

Depth as a driver of evolution and diversification of ancient squat lobsters (Decapoda, Galatheaidea, *Phylladorhynchus*)

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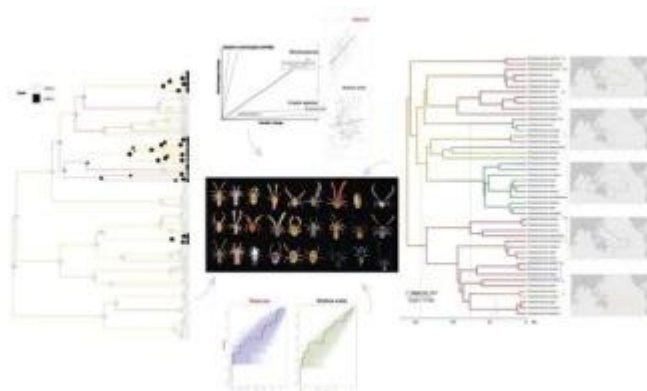
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Abstract :

The exceptional hidden diversity included in the squat lobster genus *Phylladorhynchus* and its wide bathymetric and geographic range make it an interesting group to thoroughly study its evolutionary history. Here we have analyzed the entire currently known species diversity of *Phylladorhynchus* using an integrative approach that includes morphological and molecular characters. The aim was to establish whether depth range (bathymetry) has played a role in their morphological and molecular evolution and in their diversification pathways. Phylogenetic analyses recovered the genus as monophyletic and as the sister group of *Corallioagalathea*, conforming with current systematic hypotheses, although their placement in a monophyletic Galatheaidea is doubted. All the analyzed species represent well-supported lineages, structured in ten clades, correlated in most part with the morphological phylogeny. The reconstruction of ancestral habitat showed that the most recent common ancestor of *Phylladorhynchus* most likely lived in shallow water environments. The divergence time estimation analyses dated the origin of the genus back to the Upper Jurassic, preceding the origin of all the other galatheid lineages. Morphological analyses suggested that species from deeper waters exhibit greater morphological divergences and lower genetic divergences in comparison to species from shallower waters. In *Phylladorhynchus*, the colonization of deeper waters has taken place independently multiple times since the Lower-Cretaceous. Our reconstruction of ancestral habitat suggests that shallow waters ancestors might show an acceleration in the molecular rate of evolution in comparison to deep sea lineages, and a slowdown in the rates of

morphological evolution. However, although lineages from shallow and deep sea habitats show slight differences in diversification trends, bathymetry does not significantly affect the diversification rate in *Phylladorhynchus* according to our diversification analyses.

Graphical abstract



Highlights

► The known diversity of *Phylladorhynchus* recently increased from five to 55 species. ► Multilocus and morphological phylogenies were inferred based on all known *Phylladorhynchus* diversity to test the effect of depth on the evolution and diversification of the genus. ► Our phylogenetic reconstruction showed that the sister group of *Phylladorhynchus* is *Coralliogalatea* and this clade is not closely related to other Galatheidae. ► Ten morphologically well-delimited clades are identified within the genus. ► The ancestor of the genus originated in shallow water during the Upper Jurassic and independently colonized deeper waters during diversification. ► Shallow water species present a slowdown in the morphological evolution and a higher molecular substitution rate in comparison with deep-sea species. ► Depth does not significantly affect the diversification of *Phylladorhynchus* in terms of speciation and extinction rates ► Deep-sea species of *Phylladorhynchus* tend to be sympatric whereas shallow water species present allopatric distributions

Keywords : Bathymetry, macroevolutionary analyses, Crustacea, fossil calibration, morphological evolution, substitution rate

