

# Deep-sea squat lobster biogeography (Munidopsidae: *Leiogalathea*) unveils Tethyan vicariance and evolutionary patterns shared by shallow-water relatives

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## Abstract

The ecology, abundance and diversity of galatheoid squat lobsters make them an ideal group to study deep-sea diversification processes. Here, we reconstructed the evolutionary and biogeographic history of *Leiogalathea*, a genus of circum-tropical deep-sea squat lobsters, in order to compare patterns and processes that have affected shallow-water and deep-sea squat lobster species. We first built a multilocus phylogeny and a calibrated species tree with a relaxed clock using StarBEAST2 to reconstruct evolutionary relationships and divergence times among *Leiogalathea* species. We used BioGeoBEARS and a DEC model, implemented in RevBayes, to reconstruct ancestral distribution ranges and the biogeographic history of the genus. Our results showed that *Leiogalathea* is monophyletic and comprises four main lineages; morphological homogeneity is common within and between clades, except in one; the reconstructed ancestral range of the genus is in the Atlantic and Indian oceans (Tethys). They also revealed the divergence of the Atlantic species around 25 million years ago (Ma), intense cladogenesis 15–25 Ma and low levels of speciation over the last 5 million years (Myr). The four *Leiogalathea* lineages showed similar patterns of speciation: allopatric speciation followed by range expansion and subsequent stasis. *Leiogalathea* started diversifying during the Oligocene, likely in the Tethyan. The Atlantic lineage then split from its Indo-Pacific sister group due to vicariance driven by closure of the Tethys Seaway. The Atlantic lineage is less speciose compared with the Indo-Pacific lineages, with the Tropical Southwestern Pacific being the current centre of diversity. *Leiogalathea* diversification coincided with cladogenetic peaks in shallow-water genera, indicating that historical biogeographic events similarly shaped the diversification and distribution of both deep-sea and shallow-water squat lobsters.

## KEYWORDS

allopatric speciation, comparative diversification, deep-sea speciation, Galatheoidea, historical patterns, morphological stasis

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## 1 | INTRODUCTION

Contemporary species distributions result from evolutionary forces driving the diversification of organisms, along with their own intrinsic evolutionary dynamics, and the paleogeographic and environmental history of the occupied areas. Nowadays, we can use broad-scale, time-framed phylogenies to study the historical processes that shaped patterns of current biodiversity. Despite this, knowledge of the evolutionary pathways and historical biogeography of marine invertebrates, particularly those in the deep-sea benthos (below ~200 m of depth), is still sparse (McClain & Hardy, 2010).

The deep sea is characterized by high species diversity and a complex seascape comprised of patchy habitats such as canyons, seamounts, trenches and chemosynthetic systems (Levin et al., 2001; McClain & Hardy, 2010). However, vast portions of the ocean floor remain unexplored, making it extremely difficult to characterize true levels of diversity and to determine the geographic ranges of deep-sea taxa (Rex, Stuart, & Coyne, 2000). Also, collecting this fauna is challenging and costly and sometimes results in taxonomically and geographically biased samples (Eilertsen & Malaquias, 2015; Raupach, Mayer, Maljutina, & Wägele, 2009). This bias has led to taxonomic problems, apart from those related to cryptic speciation and/or phenotypic plasticity that have been revealed by molecular phylogenies (Vrijenhoek, 2009). Phylogenies of deep-sea taxa have been mostly used to resolve evolutionary relationships, analyse global patterns of deep-sea diversity or determine colonization time frames (e.g. Lins, Ho, Wilson, & Lo, 2012; Osborn, 2009; Raupach et al., 2009; Sha & Wang, 2018), but biogeographic reconstructions of widely distributed deep-sea genera are scarce (e.g. Cabezas, Sanmartín, Paulay, Macpherson, & Machordom, 2012; Herrera, Watanabe, & Shank, 2015; Roterman, Copley, Linse, Tyler, & Rogers, 2013; Roterman et al., 2018). Therefore, studying the evolutionary history of deep-sea taxa at the genus level remains a difficult task.

The factors influencing diversification in shallow-waters, such as temperature or sea-level fluctuations, may be less important in deep-sea diversification processes (Eilertsen & Malaquias, 2015). Rather, speciation of deep-sea taxa is more likely to be driven by conditions more strongly linked to the geomorphology, bathymetry, oxygen levels or food supply, and the physiological adaptations and dispersal capacities of organisms living in such environments (Williams et al., 2013). Nevertheless, some related deep-sea (bathyal depths, 1,000–4,000 m) and shallow-water organisms such as corals (Cairns, 2007) or squat lobsters (Macpherson et al., 2010; Schnabel et al., 2011) have the same geographic centres of diversity. Historical events (e.g. convergence of tectonic plates, barrier formation,

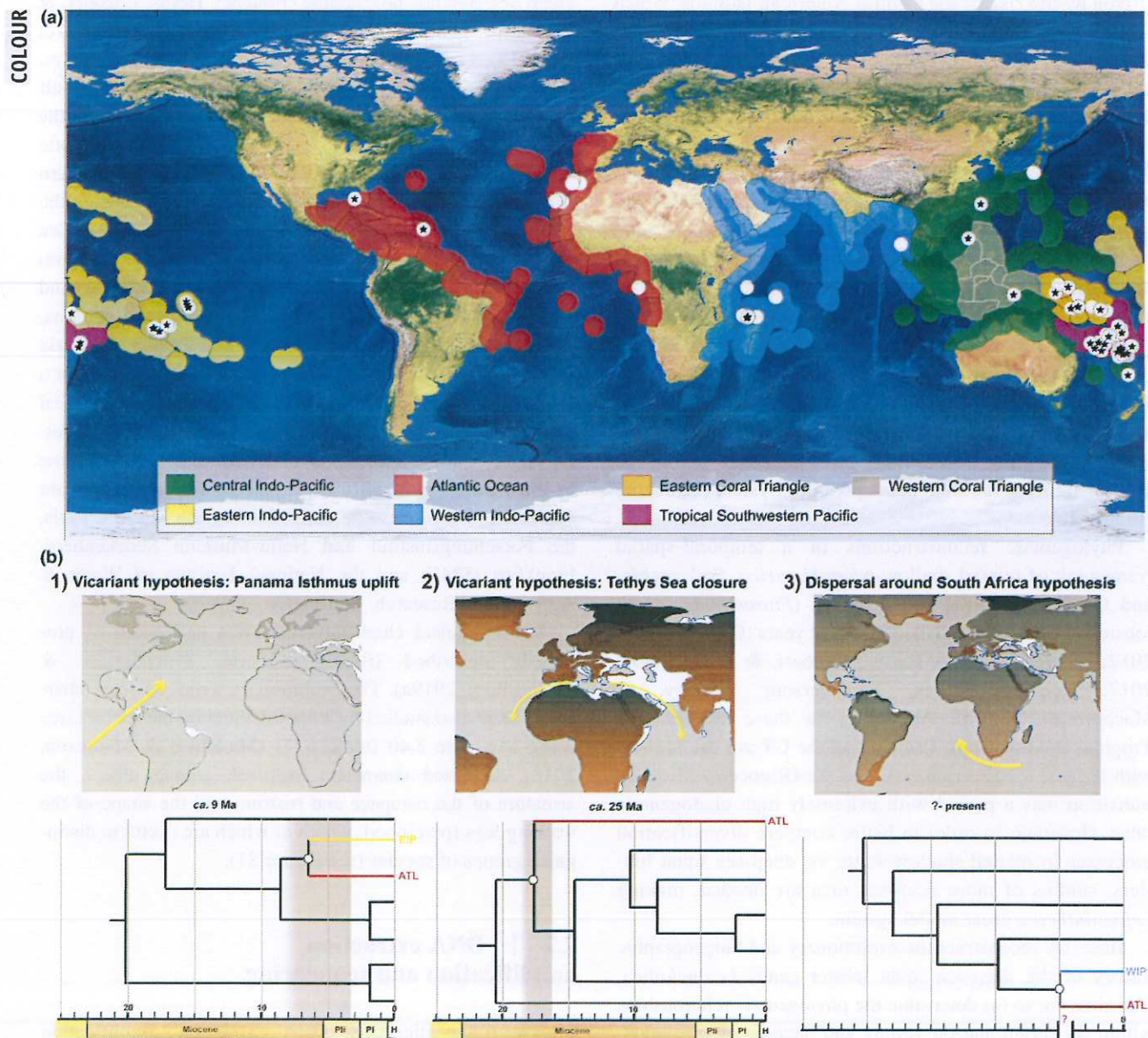
climate and ocean current changes) may similarly affect diversification processes of both coastal and deep-sea organisms (Cabezas et al., 2012; Williams et al., 2013). However, only a few comparative studies have been conducted showing how historical events might have affected deep-sea and shallow-water diversification in closely related taxa (e.g. Eilertsen & Malaquias, 2015; O'Hara, Hugall, Woolley, Bribiesca-Contreras, & Bax, 2019).

