic makeup shows that hard barrier formations (East Pacific Barrier, Terminal Tethyan event, Isthmus of the Panama) did not act as important vicariance events for this genus (Fig. 4). On the other hand, they constituted efficient barriers for *Lobophora* dispersal. However, while no sibling species were yet found across the Panama isthmus, it is not excluded that a more significant sampling effort on the Pacific side of the isthmus could disclose sibling species.

4.5. Geographical speciation processes

It is important to note that the term 'sympatric' speciation expresses here speciation within the scale considered (e.g. basin, region, realm). Within a given region, however, speciation may actually result from allopatric speciation (e.g. vicariance or founder event). Identifying actual sympatric speciation events requires working at the finest possible scale e.g. several hundred meters to several hundred kilometers.

We analyzed diversification at different scales from ocean basins to the marine realms. Virtually all speciation events occurred within ocean basins, and two-third of the speciation events occurred within marine realms. On the other hand, long-distance dispersal to adjacent realms, followed by founder speciation represents a non-negligible process in *Lobophora* diversification. It is difficult, however, to make sound conclusions regarding geographical versus ecological speciation modes based on our data. Within realms, the finest scales considered in this study, sympatric and/or allopatric speciation could have occurred. Finer phylogeographic studies, down to scales of several kilometers, in combination with ecological data, will be needed to assess the relative role of allopatric versus sympatric speciation in *Lobophora* (e.g. Billard et al., 2010; Payo et al., 2013; Pielou, 1978). The wide ecological variation in *Lobophora* hints toward an important role of ecological speciation. In addition, ecological partitioning has been shown to allow coexistence of sympatric *Lobophora* sister species (Vieira et al., 2014) often found only several meters apart.

4.6. Cladogenic drivers

Lobophora species distribution and richness are reminiscent of those of corals and coral reef fishes (Cowman and Bellwood, 2011). Several studies have already pointed to the central role of coral reef association in underpinning diversification within major marine groups (Alfaro et al., 2007; Bellwood et al., 2010; Cowman and Bellwood, 2011; Hughes et al., 2002; Renema et al., 2008). Considering the major role herbivory played in macroalgal ecology (Hay, 1997; Lubchenco and Gaines, 1981), diversification of reef algae and herbivores are very likely correlated through a co-evolutionary arms race. The development of a complex mosaic of reef habitats also probably favored reef algal speciation by providing opportunities for new habitat colonization and ecological diversification (Alfaro et al., 2007; Cowman and Bellwood, 2011). Thus, the biotic interactions between *Lobophora*, herbivores and corals may have favored diversification in coral reefs. This idea that coral reefs acted as cladogenesis drivers has already been proposed for other reef organisms, such as coral reef fishes, where coral reefs provided the mechanisms allowing both higher rates of speciation and reduced vulnerability to extinction for associated lineages (Cowman and Bellwood, 2011).

Lobophora has been considered as a potent competitor with corals. An example is its proliferation following disturbances that impacted herbivores and corals in the Caribbean in the mid-80s (De Ruyter van Steveninck and Breeman, 1987; Hughes, 1994). Timing of origination and patterns of distribution and diversity clearly show that *Lobophora* is a fully-fledged member of coral reefs and has evolved in these ecosystems since the rise of modern coral reefs (during the Cretaceous). Consequently, *Lobophora* should not be seen as a threat to corals, but instead as an indicator of coral reef health status. In fact, while following disturbances, *Lobophora* has shown the capacity to bloom in certain reefs across

the globe (De Ruyter van Steveninck and Breeman, 1987; Diaz-Pulido et al., 2009; Lesser and Slattery, 2011), and corals demonstrated resilience once conditions came back to normal (Diaz-Pulido et al., 2009). In healthy reefs, *Lobophora* has been reported only once as representing an apparent threat to corals (Vieira et al., 2015), a case of epizoism syndrome, but even then, only one species was threatened.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2017.03.007.

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