1. INTRODUCTION

The effect of depth on biological adaptations and diversification in the oceans remains the subject of many studies. A number of authors have explored deep sea speciation, phylogenetic relationships of invertebrates from the coast to the abyssal plains, and the patterns and directions of colonization (Jacobs and Lindberg, 1998; Faure et al., 2009; Raupach et al., 2004, 2009; Lidner et al., 2008; Osborn et al., 2012; Pante et al., 2012; Thuy et al., 2012, Prada and Hellberg, 2021). Many studies on the evolution of marine invertebrates have centered on the origin of deep sea taxa, the horizontal barriers affecting speciation and the timing of cladogenesis (e.g., Cabezas et al., 2012; Lins et al., 2012; Priede and Froese, 2013; Eilertsen and Malaquias, 2015; Herrera et al., 2015). The overall results suggest a main path of colonization of deep sea fauna from the shallow to the deep ocean and a timing of these events during the Upper Mesozoic or Lower Cenozoic (Jablonski and Bottjer, 1990, McClain and Hardy, 2010; Thuy et al., 2012). Only a few studies have explored the effect of the depth in the morphological evolution of marine invertebrates (e.g., Rex and Etter, 1998; McClain et al., 2004; McClain, 2005) and compared the rates of diversification between deep sea and shallow water environments (O'Hara et al., 2019; Modica et al., 2020).

Squat lobsters can be excellent biological models to study the evolution and adaptation in both the shallow and the deep sea. They are extremely diverse, including more than 1300 species and occur down to abyssal depths across all oceans (Baba et al., 2008; Schnabel et al.,

2011a; Baba, 2018, Schnabel, 2020). They constitute an old group, with a crown age dating back to the Middle Jurassic followed by a radiation that co-occurred with brachyuran decapods during the Upper Jurassic (Schweitzer and Feldmann, 2010; Robins et al., 2012).

Representatives of all currently known galatheoid families appeared in the fossil record during the Mesozoic, also including other extinct families (Robins et al., 2013, 2016; Robins and Klompmaker, 2019). The squat lobsters of the superfamily Galatheoidea Samouelle, 1819 are the most diverse and include three morphologically, genetically and ecologically distinct families: the family Galatheidae Samouelle, 1819 includes mostly shallow water species; species of the family Munididae Ahyong, Baba, Macpherson & Poore, 2010 are predominantly found in the continental shelf and slope; finally, the species of the family Munidopsidae Ortmann, 1892 are usually found in bathyal and abyssal environments (Schnabel et al., 2011a). In the last decades, molecular studies have identified an origin of diversification in shallow water squat lobsters during the Paleocene-Eocene (Palero et al., 2017; Rodríguez-Flores et al., 2018) and rapid radiation in the Miocene was observed in deep sea genera (Machordom and Macpherson, 2004; Cabezas et al., 2012; Rodríguez-Flores et al., 2020). However, differences in trends of diversification between shallow and deep- lineages remain under-investigated (Rodríguez-Flores et al., 2020).

Previous approaches have led us to hypothesize the effect of depth transitions of species distributions on the evolution of squat lobsters (Schnabel et al., 2011a; Rodríguez-Flores et al., 2018, 2020). (1) *Environmental change can affect rates of molecular and morphological evolution*: if rates of morphological and molecular evolution are decoupled, they can produce high phenotypic plasticity within species, for instance after ecological adaptation (Wagner et al., 2012). On the other extreme, a slowdown or lack of morphological change among the evolutionary units, while presenting high genetic divergences can result in cryptic species (Struck et al., 2019) (Fig 1A). Shallow water squat lobsters are mostly characterized by their smaller size and there is a tendency of character miniaturization, cryptic diversity, and a low morphological diversity (e.g., genera *Lauriea* Baba, 1971, *Galathea* Fabricius, 1793, *Sadayoshia* Baba, 1969 and *Coralliogalathea* Baba & Javed, 1974) (Schnabel et al., 2011a; Macpherson and Robainas-Barcia, 2013, 2015; Macpherson and Baba, 2012; Rodríguez-Flores et al., 2018). Moreover, those shallow water lineages seem to exhibit longer branches in phylogenetic trees compared to deep sea taxa (Rodríguez-Flores et al., 2018). However, longer branches could be an effect of the antiquity of the lineages with significant extinctions, and morphological stasis seems to be a tendency within the whole Galatheoidea, since it is also