Since the Eocene [~50 million years ago (Ma) to present], circum-tropical marine realms have been dramatically affected by geological history and paleoclimatic events. The Central Indo-Pacific (CIP) region, which includes the Coral Triangle (CT), currently constitutes the major marine biodiversity centre in the world, with a latitudinal and longitudinal species gradient (Briggs, 1999; Hoeksema, 2007; Veron et al., 2009). Historically, however, during the first half of the Cenozoic, the global centre of marine biodiversity was located in the western Tethys Sea (Vermeij, 2001) and the CIP harboured much less species diversity (Briggs, 1999). The Tethyan tropical peak of diversity was displaced eastwardly over time to its current location in the CT (Renema et al., 2008). The closure of the Tethyan Seaway during the so-called Terminal Tethyan Event (TTE) during the Early to Middle Miocene (14–18 Ma) drove isolation, allopatric fragmentation and diversification of local faunas (Hou & Li, 2018; Liu, Li, Ugolini, Momtazi, & Hou, 2018; Malaquias & Reid, 2009). More recently, the complete uplifting of the Isthmus of Panama (IOP) during the Pliocene has interrupted connectivity between the Atlantic and the Indo-Pacific oceans through the Central American Seaway (~3 Ma) (O'Dea et al., 2016). Tropical organism exchange between Atlantic and Pacific oceans through the western Indian Ocean was already in decline after the TTE and IOP; however, this break was further intensified by the Pliocene establishment of a cold-water barrier (Benguela upwelling system) in the southernmost part of Africa that is rarely crossed by tropical taxa (Macpherson, 1991; Rocha et al., 2005). These historical processes have been invoked to explain the biogeography and the current distribution patterns of shallow-water organisms (Briggs & Bowen, 2012, 2013; Cowman & Bellwood, 2013a), and they are often used in biogeographic hypotheses for deep-sea taxa. However, direct comparisons of related deep-sea and shallow-water taxa are needed to identify the historical biogeographic processes affecting deep-sea versus shallow-water organisms.

Squat lobsters (Crustacea, Decapoda, Galatheaidea) represent an ideal group to approach this topic. They are extremely diverse in terms of species richness and ecological adaptations and occupy a vast plethora of marine environments, from coasts to depths of more than 5,000 m. Taxonomic interest in squat lobsters over the last two to three decades (e.g. Baba et al., 2008) has led to a dramatic

1 increase in the number of recognized species (Macpherson  
2 & Robainas-Barcia, 2015; Rodríguez-Flores, Macpherson,  
3 & Machordom, 2019a). However, we are far from knowing  
4 the true level of diversity of many genera in this group, in-  
5 cluding *Leiogalatea* spp., which comprises deep-sea spe-  
6 cies commonly found on continental shelves, seamounts  
7 and outer slopes (Baba et al., 2008). The genus belongs  
8 to the deep-sea family Munidopsidae and is distributed

worldwide from continental shelf to bathyal depths (163–  
1,480 m), mostly in tropical latitudes of all major oceans,  
with the highest latitude records in New Zealand in the  
South and Japan and northwest Africa in the North  
(Figure 1a). *Leiogalatea* is characterized by extreme mor-  
phological conservatism (cryptic species), high incidence  
of endemic species (described from one single archipel-  
ago) together with some broadly distributed species in the



**FIGURE 1** (a) Map showing the distribution of *Leiogalatea* within the different biogeographic areas. White dots indicate localities, and black stars indicate those localities from which material was sequenced. (b) Biogeographic scenarios to explain *Leiogalatea* species colonization of the Atlantic by vicariance or, alternatively, by dispersal: (1) vicariance driven by the rise of the Central American Isthmus, (2) vicariance driven by the Tethys Seaway closure and (3) dispersal around southern Africa from the western Indian Ocean. ATL: Atlantic, EIP: Eastern Indo-Pacific, WIP: Western Indo-Pacific. Marine Ecoregions of the World (MEOW) (Spalding et al., 2007) data were obtained from <http://marineregions.org/>. Paleoshorelines are based on Heine, Yeo, and Müller (2015). Shapefiles were obtained from <https://www.natureearthdata.com>. Maps were created with Qgis v 3.6.2 (<https://qgis.org/en/site/>)

1 Indo-Pacific region and comparatively poor diversity in  
2 the Atlantic Ocean (16 vs. 2 species) (Rodríguez-Flores,  
3 Macpherson, & Machordom, 2019a). The patterns of di-  
4 versity and distribution of the Atlantic taxa raise questions  
5 about the origin and evolution of these lineages. Briggs  
6 and Bowen (2013) explained the origin of the current  
7 Atlantic fauna on the basis of different biogeographic sce-  
8 narios. We consider the same scenarios here to account  
9 for the current distribution of *Leiogalathea*: (a) vicariance  
10 driven by the rise of the Central American Isthmus, which  
11 would have promoted cladogenesis between Atlantic and  
12 Eastern Indo-Pacific (EIP) lineages, and the closing of  
13 deep-water passages 9.2 Ma (O’Dea et al., 2016); (b) vi-  
14 cariance driven by closure of the Tethys Seaway leading  
15 to cladogenesis between Atlantic and Indo-Pacific lineages  
16 during the Early to Middle Miocene, around the TTE (14–  
17 18 Ma). Estimating the timing of cladogenesis between the  
18 Atlantic *Leiogalathea* and the other lineages would lead  
19 to reject and accept one of these vicariant hypotheses;  
20 however, (c) if vicariance is rejected, the default hypoth-  
21 esis of colonization by dispersal can be proposed (Crisp,  
22 Trewick, & Cook, 2011). *Leiogalathea* species could have  
23 colonized the Atlantic Ocean via dispersal around south-  
24 ern Africa from the western Indian Ocean. In this case, it  
25 would be difficult to establish an accurate temporal frame-  
26 work, although it would likely have happened before the  
27 cooling trend of the Benguela upwelling system (Pliocene)  
28 (Figure 1b).

29 Phylogenetic reconstructions in a temporal-spatial  
30 framework of related shallow-water (*Lauriea*, *Sadayoshia*,  
31 and *Coralligalathea*) and deep-sea (*Paramunida*) squat  
32 lobsters have been published in recent years (Cabezas et al.,  
33 2012; Palero, Robainas-Barcia, Corbari, & Macpherson,  
34 2017; Rodríguez-Flores, Macpherson, Buckley, &  
35 Machordom, 2019b). According to these studies, the  
36 Tropical Southwestern Pacific and the CT are the regions  
37 with highest species richness, and the Oligocene–Miocene  
38 transition was a period with extremely high cladogenetic  
39 rates. However, in order to better compare diversification  
40 processes in related shallow-water vs. deep-sea squat lob-  
41 sters, studies of more deep-sea taxa are needed, making  
42 *Leiogalathea* a great model system.

Here, we reconstruct the evolutionary and biogeographic  
history of the deep-sea squat lobster genus *Leiogalathea*.  
Our aims are to (a) determine the phylogenetic relationships  
within the group and the timing and patterns of speciation,  
(b) analyse its ancestral distribution to consider alternative  
hypotheses on the Atlantic Ocean colonization and to discuss  
drivers of current patterns of species distribution (historical  
biogeography), and (c) contrast patterns and historical pro-  
cesses affecting shallow-water versus. deep-sea squat lobster  
genera.

## 2 | MATERIAL AND METHODS

### 2.1 | Sampling, bathymetry, geography and morphological examination

Specimens were collected by trawling and dredging in the  
Atlantic, Indian and Pacific oceans during several deep-sea  
cruises, most of which were organized by the Muséum na-  
tional d’Histoire naturelle (MNHN) through the Tropical  
Deep Sea Benthos programme (Bouchet, Héros, Lozouet, &  
Maestrati, 2008; Poupin & Corbari, 2016; Richer de Forges et  
al., 2013). The sampling depths ranged from 163 to 1,500 m.  
Sampling areas included off the coast of Florida in the Gulf  
of Mexico and Guadeloupe Island in the Caribbean Sea; the  
northwestern coast of Africa in the eastern Atlantic; Mayotte  
and Glorieuses Islands and the Seychelles in the western  
Indian Ocean; Kai and Tanimbar islands in Indonesia; the  
Solomon Islands, Papua New Guinea in the Solomon Sea  
and New Ireland Island in the Bismarck Sea; the Solomon  
Islands, the Vanuatu archipelago, New Caledonia and  
Chesterfield Islands in the Coral Sea; Wallis and Futuna,  
Tonga Island, the Marquesas Islands and French Polynesia  
in the EIP (Figure 1). We also analysed sequences from a  
specimen from New Zealand. We conducted a morphological  
analysis of 436 specimens from approximately 120 localities.  
Of these, 70 were selected for molecular analyses, but some  
of them failed to amplify or sequence. The specimens are  
deposited in the scientific collections of the MNHN, Paris,  
the Forschungsinstitut und Natur-Museum Senckenberg,  
Frankfurt (SMF) and the National Institute of Water &  
Atmospheric Research, Wellington (NIWA).

Morphological characterization was performed as pre-  
viously described (Rodríguez-Flores, Macpherson, &  
Machordom, 2019a). The evolutionary trends of some char-  
acters were also studied by mapping them on the species tree  
using Mesquite 3.40 (build 877) (Maddison & Maddison,  
2018). Analysed characters included, among others, the  
armature of the carapace and rostrum and the shape of the  
walking legs (pereopods), both of which are useful to distin-  
guish groups of species (see Figure S1).

### 2.2 | DNA extraction, amplification and sequencing

Muscle tissue digestion, DNA extraction, amplification  
and sequencing were performed as previously described  
(Rodríguez-Flores, Macpherson, Buckley, et al., 2019b;  
Rodríguez-Flores, Macpherson, & Machordom, 2019a).  
Partial sequences of five genes, two mitochondrial (coding  
and ribosomal) and three nuclear (one coding and two ribo-  
somal), were amplified for molecular analyses: the barcoding

1 region of cytochrome c oxidase subunit I (COI), the mito-  
2 chondrial large subunit ribosomal RNA (16S), the coding  
3 region of Histone 3 (H3) and fragments of two ribosomal nu-  
4 clear genes (28S and 18S) (for the list of primers used in this  
5 study, see Table S2). As multiple copies of the 28S fragment  
6 were detected, we cloned the fragment using the pGEM-T  
7 Vector System (Promega). Sequencing of both strands of  
8 each fragment was performed by Secugen (Madrid) using  
9 BigDye Terminator and an ABI 3,730 genetic analyzer. New  
10 sequences were deposited in GenBank (Table S3).

### 13 | 2.3 | Sequence alignment and 14 phylogenetic analyses

15 All DNA sequences were revised and assembled using  
16 Sequencher v4.8 (Gene Codes Corporation). Ribosomal gene  
17 sequences were first aligned automatically using MAFFT  
18 (Kato, Misawa, Kuma, & Miyata, 2002) then manually cor-  
19 rected in the Se-AL alignment editor ([http://tree.bio.ed.ac.uk/  
20 software/seal/](http://tree.bio.ed.ac.uk/software/seal/)). To detect whether pseudogenes were present,  
21 COI sequences were translated with the invertebrate mito-  
22 chondrial genetic code to look for internal stop codons using  
23 ExPASy (<https://web.expasy.org/translate/>).

24 Phylogenetic relationships were inferred through Bayesian  
25 inference (BI), maximum likelihood (ML) and maximum  
26 parsimony (MP) methods. In the BI approach, two paral-  
27 lel runs of four Metropolis-Coupled Markov Chains Monte  
28 Carlo (MC<sup>3</sup>) were run for 10<sup>7</sup> generations in MrBayes v3.2.1  
29 (Ronquist & Huelsenbeck, 2003), sampling every 1,000 gen-  
30 erations and using a mixed model to average among substi-  
31 tution models to obtain the posterior probabilities. The first  
32 25% of the initial trees were discarded as burn-in. The analy-  
33 ses were run combining mitochondrial and nuclear markers in  
34 two partitions and with the full concatenated data set. The ML  
35 tree was built with phyML v3.1 (Guindon & Gascuel, 2003)  
36 after obtaining the best substitution model estimated for the  
37 concatenated data sets (mitochondrial and global data) using  
38 the program jModelTest 2.1.5 (Darriba, Taboada, Doallo, &  
39 Posada, 2012) following the Bayesian information criterion  
40 (BIC). The MP analyses were implemented in PAUP\* v4.0a,  
41 applying a full heuristic search with a tree-bisection recon-  
42 nection (TBR) branch swapping algorithm with reconnection  
43 limit = 8, ten random stepwise additions, and gaps treated as  
44 a new state ('fifth base'). Non-parametric bootstrap analyses  
45 for ML and MP were conducted with 1,000 pseudo replicates.

### 46 | 2.4 | Species tree and divergence 47 time estimation

48 To explore conflicts between different loci (e.g. incongru-  
49 ence of the information of each gene), we built a species tree

with mitochondrial and nuclear matrices using StarBEAST2  
(Heled & Drummond, 2010) and compared the resulting tree  
with those of the individual genes.

There are no known *Leiogalatea* fossils to calibrate a  
molecular clock. Therefore, we calibrated the analysis with  
secondary calibration points derived from previous broad-  
scale phylogenetic studies. According to Rodríguez-Flores,  
Macpherson, Buckley, et al. (2019b), who used fossil calibra-  
tion and ages obtained from several other works, the diver-  
gence of *Leiogalatea* from its Munidopsidae relatives took  
place 74–120 Ma (average of 99 Ma), and the age of the most  
recent common ancestor (MRCA) of the outgroups used in  
the present study (*Munidopsis crenatirostris* and *Galacantha*  
*subspinosa*, Munidopsidae) was 61 Ma (40–85 Ma).

Divergence time estimation was carried out in BEAST  
v2.5.1 (Bouckaert et al., 2014). This program uses relaxed  
clock models and allows for missing data and flexibility of  
model parameters. Before estimating divergence times, we  
first estimated the best partition scheme fitting the data with  
PartitionFinder v1.1.0 (Lanfear, Calcott, Ho, & Guindon,  
2012) in order to determine which partitions following the  
same substitution pattern can be linked in the species tree and  
divergence estimation.

We selected an 'analytical population size integration'  
for the population model as there was no need to estimate  
exact population sizes for each species. A 'beastmodeltest'  
selecting 'TransitionTransversionSplit' was chosen for the  
site model to average among substitution models while esti-  
mating the posterior probability of the parameters (Bouckaert  
& Drummond, 2017). An uncorrelated relaxed log normal  
clock model was implemented with values drawn from a dis-  
tribution with a mean of 0.002 and a standard deviation of  
0.1 for the 16S clock rate. These rates were based on previ-  
ously reported mitochondrial DNA rates of substitution for  
related crustaceans (Cabezas et al., 2012). Mean substitution  
rates were estimated for each gene, for which we assigned  
non-informative priors for the substitution rates (gamma dis-  
tribution setting values for alpha and beta parameters as 0.01  
and 100, respectively). We also used a birth–death model for  
the tree prior. Normal distributions were chosen as temporal  
priors for the calibration points (mean = 100, stdv = 10 for  
the root of the tree; and mean = 60, stdv = 10 for the MRCA  
of the outgroup *Galacantha subspinosa* and *Munidopsis*  
*crenatirostris*). The Markov Chains Monte Carlo (MCMC)  
was run for 5 × 10<sup>8</sup> generations per run, and parameters were  
logged every 5 × 10<sup>4</sup> generations. BEAST analyses were run  
in the CIPRES Science Gateway v3.1 (Miller, Pfeiffer, &  
Schwartz, 2010).

Convergence of the chains (trace and effective sample  
sizes, ESSs) was assessed in Tracer v1.7. The results were  
summarized and annotated in a Maximum Clade Credibility  
(MCC) tree generated with Tree Annotator v2.5.1 (Rambaut  
& Drummond, 2014) after discarding the first 25% of the

1 trees as burn-in. The resulting MCC trees from each analysis  
2 were edited in FigTree v1.4.3 (Rambaut, 2014).

## 3 2.5 | Ancestral range estimation

4  
5  
6  
7 Biogeographic areas were defined following the ‘Marine  
8 Ecoregions of the World’ (MEOW) global classification sys-  
9 tem (Spalding et al., 2007), which uses patterns of mapped  
10 marine biodiversity to delimit realms, provinces and ecore-  
11 gions. This system was previously used to reconstruct the  
12 biogeographic history of related shallow-water squat lobsters  
13 (e.g. Palero et al., 2017; Schnabel et al., 2011). Our samples  
14 covered four realms: Tropical Atlantic, Western Indo-Pacific,  
15 Central Indo-Pacific and Eastern Indo-Pacific. We delimited  
16 six areas within these realms to consider geographic patterns  
17 of diversity in *Leiogalathea* (see Figure 1): (A) Atlantic, (N)  
18 Tropical Southwestern Pacific, (P) Eastern Coral Triangle,  
19 (I) Western Coral Triangle, (F) Eastern Indo-Pacific and (W)  
20 Western Indian Ocean (modified from Spalding et al., 2007).  
21 The New Zealand specimen of *L. ascanius* was genetically  
22 identical to those from New Caledonia and was included in  
23 the tropical southwestern Pacific region (Figure 2).

24 Historical biogeographic analyses were performed in the  
25 R package BioGeoBEARS (Matzke, 2013), which permits  
26 biogeographic model comparison, and then in RevBayes  
27 (Höhna et al., 2016) to reconstruct the geographic ancestral  
28 states and the evolution of geographic ranges. We first se-  
29 lected the best fit model for our data in BioGeoBEARS, which  
30 includes and compares the following models: Dispersal-  
31 Extinction-Cladogenesis (DEC) (Ree & Smith, 2008),  
32 Dispersal-Vicariance Analysis (DIVALIKE), BayArea (the  
33 range evolution model) and the Bayesian Binary Model of  
34 RASP (Yu, Harris, Blair, & He, 2015). We also allowed  
35 founder-event speciation processes (+J) to be integrated into  
36 all models. We then reconstructed the history of geographic  
37 ranges in a Bayesian framework using RevBayes, which also  
38 estimates migration rates (range expansion), extirpation rates  
39 (range contraction) and the probability of allopatry versus  
40 sympatry according to the data.

41 In order to test the vicariant events, we ran an epoch DEC  
42 model in RevBayes, following the results from the model se-  
43 lection test in BioGeoBEARS (see below). We specified a  
44 time matrix with three epochs: 35–32 Ma, age of the MRCA  
45 of the ingroup; 16–14 Ma to represent the Terminal Tethyan  
46 Event; and the Present. We assigned three connectivity

47 matrices to these epochs to represent paleo-connectivity  
48 among areas. Specifically, we coded the matrices to repre-  
49 sent the disconnection and unlikely presence of *Leiogalathea*  
50 species in French Polynesia (F) at the root of the tree and the  
51 current disconnection of Atlantic and Indo-Pacific areas. A  
52 distance matrix between areas was generated to scale disper-  
53 sal rates and probabilities. This was not an absolute distance  
54 matrix; rather, we coded relative distances between areas as  
55 adjacent (1), separated (100) and very far away (1,000). We  
56 constrained ancestral ranges to have a maximum of four areas  
57 to minimize the number of potential ancestral states. None  
58 of the current species is present in more than three discrete  
59 biogeographic areas. Four independent analyses for 25,000  
60 generations were run. We visually and statistically checked  
61 for convergence and proper mixing of the MCMC analyses  
62 in Tracer v1.7 and the R package Bonsai (<https://github.com/mikeryanmay/bonsai>), respectively. Results from the  
63 four analyses were combined to generate the final biogeo-  
64 graphic reconstructions, which were visualized and edited  
65 with RevGadgets in R. All matrices and scripts are provided  
66 in Supporting Information (S4).