observed in deep sea species (Machordom and Macpherson, 2004). (2) *Environmental colonization (shallow vs. deep) could affect diversification (cladogenesis)*: McClain and Schlacher (2015) suggested that the long-term stability in deep habitats could increase the diversification rate through fine-niche partitioning. They propose that diversification rates and cladogenesis could increase with depths, which may result in decreasing average genetic and taxonomic distances between deep lineages (McClain and Schlacher, 2015). Therefore, if depth has a direct effect on the diversification rate, differences in the parameters of net diversification, extinction (μ) and speciation (λ) among species from shallow vs. deep waters, would be expected (Fig 1B). (3) *Depth distribution can influence geographic lineage ranges and geographic speciation patterns*: colonization of deeper waters may be expected to shape current ranges of vertical or horizontal distribution, as species from deeper waters are expected to present wider geographic ranges (McClain and Hardy, 2010), which may be the result of changes in dispersal patterns, isolation by distance, vicariance or sympatric speciation. These hypotheses remain to be tested in squat lobsters by including morphological/molecular change quantification and diversification analyses of closely related species across a range of depths. In contrast to most other genera, the diverse genus *Phylladorhynchus* is well suited to this approach. Until very recently, the genus included only 5 species (Baba, 1991; Baba et al., 2008). After the revision of material collected in the last decades, more than 40 new species have been described in the past three years (Schnabel and Ahyong, 2019; Rodríguez-Flores et al., 2021). *Phylladorhynchus* currently contains 55 species with representatives from the intertidal zone to more than 1000 m depth. The genus is distributed throughout the tropical and sub-tropical Indian and Pacific oceans (Fig 1C), with many species from shallow water coral reefs, living in dead coral rubbles, and several others from the continental shelf and slope (Miyake and Baba, 1965, 1966; Fujita, 2007; Baba et al., 2008, 2009; Dong and Li, 2013; Lee et al., 2019a; Schnabel and Ahyong, 2019; Rodríguez-Flores et al., 2021). Their body-size range is small, between 1.0 and about 7.0 mm of carapace length (Schnabel and Ahyong, 2019; Rodríguez-Flores et al., 2021). The highest latitudinal records are in New Zealand in the south, and Korea and Japan in the north (Lee et al., 2019a; Schnabel and Ahyong, 2019). The genus also includes high regional diversity and endemism but also a few broadly distributed species (Schnabel and Ahyong, 2019; Rodríguez-Flores et al., 2021). The diversity of *Phylladorhynchus* includes some species that are barely distinguishable using morphological characters but presenting high genetic distances (Schnabel and Ahyong, 2019; Rodríguez-Flores et al., 2021). Therefore, the morphological and genetic diversity, and their bathymetric,

and geographic distributions, make it an ideal group for detailed study of the evolution in shallow versus deep habitats.

In this study, we present the first phylogeny of the diverse squat lobster *Phylladorhynchus*. We analyze six (mitochondrial and nuclear) gene sequences and morphological characters for all *Phylladorhynchus* species inhabiting the different Indo-Pacific biogeographical provinces, from East Africa to French Polynesia and Hawai'i, and using comparative macroevolutionary phylogenetic methods, to test the previously proposed three hypotheses related with the environmental change. We aim to explore (1) the systematics and phylogenetic relationship within Galatheoidea, including the timing of diversification of the genus, (2) the patterns of inshore/offshore colonization during their evolutionary history, (3) the potential effect of depth in their molecular, morphological evolution and (4) in their diversification patterns (speciation and extinction); and (5) to discuss the relation between depth with geographic lineage range and the speciation patterns.