## 67 3 | RESULTS

68 Most (85%) of the 18 *Leiogalathea* species described to  
69 date were included in our phylogenetic analyses (Table S3).  
70 *Leiogalathea laevirostris*, *L. imperialis* and *L. aeneas* sam-  
71 ples were excluded as they were preserved in formalin. Our  
72 results (Figures 2–4, Figure S1) show the potential existence  
73 of one undescribed species (*Leiogalathea* sp. in the phyloge-  
74 netic tree), which would increase the number of known spe-  
75 cies to 19. The complete alignment of the five partial genes  
76 consisted of 3,748 characters: 658 base pairs (bp) for COI;  
77 533 bp for 16S; 331 bp for H3; 902 bp for 28S; and 1,324 bp  
78 for 18S. In most cases, phylogenetic analyses based on the  
79 mitochondrial and the concatenated matrices recovered con-  
80 gruent topologies, although lower clade supports were ob-  
81 served in the mitochondrial phylogeny (Figure 2).

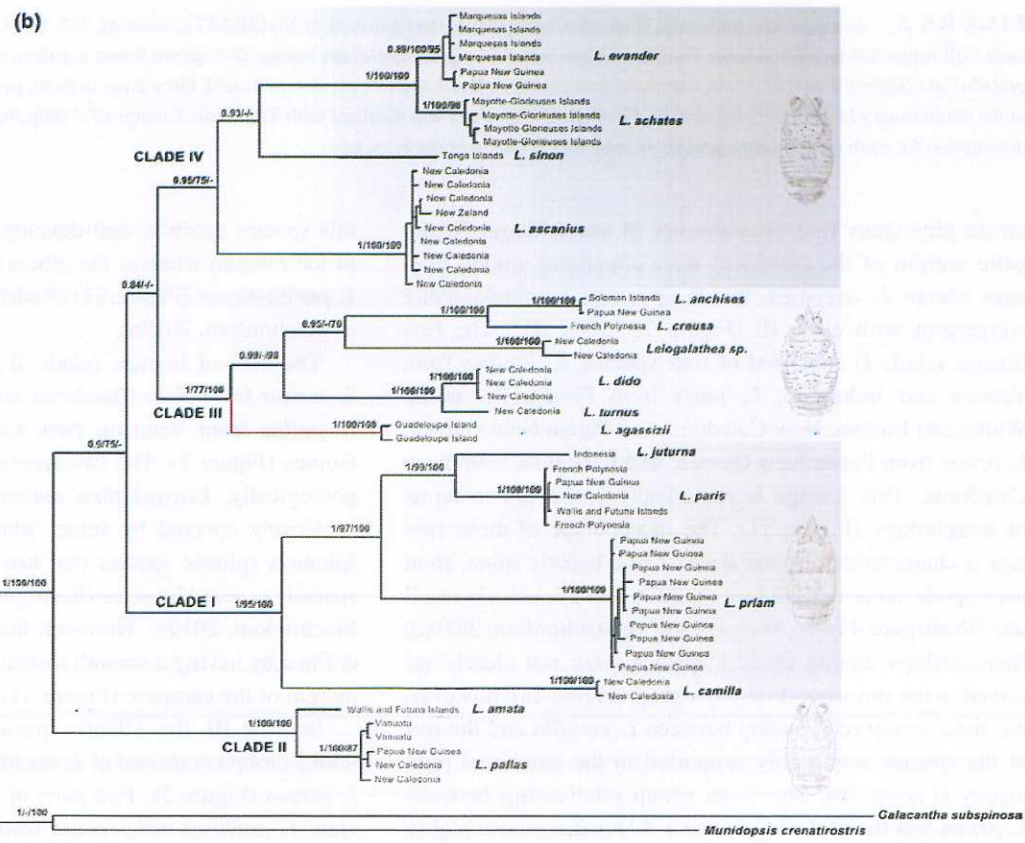
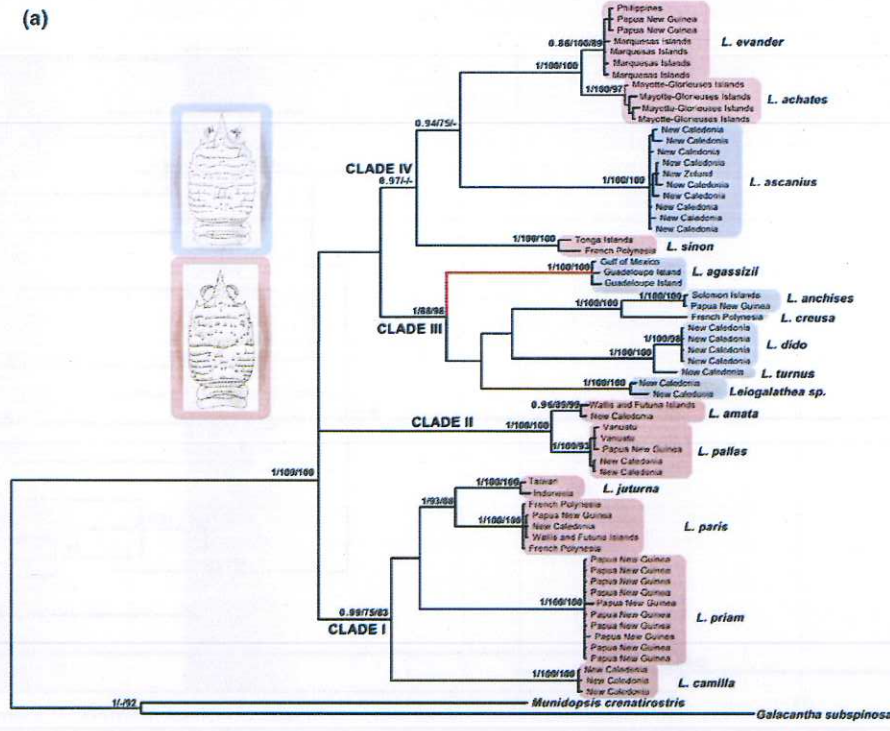
### 82 3.1 | Phylogenetic analyses and morphological character evolution

83 The genus *Leiogalathea* was recovered as a monophyletic  
84 clade in all analyses [posterior probability (pp):1; bootstrap

**FIGURE 2** Phylogenetic tree based on (a) concatenated mitochondrial data and (b) concatenated nuclear plus mitochondrial data. The geographic location of each specimen is provided at the tips. The morphotypes of the main clades (I, II, III and IV) based on the spinulation of the hepatic margin of the carapace (blue spinose, pink unarmed) are also shown. The red branch indicates the Atlantic species, and, in B, the typical morphotype of each major clade is represented by an illustration of the carapace. Numbers above branches indicate posterior probability and bootstrap support values for the BI and ML analyses, respectively. Hyphens (–) indicate mean node unsupported in the corresponding analysis (Bayesian posterior probability lower than 0.85, MP and ML bootstrap support lower than 70)

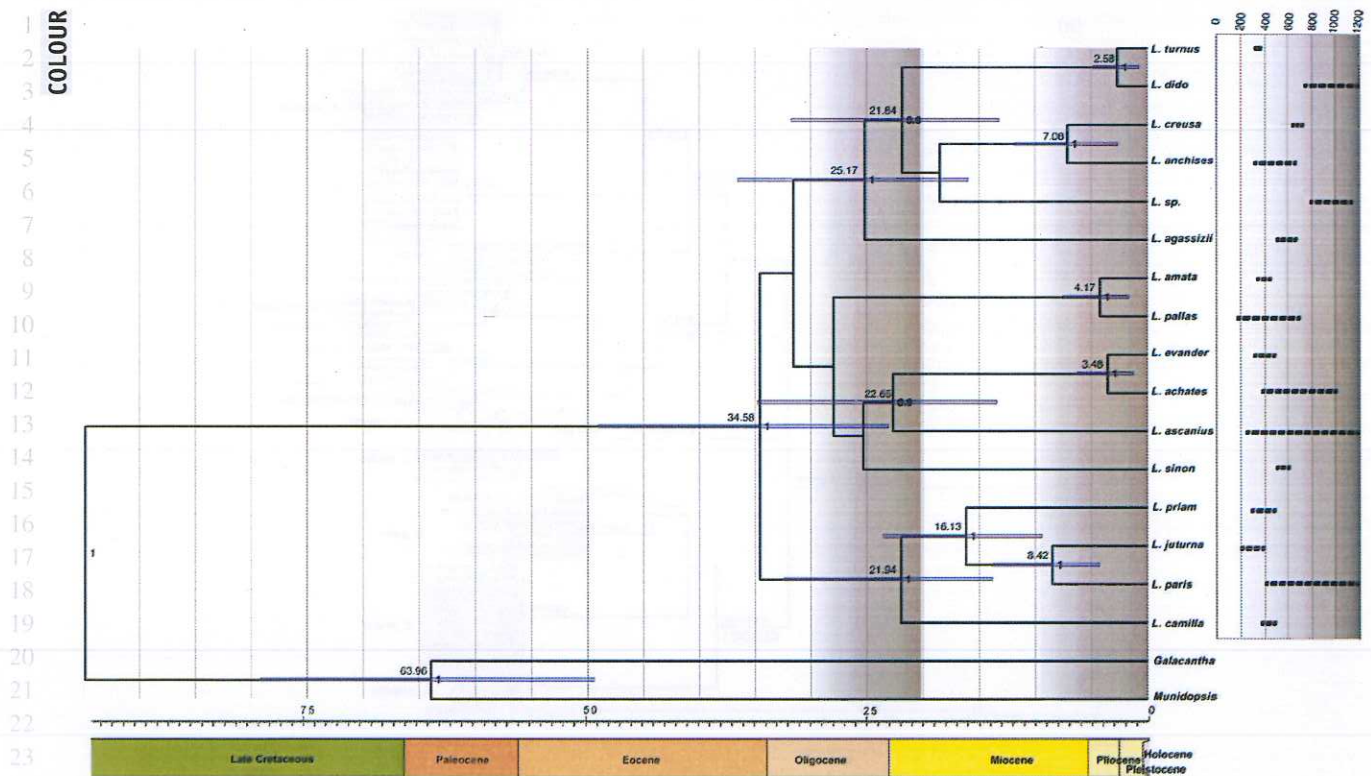
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supports (bs): 100] (Figure 2). *Leiolgalthea* species were grouped in four main lineages that, in most cases, presented different combinations of morphological synapomorphies