2. MATERIAL AND METHODS

2.1. Sampling and data collection

The material studied here is deposited in the following scientific museum collections: Muséum national d'Histoire naturelle, Paris (MNHN), National Institute of Water and Atmospheric Research, Wellington (NIWA), Florida Museum of Natural History, Florida (UF), Western Australian Museum, Perth (WA), National Taiwan Ocean University, Keelung (NTOU), National Museum of Marine Biology & Aquarium, Pingtung (NMMB), Museum of Evolution of Uppsala University, Uppsala universitet Evolutionsmuseet (UPSZTY), and National Museum of Natural History of the Smithsonian Institution (USNM). Specimens in these collections were collected from the Indian and Pacific oceans over the course of deep sea cruises and biodiversity surveys carried out by different institutions (e.g., Biodiversity surveys operated by MNHN under the exploration program "Our planet reviewed"), from the intertidal zone (0 m) to bathyal depths (1261 m). Shallow waters specimens were collected by scuba diving using different tools and procedures such as dead coral brushing, vacuum cleaning, hand-picking, or they were retrieved from previously deployed Autonomous Reef Monitoring Structures (ARMS). Specimens from the continental shelf and slope were collected by dredging and trawling and by retrieving previously deployed tangle nets. The examined material,

collection data and its sources are detailed in Schnabel and Ahyong (2019) and in Rodríguez-Flores et al. (2021).

Morphological characters were analyzed for a total of 55 species of *Phylladiorhynchus* from the Pacific Ocean (Chile, Hawaii, French Polynesia, Kiribati, Mariana Islands, American Samoa, Japan, Philippines, Taiwan, New Caledonia, New Zealand, Queensland, Indonesia, Papua New Guinea, Vanuatu, Chesterfield Islands) and from the Indian Ocean (Western Australia, Chagos Archipelago, Reunion Island, Comores and Mayotte Islands, Madagascar and Walters Shoal and Red Sea) (Fig. 1C). Except for *Phylladiorhynchus bengalensis* Tirmizi & Javed, 1980, a rare species collected from the Gulf of Bengal and known only from the broken holotype, and *Phylladiorhynchus ikedai* (Miyake & Baba, 1965), morphological data was extracted from the examined museum specimens by either direct visits or on loan. Morphological data of *P. bengalensis* and *P. ikedai* was obtained from the original descriptions (Miyake and Baba, 1965; Tirmizi and Javed, 1980). The methodology for collecting morphological data and morphometric measurement of each specimen follows Rodríguez-Flores et al. (2021). After the examination of this material (more than 2000 specimens), 280 specimens were selected for genetic analyses.

We collected depth data from each examined lot (including one or more specimens) that had an associated station with depth values recorded at the time of the collection event. Those collection events included data from research vessel operations (dredge, trawl) or depth registered by divers at the station where the specimen was collected. Depth data here analyzed is reunited in Table S1, and the whole station data of the examined material can be found in Rodríguez-Flores et al. (2021) and Schnabel and Ahyong (2019). For each species we calculated: a) the bathymetric range, i.e., the maximum and minimum depths where specimens of a given species were collected, and b) the median depth. In some stations depth was measured as a range of maximum and minimum depths of the collection event (e.g., the depth when the dredge is cast and deployed or at the beginning and the end of the dive) or by a single value (sampling at constant depth). When depth was measured as a range, the mean of these values was calculated, but only when the difference between the minimum and maximum depths at a given sampling station did not exceed 200 m. Those stations with a depth range difference higher than 200 m were not considered for the calculation of the median depth of the species. The mean values of each station were used to calculate the general median bathymetric depth of a given species using the formula $(n+1) / 2$ in Microsoft Excel (2021). When stations were sampled at constant depth, the same depth value was considered as the

mean value (in most shallow water stations). Some species were represented by a singleton, and in this case the median depth is represented by the unique known value or the median value of the minimum and maximum depth of the station. This procedure was repeated for the total of 730 sampling stations (Table S1).

2.2. Molecular laboratory and sequence processing

We obtained molecular data from around 175 specimens corresponding to 47 species (83% of the known diversity) of *Phylladorhynchus*, with an extraction success of about 65%. The partial genes here employed were selected based on their resolution for species delimitation, their capacity to resolve deep or ancient nodes, their availability in databases for further comparisons with other taxa and their demonstrated utility with Decapoda (e.g., Bracken-Grissom et al., 2013): mitochondrial cytochrome c oxidase subunit one (COI) and 16S rDNA (16S), and the nuclear DNA 18S rDNA (18S), 28S rDNA (28S), histone H3 (H3) and phosphoenolpyruvate carboxykinase (PEPCK).