(following the morphological characterization by Rodríguez-Flores, Macpherson, & Machordom, 2019a) but lacked a clear geographic structure. The two morphotypes mapped



**FIGURE 3** *Leiogalathea* maximum clade credibility (MCC) tree inferred by StarBEAST2, showing 95% HPD credibility intervals for each well supported recovered node. Numbers above branches represent average lineage divergence times; numbers in nodes represent posterior probabilities (higher than 0.9). Main morphological clades (I, II, III and IV) are also indicated. Grey areas indicate periods of intense cladogenesis in the evolutionary history of *Leiogalathea*. Geological time chart was obtained with TimeScale Creator v7.3 (<http://www.tscreator.org>). Depth distribution for each *Leiogalathea* species is indicated at the tip of the branches

on the phylogeny (presence/absence of one spine on the hepatic margin of the carapace) were congruent among lineages except *L. ascanius*, which appeared morphologically convergent with clade III (Figure 2, Figure S1). The first lineage (clade I) consisted of four species: *L. juturna* from Taiwan and Indonesia; *L. paris* from French Polynesia, Wallis and Futuna, New Caledonia and Papua New Guinea; *L. priam* from Papua New Guinea; and *L. camilla* from New Caledonia. This lineage is remarkably conserved in terms of morphology (Figure S1). The morphotype of these species is characterized by the absence of a hepatic spine, stout pereopods, an armed spinose rostrum, and a relatively small size (Rodríguez-Flores, Macpherson, & Machordom, 2019a). Relationships among clade I species were not clearly resolved in the mitochondrial phylogeny (Figure 2a); however, the sister group relationship between *L. camilla* and the rest of the species was highly supported in the combined phylogeny (Figure 2b). The sister group relationship between *L. priam* and the clade *L. juturna* + *L. paris* was also highly supported in the combined phylogeny (Figure 2b). The clade *L. juturna* + *L. paris* was well supported in both phylogenies. The morphology of the species also supports the phylogenetic distinction of *L. camilla* from the other clade I species:

this species exhibits well-developed spines in the armature of the rostrum whereas the others (*L. priam*, *L. juturna*, and *L. paris*) do not (Figure S1) (Rodríguez-Flores, Macpherson, & Machordom, 2019a).

The second lineage (clade II) comprised two species: *L. amata* from New Caledonia and Wallis and Futuna and *L. pallas* from Vanuatu, New Caledonia and Papua New Guinea (Figure 2). The two species are quite different morphologically. *Leiogalathea amata* is a small species that is densely covered by setae, whereas *L. pallas* is a conspicuous spinose species that has a carapace and abdomen sparsely covered by setae (Rodríguez-Flores, Macpherson, & Machordom, 2019a). However, the clade is morphologically defined by having a smooth rostrum and an unarmed hepatic margin of the carapace (Figure S1).

In clade III, the Atlantic species *L. agassizii* was united with a group comprised of *L. anchises*, *L. creusa*, *L. dido* and *L. turnus* (Figure 2). Two pairs of sister species were recovered: *L. anchises* + *L. creusa* from Papua New Guinea and Polynesia, respectively, and *L. dido* + *L. turnus*, both from New Caledonia. These pairs were also related to a new species (*Leiogalathea* sp.) from New Caledonia. However, the relationship among them and with respect to the Atlantic



1 taxon was unresolved in the mitochondrial tree (Figure 2a).  
2 In the combined tree, the new species was recovered as sister  
3 species of *L. anchises* + *L. creusa* (Figure 2b). The morpho-  
4 logic of clade III species is also very conserved: they are  
5 conspicuous, have a rostrum margin that is armed with several  
6 spines (5–7) and a carapace with 6–7 spines, including the  
7 hepatic spine (Figure 2a, Figure S1) (Rodríguez-Flores,  
8 Macpherson, & Machordom, 2019a).

9 The fourth lineage (clade IV) was only supported in  
10 the BI analyses and included diverse morphotypes. The  
11 sister species *L. evander* and *L. achates* from the Central  
12 Pacific–Polynesia and the West Indian Ocean, respectively,  
13 clustered with *L. ascanius* from New Caledonia and New  
14 Zealand (Figure 2a). *Leiogalathea sinon* from Polynesia was  
15 sister species to this group in the mitochondrial tree and  
16 to *L. evander* + *L. achates* in the combined tree; however,  
17 neither relationship was fully supported in all of the analyses.  
18 Clade IV species, except *L. ascanius*, lack a spine on  
19 the hepatic margin of the carapace (Figure 2a, Figure S1)  
20 (Rodríguez-Flores, Macpherson, & Machordom, 2019a),  
21 indicating morphological convergence of this trait with respect  
22 to clade I species.

### 23 24 25 3.2 | Species tree, divergence time 26 estimation, rates of evolution and 27 bathymetric ranges

28  
29 The topology obtained from the \*BEAST analyses was  
30 congruent with the combined nuclear and mitochondrial  
31 phylogenetic tree and recovered the same main lineages  
32 and relationships (pp > 0.95; only clade IV had a  
33 pp < 0.95) (Figure 3). Nodes that were not well resolved  
34 were not considered for the time estimates. The MRCA of  
35 the genus was estimated around 35 Ma [highest 95% posterior  
36 density interval (HPD<sub>95%</sub>) 23–49 Ma] and those of the main  
37 clades around 20–25 Ma (Figure 3). For instance, the first  
38 lineage branching off in clade III was the Atlantic species  
39 *L. agassizii* around 25 Ma (HPD<sub>95%</sub> 16–36 Ma). As shown in  
40 Figure 3, the Oligocene/Miocene boundary was an active  
41 period of diversification for the group, although within-clade  
42 diversification occurred mainly during the Miocene/Pliocene.  
43 Only one cladogenetic event definitively occurred during the  
44 Plio/Pleistocenic (diversification of *L. turnus*/*L. dido*).

45 The following average substitution rates were estimated  
46 for each gene:  $5.6 \times 10^{-3}$  (COI),  $2 \times 10^{-3}$  (16S),  $3 \times 10^{-3}$   
47 (28S),  $5.5 \times 10^{-4}$  (18S) and  $1.1 \times 10^{-4}$  (H3).

48 A general overlap in the species depth distribution was  
49 observed (Figure 3) with wide bathymetric ranges, most of them  
50 appearing at 600–800 m, only a few records below 1,000 m  
51 (*L. ascanius* and *L. paris*) and only two species mainly restricted  
52 below this depth (*L. dido* and *Leiogalathea* sp).

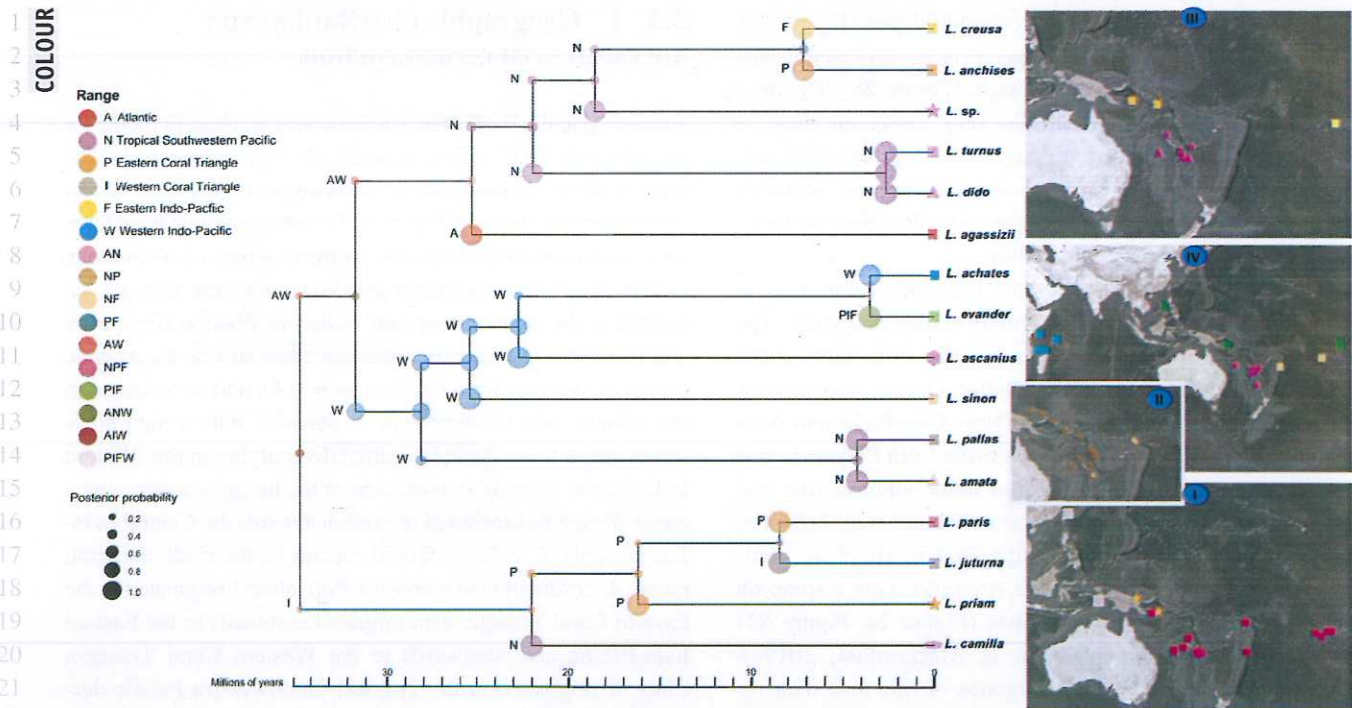
### 3.3 | Geographic distribution and ancestral area reconstruction