The methodology implemented in the laboratory for DNA extraction, amplification and purification follows previous studies (Rodríguez-Flores et al., 2018, 2019a, b, 2020), using both published and newly designed primers (Table S2). Sanger sequencing of the amplicons was performed by Secugen (Madrid). Both strands of DNA sequences were revised using Sequencher v.4.8 (Gene Codes Corporation). Ribosomal gene sequences were aligned with MAFFT (Kato et al., 2002), using the iterative method L-INS, which is recommended for sequences with one conserved domain and long gaps, like the genes here analyzed, especially the 28S. A posterior manual checking and correction of the alignments was carried out in AliView (Larsson, 2014). Coding genes were aligned manually after checking for pseudogenes using the online tool Expasy (<https://web.expasy.org/translate/>) considering the invertebrate mitochondrial genetic code. The matrix was built with all concatenated genes in PAUP v.4.0a (build 169; Swofford, 2002) and included a total of 4667 molecular characters including gaps.

2.3. Molecular phylogenetic analyses

To provide phylogenetic context of *Phylladorhynchus* within the wider Galatheaidea phylogenetic framework we included outgroups from all families of galatheid squat lobsters. According to previous data, genetic distances among species of *Phylladorhynchus* largely surpass those found for species from different genera and even different families (see Schnabel and Ahyong, 2019; Rodríguez-Flores et al., 2021). Therefore, we designed the taxonomic

sampling aimed to test (a) the monophyly of the genus *Phylladiorhynchus* and (b) its phylogenetic position among other galatheoidean squat lobsters. In the analyses, we included data from 31 other squat lobsters of the families Galatheidae (*Alainius* Baba, 1991, *Allomunida* Baba, 1988, *Allogalatea* Baba, 1969, *Coralliogalatea*, *Fennerogalatea* Baba, 1988, and several species of *Galatea*), Munidopsidae (*Galacantha* A. Milne Edwards, 1880, *Leiogalatea* Baba, 1969, and *Munidopsis* Whiteaves, 1874), and a wide taxonomic sampling of Munididae, considering the polyphyly of *Munida* Leach, 1820 and the evolutionary units at genus level that are currently being delimited (Machordom et al., in prep). Munidid representatives include *Agononida* Baba & de Saint Laurent, 1996, *Anomoeomunida* Baba, 1993, *Babamunida* Cabezas, Macpherson & Machordom, 2008, *Crosnierita* Macpherson 1998, *Munida*, *Hendersonida* Cabezas & Macpherson, 2014, *Heteronida* Baba & de Saint Laurent, 1996, *Onconida* Baba & de Saint Laurent, 1996, *Paramunida* Baba, 1998, *Sadayoshia* Baba, 1969, and some independent lineages currently included under the name *Munida* sensu lato. A porcellanid crab [*Porcellana sayana* (Leach, 1820), Porcellanidae, Galatheoidea], was employed to represent the most closely related group of galatheoid squat lobsters (Palero et al., 2019) and the phylogenetic analyses were rooted with *Calcinus laevimanus* (Randall, 1840) (Paguroidea, Diogenidae). Details of the taxonomic sampling and the analyzed specimens for molecular analyses are in Table S3. Exploratory analyses were run to study the effect of distant outgroups in the topology/support of the ingroup: a) including only the ingroup with *Coralliogalatea* as outgroup, and b) removing *Calcinus laevimanus* and with *Porcellana sayana* as outgroup, in both cases conforming with recently proposed phylogenetic hypotheses (Palero et al., 2019; Rodríguez-Flores et al., 2018; Roterman et al., 2019).