53 According to the BioGeoBEARS analysis, the best fit model for  
54 our data was DEC with no founder event speciation (+J). The  
55 biogeographic reconstruction following an epoch DEC model  
56 in RevBayes is shown in Figure 4. The analysis considered three  
57 areas with moderate probability for the root (pp = 0.4): Atlantic  
58 Ocean, Western Indo-Pacific and Western Coral Triangle, all  
59 located in the westernmost part of the distribution (Figure 1).  
60 The reconstructed ancestral range for clade III was the Atlantic  
61 Ocean + Western Indo-Pacific (pp = 0.4), and an ancestor in  
62 the Atlantic was recovered for *L. agassizii* with a high probability  
63 (pp = 0.8). Clade IV started diversifying in the Western  
64 Indo-Pacific (pp = 0.8), with each of the lineages undergoing a  
65 range change that included migration towards the Central Indo-  
66 Pacific; only *L. achates* would remain in the clade ancestral  
67 range. According to the reconstruction, clade I originated in the  
68 Eastern Coral Triangle then migrated eastwards to the Eastern  
69 Indo-Pacific and westwards to the Western Coral Triangle.  
70 Clade II originated in the Tropical Southwestern Pacific during  
71 the Pliocene but subsequently underwent a range expansion  
72 towards the Eastern Coral Triangle. Speciation processes in  
73 *Leiogalathea* were predominantly by allopatry (pp = 0.6) than  
74 sympatry (pp = 0.4). A high rate of extirpation (local extinction  
75 in part of the ancestral range) was also observed [0.98/Myr  
76 (million years), HPD<sub>95%</sub> 0.22–1.97]. Migration rates (migration  
77 events/Myr) ranged from 0.03 to 0.53 (HPD<sub>95%</sub>, mean: 0.12).  
78 Range stasis was observed in the lineage leading to *L. dido* and  
79 *L. turnus*, and in *Leiogalathea* sp. and *L. camilla*, while range  
80 expansion was detected in the rest of the lineages.

## 4 | DISCUSSION

### 4.1 | *Leiogalathea* speciation patterns

81 Molecular studies of deep-sea fauna are crucial to unravel the  
82 taxonomic incongruences, such as those related to previously  
83 described morphospecies, that were obscuring evolutionary  
84 patterns in deep-sea taxa (Cabezas et al., 2012; Vrijenhoek,  
85 2009). These studies have also indicated how diversity has  
86 been greatly underestimated in these taxa (Ritchie, Jamieson,  
87 & Piertney, 2015). *Leiogalathea* is a clear example: only  
88 two species were recognized (Baba et al., 2008) until a recent  
89 revision of the genus showed the existence of 18 species  
90 (Rodríguez-Flores, Macpherson, & Machordom, 2019a). Our  
91 results show, in general, that the genus is monophyletic,  
92 presents a high level of morphological convergence or homoplas-  
93 y, having thus few morphological traits of phylogenetic  
94 value, exhibits overlap among most species depth ranges  
95 and contains pairs of sister species that show allopatric and  
96 sympatric speciation patterns (in a biogeographic sense).



**FIGURE 4** Range area reconstruction based on a Bayesian Dispersal-Extinction-Cladogenesis (DEC) reconstruction of the spatio-temporal evolution of *Leiogalthea* spp. using the MCC tree obtained in starBEAST2. The biogeographic areas and the posterior probabilities of the biogeographic scenarios are also represented in the figure. Coloured shapes at the branch tips indicate contemporary distributions of the taxa. Maps illustrate geographic distribution of clades I, II, III (excluding the Atlantic *L. agassizii*) and IV

Speciation in the same geographic area occurred at least once in each major lineage of *Leiogalthea*. Interestingly, sympatric versus. allopatric speciation events in *Leiogalthea* have generated highly distinct species in terms of morphology. Divergence of the morphologically well-differentiated sister species *L. dido* and *L. turnus*, which have overlapping distributions around New Caledonia, constitutes the most recent speciation event within the genus. Differential niche occupation may explain the speciation: *L. turnus* has a bathymetric range of 333–375 m, whereas most of *L. dido* specimens have been recorded below 1,000 m and exhibit a conspicuous reduction in the ocular orbit (Figure 3, Figure S1.5; Rodríguez-Flores, Macpherson, & Machordom, 2019a). In this case, bathymetry might have driven/affected speciation in the absence of geographic isolation, as has been shown in hadal amphipods (Ritchie et al., 2015). On the other hand, the older speciation events seem to have been due to allopatry/vicariance and occurred without conspicuous morphological changes. For example, the sibling species *L. juturna* and *L. paris*, which are exceptionally similar and can only be differentiated by inconspicuous diagnostic characters (Rodríguez-Flores, Macpherson, & Machordom, 2019a), diverged and migrated towards the Western Coral Triangle in a comparatively ancient process compared with the morphologically distinctive species *L. dido* and *L. turnus* (8.4 vs. 2.6 Ma) (see Figure 4), occupy also a vicariant vertical

distribution (Figure 3). Increased phenotypic differences related to sympatric speciation are not an uncommon phenomenon and are likely related to divergence in ecological traits (such as differences in microhabitat exploitation) and assortative mating phenomena (e.g. Moritz et al., 2018; Puritz et al., 2012). There are also several examples of cryptic species presenting allopatric distributions (e.g. Vrijenhoek, 2009). Ecological speciation processes, including those involving explosive radiations, have been shown to be generally faster than those due to vicariance (for instance, in *Drosophila*: 200,000 years vs. 2.7 Ma), and cases of rapid speciation have been detected in marine animals (sea stars, snails and fishes) (Bowen, Rocha, Toonen, & Karl, 2013). Genetic drift is hypothesized to lead to sexual isolation slower than isolation mediated by selective pressures, which could have a clear effect in just a few generations (Hendry, Wenburg, Bentzen, Volk, & Quinn, 2000; Puritz et al., 2012). Quantifying morphological change through time between sister species would help to determine whether speciation mode (allopatric vs. sympatric) is correlated with morphological evolution in *Leiogalthea*.

Finally, in the case of the sister species *L. achates* and *L. evander*, we identified speciation involving dispersal. The known distribution ranges of the two species are restricted (localized) and separated from each other by more than 8,000 km (straight line distance) (SW Indian Ocean and Papua

1 New Guinea/French Polynesia, respectively). A relatively re-  
2 cent long-term dispersal event between the western Indian  
3 Ocean and the CIP might explain this pattern. Vicariant sister  
4 species separated by thousands of kilometres have been  
5 also reported in *Corallioagalathea* (*C. humilis* vs. *C. minuta*)  
6 (Rodríguez-Flores, Macpherson, Buckley, et al., 2019b). As  
7 in related galatheid species, for instance *Lauriea punctata*,  
8 *Sadayoshia edwardsii* or *Allogalathea babai* (Baba et al.,  
9 2008; Palero et al., 2017), some *Leiogalathea* species exhibit  
10 a wide geographic distribution. Although not known for this  
11 genus, other related squat lobster species have free-swim-  
12 ming planktonic larvae (Baba, Fujita, Wehrmann, & Scholtz,  
13 2011) that might occasionally drift with the ocean currents,  
14 making long-distance dispersal events followed by establish-  
15 ment conceivable. Long-distance drifting is evidenced  
16 by genetic uniformity across immense geographic distances,  
17 which has been observed in many marine organisms includ-  
18 ing algae, mollusks, isopods and amphipods (Gillespie et al.,  
19 2012). Indeed, widely distributed *Leiogalathea* species (e.g.  
20 *L. paris*) exhibited genetic homogeneity among very distant  
21 populations (see Figure 2).

## 24 | 4.2 | Historical biogeography

26 Our results indicate that the MRCA of *Leiogalathea* likely  
27 lived during the Late Eocene to Early Oligocene. The re-  
28 constructed ancestral range was located in the westernmost  
29 part of the genus current distribution (Atlantic and western  
30 Indian Ocean) and dated to the Late Eocene (Figures 3 and  
31 4), both of which suggest a geographic origin in the Tethys  
32 realm. The Atlantic lineage currently includes only two spe-  
33 cies (*L. agassizii* and *L. aeneas*) and is characterized by a  
34 poor cladogenetic history compared with the Indo-Pacific  
35 lineages, which consist of more than 16 species (Rodríguez-  
36 Flores, Macpherson, & Machordom, 2019a).

37 The hypotheses for the origin of the Atlantic *Leiogalathea*  
38 were proposed as: (a) IOP vicariance, (b) TTE vicariance  
39 and (c) colonization from Indo-Pacific lineages surrounding  
40 southern Africa (Figure 1).

41 If the vicariance was driven by the IOP as suggested by  
42 the first vicariant hypothesis, Eastern Pacific and Western  
43 Atlantic would share lineages with a divergence estimated  
44 around the rise of the Isthmus (Cowman & Bellwood, 2013b).  
45 The genus is supposedly currently missing in the Eastern  
46 Pacific; therefore, if this particular biogeographic scenario  
47 happened, current Eastern Indo-Pacific lineages would be  
48 closely related to the Atlantic species, not observed in our  
49 results. Moreover, the estimated divergence between Atlantic  
50 and Pacific lineages, at the end of the Oligocene, largely pre-  
51 cedes the closure of the Panamanian Isthmus.

52 On the other hand, a scenario of Atlantic colonization  
53 via dispersal from southmost tip of Africa (third hypothesis)

54 requires a sister relationship among Indian and Atlantic  
55 lineages (Lessios & Robertson, 2013; Rocha et al., 2005).  
56 However, this relationship was not observed either.

57 In the second biogeographic hypothesis, ancient relict  
58 Tethyan lineages should be detected, with an early to middle  
59 Miocene age (14–20 Ma) (Hou & Li, 2018; Liu et al., 2018).  
60 The reconstruction results are in line with the second hypoth-  
61 esis (see Figure 1b): colonization of the Atlantic following  
62 a vicariant event caused by the Tethys closure. The Tethyan  
63 origin hypothesis is supported by the richness and abundance  
64 of related squat lobster fossils in the west Tethys during the  
65 second half of the Mesozoic and Early Cenozoic (e.g. Robins,  
66 Feldmann, & Schweitzer, 2013; Robins & Klompmaker,  
67 2019). According to our divergence time estimates, diver-  
68 gence of the Atlantic lineage (25 Ma) slightly predates the  
69 Terminal Tethyan Event (TTE) (12–18 Ma), though the age  
70 of this episode overlaps with our estimated range of diver-  
71 gence (16–36 Ma). Vicariant patterns between Atlantic and  
72 Indo-Pacific lineages have been extensively studied in shal-  
73 low-water taxa, with divergence estimations ranging from 12  
74 to 36 Ma and associated with vicariance driven by the TTE  
75 scenario (e.g. Cowman & Bellwood, 2013b; Liu et al., 2018;  
76 Thacker, 2015). However, there are several instances of other  
77 taxa with lineage divergences predating the TTE, some as far  
78 back as the Cenozoic to the early Eocene (e.g. Malaquias &  
79 Reid, 2009; Uribe, Williams, Templado, Buge, & Zardoya,  
80 2017). The global cooling that characterized the end of the  
81 Eocene likely promoted extinction and diversification in  
82 some of these instances (Harzhauser et al., 2007). However,  
83 these estimates can also be explained by tectonic events pre-  
84 vious to the Tethys closure (from the Eocene to the Miocene)  
85 (Hou & Li, 2018), lineage extinction (and/or incomplete sam-  
86 pling) and calibration inaccuracy (Malaquias & Reid, 2009).  
87 In the case of *Leiogalathea*, the most probable explanation of  
88 the time estimate is that deep-sea organisms might have been  
89 affected earlier by closure of the Tethys Seaway than their  
90 shallow-water counterparts (Eilertsen & Malaquias, 2015)  
91 due to the progressive disappearance of deep-water passages.  
92 In the Tethyan vicariance scenario, the level of genetic con-  
93 nectivity/isolation would vary depending on depth ranges on  
94 both sides of the barrier; therefore, the TTE might have af-  
95 fected bathyal marine organisms earlier than intertidal and  
96 shallow-water organisms (Liu et al., 2018). Comparisons of  
97 divergence times between sister species of related deep-sea  
98 and shallow-water taxa distributed at both sides of a biogeo-  
99 graphic barrier remain to be examined in detail to test this  
100 hypothesis.

101 Other squat lobsters have a distribution pattern sim-  
102 ilar to *Leiogalathea* in the Atlantic. For instance, very  
103 few *Agononida*, *Galathea* or *Eumunida* species are found  
104 in the Atlantic compared with the CIP (Baba et al., 2008;  
105 Macpherson & Robainas-Barcia, 2015). Indeed, global diver-  
106 sity of squat lobsters is quite poor in the Atlantic compared

with the CIP (Macpherson et al., 2010; Schnabel et al., 2011), an area that has clearly been acting as a centre of diversification over the last 20 Myr. Conversely, the Atlantic is considered an independent and isolated region in terms of species diversity (Cowman & Bellwood, 2013a; Macpherson, 1991; Rocha et al., 2005). The poor cladogenetic history of *Leiogalathea* and related squat lobsters in the Atlantic might be a result of a high rate of extinction and poor lineage replenishment from the Indo-Pacific due to a history of isolation generated by the formation of new barriers and the establishment of the South African (Benguela) cold-water current (Briggs & Bowen, 2013; Cowman & Bellwood, 2013a). A high rate of extinction in the Atlantic has already been demonstrated for fishes, echinoderms, bryozoans and plants (Antonelli & Sanmartín, 2011; Cowman & Bellwood, 2011; Di Martino, Jackson, Taylor, & Johnson, 2018). In addition, at the Eocene–Oligocene boundary, the deep sea underwent a dramatic turnover in fauna (Whatley & Coles, 1991), which might have been related to environmental changes associated with this progressive isolation.

Our analyses of colonization patterns for the whole genus *Leiogalathea* suggest that the most likely path of dispersal from the Tethys was migration eastwards to the CIP, which is consistent with the pattern observed for some shallow-water taxa (Renema et al., 2008). Most *Leiogalathea* lineages were established in the CIP during the Pliocene after Miocene cladogenetic events, although the MRCA of clade I was already in the Eastern Coral Triangle by the Early Miocene (20 Ma). High diversity of coral reef fauna was already well established by the Late Miocene (Briggs, 1999). Consistent with this, our analyses showed an increase in diversity of *Leiogalathea* lineages at this time and in this place. Thus, the CIP and, within it, the Tropical Southwestern Pacific might have initially acted as a centre of accumulation (Bowen et al., 2013; Cowman & Bellwood, 2013a), after they had expanded their range. The CIP area then might have acted progressively as a centre of origin, promoting cladogenesis and rapid speciation (Williams & Duda, 2008; Williams et al., 2013). These hypotheses have been widely proposed and tested to explain the distribution patterns of coral reef and intertidal fauna in the CT (Bowen et al., 2013; Gaither et al., 2011). However, comparisons of diversification and biogeographic patterns with deep-sea taxa, such as *Leiogalathea* and other squat lobsters, were, until now, not possible.

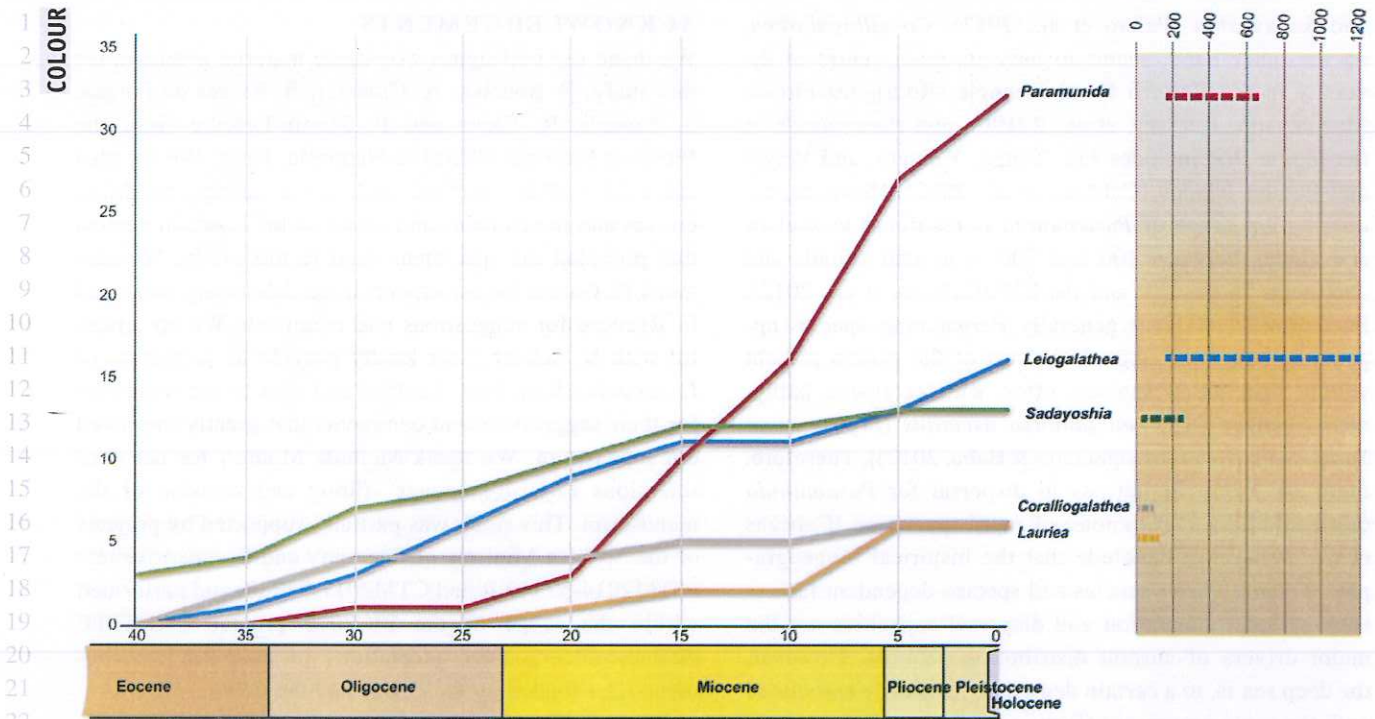
### 4.3 | Comparisons of diversification and biogeographic patterns between shallow-water and deep-sea taxa

As observed in Galatheoidea and Chirostyloidea (Macpherson et al., 2010; Schnabel et al., 2011), *Leiogalathea* also has its

centre of diversity in the Tropical Southwestern Pacific (nine species) with the number of species decreasing with distance, for instance, in the Eastern Coral Triangle and Eastern Indo-Pacific (Polynesia) (five species). A lower species richness is observed in all the others areas. Nine *Leiogalathea* species are found in New Caledonia, some of which have only been found in this area (e.g. *L. camilla*, *L. dido*, and *L. turnus*). Samadi, Bottan, Macpherson, Forges, and Boisselier (2006) argued that this region is highly productive, which would lead to an accumulation of squat lobster species instead of being a centre of speciation. Therefore, it is likely that these species have a broader distribution range.

Time-calibrated molecular phylogenies at the species level reflect the complex biogeographic history of the marine circum-tropical belt as far back as the Mesozoic. Our findings indicate that a major period of cladogenesis in *Leiogalathea* occurred 25–15 Ma (Late Oligocene to Early Miocene). Major diversification of coral reef fauna in the CIP is thought to have occurred approximately 25–20 Ma during the Paleogene–Neogene transition (Palero et al., 2017; Rodríguez-Flores, Macpherson, Buckley, et al., 2019b; Williams & Duda, 2008) when the most important Cenozoic plate boundaries were reorganized (Hall, 2002). Intense diversification was also occurring in deep-sea taxa during this period (Cabezas et al., 2012; Eilertsen & Malaquias, 2015). Comparison of the timing of cladogenetic events and lineage diversity among *Leiogalathea* and other squat lobster genera (i.e. *Corallioagalathea*, *Lauriea*, *Paramunida* and *Sadayoshia*) revealed general evolutionary speciation trends affecting these tropical marine organisms (Figure 5). These genera are excellent candidates to compare evolutionary trends between shallow-water and deep-sea organisms because they present (a) overlapping geographic distributions, (b) comparable species diversity and (c) are phylogenetically related but (d) differ in their bathymetric ranges (depth distribution mostly above of 200 m in *Corallioagalathea*, *Lauriea* and *Sadayoshia*, and below 200 m in *Paramunida* and *Leiogalathea*; see Figure 5). The MRCA of these genera dates to the Middle to Late Eocene, a period characterized by anoxic events in the deep sea (McClain & Hardy, 2010) and progressive global cooling (Harzhauser et al., 2007), which seems to have had a key role in the evolution of the Anomura (Davis, Hill, Astrop, & Wills, 2017).

During the Oligocene to Miocene transition, high tectonic activity and climate and ocean current changes could have promoted speciation in both shallow-water and deep-sea squat lobsters (Cabezas et al., 2012). Consistent with this, increased cladogenesis during this period is observed in both groups (Figure 5). With the exception of the deep-sea genus *Paramunida*, diversification stasis was observed around the Middle Miocene for all genera. Hence, other processes such as lineage extinction and local adaptation might have unequally affected these taxa. Furthermore,



**FIGURE 5** Graph showing evolutionary speciation trends in squat lobsters of the superfamily Galatheoidea: number of reconstructed lineages, estimated in increments of 5 Ma, for *Leiogalatheia* and other galatheid squat lobsters from shallow-waters (*Coralliogalatheia*, *Lauriea*, *Sadayoshia*) and the deep sea (*Paramunida*) that overlap in their distribution (data for trend analysis compiled from this study and those of Rodríguez-Flores, Macpherson, Buckley, et al., 2019b, after re-treatment of the data from Cabezas et al., 2012 and Palero et al., 2017). Depth distribution for each squat lobster genus is indicated on the right of the graph

the shallow-water genera *Coralliogalatheia*, *Lauriea* and *Sadayoshia*, all of which are associated with coral reefs, show an absence of cladogenesis for the last 5 Myr (Palero et al., 2017; Rodríguez-Flores, Macpherson, Buckley, et al., 2019b). In this sense, Pliocene extinctions have had a relatively limited effect on shallow-water taxa in the tropical Indo-Pacific compared with the Atlantic (Malaquias & Reid, 2009; Palero et al., 2017; Vermeij, 2001; Williams & Duda, 2008). However, in the deep-sea genera *Paramunida* (Cabezas et al., 2012) and *Leiogalatheia*, speciation, likely associated with the progressive cooling of the deep-sea bottom (Davis et al., 2017), appears to have been promoted during the Pliocene, as has been observed in other deep-sea invertebrates [e.g. deep-sea barnacles (Herrera et al., 2015) or yeti crabs (Roterman et al., 2018)]. Moreover, geographic isolation due to drastic changes in sea level (for instance, after the climatic changes in the Late Pleistocene) could have had a greater impact on reef fauna (Gaither et al., 2011) than on deep-sea fauna, in which processes related to water chemistry, temperature, nutrients and dispersal method might have been more influential for speciation (Ritchie et al., 2015). For instance, differences in dissolved oxygen levels seem to affect the composition and the vertical distribution of squat lobsters in the Gulf of California (Hendrickx & Serrano, 2014). Therefore, hypoxic and anoxic zones might

have acted as vertical barriers, generating isolation and ultimately speciation. In line with this hypothesis, branch lengths in a previously published phylogenetic reconstruction seem to be different among shallow- and deep-water squat lobsters (Rodríguez-Flores, Macpherson, Buckley, et al., 2019b). Diverse coalescence times or distinct rates of evolution in deep-sea versus shallow-water taxa may account for these differences since barriers to gene flow, dispersal pathways and selective pressures are highly dissimilar in both environments (McClain & Hardy, 2010). Comprehensive studies of how bathymetry affects evolutionary rates are still needed to establish which of these hypotheses are best supported.

Given the distribution overlap of these genera, the fact that their major centres of diversification coincide may not be surprising; however, there are slight geographic differences. For instance, only *Leiogalatheia* presents extant Atlantic species, although there is one fossil species of *Sadayoshia* from coral reefs in the Western Tethys (Late Eocene; Müller & Collins, 1991), which might support also a Tethyan ancestral area for the genus, as in other squat lobsters (Ahyong, Schnabel, & Macpherson, 2011). For *Leiogalatheia*, the Tropical Southwestern Pacific, specifically New Caledonia, constitutes its major current centre of diversity, similar to the shallow-water genera *Lauriea*

and *Sadayoshia* (Palero et al., 2017). *Coralliogalatea*, on the other hand, seems to have its main centre of diversity in the Eastern Coral Triangle (Rodríguez-Flores, Macpherson, Buckley, et al., 2019b), and *Paramunida* in the region that includes Fiji, Tonga, Vanuatu, and Wallis and Futuna Islands (Cabezas et al., 2012). However, the distribution range of *Paramunida* is restricted to shelves and slopes between 200 and 700 m around islands and continents in the CIP and the EIP (Cabezas et al., 2012). Furthermore, whereas generally *Paramunida* species appears narrowly distributed, the rest of the genera present widely distributed species, often with extensive bathymetric ranges [e.g. *Leiogalatea ascanius* (Figure 3) or *Sadayoshia lipkei* (Macpherson & Baba, 2012)]. Therefore, there are likely limitations to dispersal for *Paramunida* that could act as a promoter of rapid speciation (Cabezas et al., 2012). We conclude that the historical biogeography of squat lobster species and species-dependent factors such as local adaptation and dispersal capacities are the major drivers of current distribution patterns. However, the deep sea is, to a certain degree, dynamically associated with the same processes affecting the surface (Levin et al., 2001) and, therefore, deep-sea and shallow-water squat lobsters are also similarly affected by the same historical processes.

Extinction and geographic persistence of lineages must be considered more accurately in these kind of inferences (Crisp et al., 2011). As such, we must consider the limitations of our interpretation of the results: (a) the lack of a fossil record for *Leiogalatea* limits the accuracy of the molecular clock calibration and hinders the inference of more accurate speciation/extinction rates; (b) sampling is biased towards the New Caledonia (or SW Pacific) region (Bouchet et al., 2008; Richer de Forges et al., 2013) (though other squat lobster genera such as *Paramunida* and *Coralliogalatea* show different diversification centres despite greater sampling of this area; Cabezas et al., 2012, Rodríguez-Flores, Macpherson, Buckley, et al., 2019b); and (c) we cannot discard other factors that could affect our biogeographic reconstructions including extinction of lineages from the Eastern Pacific (or from the Western Indo-Pacific), incomplete geographic sampling, or the existence of undescribed species from this and other under-sampled areas (see Baba, 2018; Baba & Wicksten, 2019; Rodríguez-Flores, Macpherson, & Machordom, 2019a). The historical biogeography of most deep-sea invertebrates is still a conundrum. However, the reconstruction we have presented here was based on the most comprehensive taxonomic and geographic sampling performed to date of any circum-tropical, deep-sea invertebrate, and thus, is expected to serve as an invaluable baseline study for future research.

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### 10 SUPPORTING INFORMATION

11 Additional supporting information may be found online in  
12 **3** the Supporting Information section.

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