Phylogenetic analyses were conducted using Bayesian Inference (BI), maximum likelihood (ML), and Bayesian time estimation by sampling trees using coalescence to obtain an ultrametric tree in BEAST v2.6.3 (Drummond and Bouckaert, 2014; Bouckaert et al., 2014) that will serve as input for further phylogenetic comparative methods. We explored the best partition scheme using the model selection finder tool in W-IQ-TREE (Trifinopoulos et al., 2016). The concatenated alignment of the six genes were used as input selecting the following parameters: Bayesian Information Criteria (BIC) and considering partition merging for those partition than may have the same model. We compared the best scheme with the results obtained with PartitionFinder v1.1.0 (Lanfear et al., 2012) and, considering both results, selected a scheme with six partitions, by gene, with models TIM+F+I+G4 (COI, 16S), GTR+F+I+G4 (H3, 18S), TIM3e+G4 (28S) and TIM2e+I+G4 (PEPCK). To estimate the

phylogenetic relationships and posterior probabilities in BI, two parallel runs of four Metropolis-coupled Markov chains Monte Carlo (MCMC) were run for 10^8 generations, sampling every 10,000 generations, in MrBayes v.3.2.1 (Ronquist and Huelsenbeck, 2003), employing a mixed model to average among substitution models. The first 25% of the trees were discarded as burn-in. The ML tree was inferred with W-IQ-TREE online v.1 (Trifinopoulos et al., 2016). Bootstrap support values were calculated with 1000 pseudoreplicates and the other parameters were set as default. Nodes were considered supported when bootstrap values were higher than 70 and posterior probability higher than 0.95. BI and ML analyses were carried out with all genes concatenated, with a previous exploration with BI for each gene partition to explore incongruences among markers.

An ultrametric tree was obtained with BEAST v2.6.3 in order to recover molecular substitution rates considering clock models that allow for rate variation among branches. We employed a partial dataset including three concatenated genes (COI, 16S and H3). This data subset was chosen to address difficulties during the amplification of large nuclear gene markers (due to DNA degradation) and these three markers presented the best representation of our sampling and minimized the overall impact of missing data in obtaining the molecular substitution rates. For the substitution model selection, we used the model averaging package bModelTest in BEAST2 (Bouckaert and Drummond, 2017) for selecting the best substitution model fitting our data set (Barido-Sottani et al., 2018). We ran and compared parallel analyses in BEAST2 in order to select the best clock model and best tree prior. We compared two clock models: a relaxed uncorrelated lognormal clock model (where every branch can have a different rate of evolution), and a random clock model (where only a limited series of local changes could be required) (Drummond and Suchard, 2010). Best tree prior was selected between a Birth–Death model and a Birth–Death Skyline Contemporary (Stadler et al., 2013). Clock rates values were set in $M=0.002$, $S=1.0$, for the 16S; $M=0.006$, $S=1.0$ for the COI and $M=0.0001$, $S=1.0$ for the H3 [rates obtained from previous studies on squat lobsters: Cabezas et al. (2012) and Rodríguez-Flores et al. (2018, 2020)]. Convergence of chains and Effective Size Samples (ESS) parameters were checked with Tracer 1.7.1 (Rambaut and Drummond, 2007; Rambaut et al., 2018). We selected the best model after a comparison of the marginal likelihoods with a Bayes factor test run in Tracer 1.7.1. MCMC were run for 10^8 generations, sampling every 10,000. The first 25% of the trees were removed as burn-in when building the Maximum Clade Credibility (MCC) tree with Tree Annotator v2.5.1 (Rambaut and Drummond, 2007).

2.4 Morphological analyses

A matrix including 46 morphological characters was built for all the currently known species of *Phylladiorhynchus* (55). The chosen outgroup for rooting the morphological tree was *Coralliogalatea humilis*, since *Phylladiorhynchus* and *Coralliogalatea* were proposed as related lineages according to morphological characters (Rodríguez-Flores et al., 2018). We performed morphological analyses in order to (a) determine the phylogenetic position of species that lack molecular data and (b) characterize morphological variation among species. Coding of the morphological characters included discrete characters with as many as four states per character. The matrix included different traits from the carapace and rostrum (e.g., dorsal ornamentation, presence of ridges, and numbers of spines, etc.), and traits from the appendages (pereopods, antennula, antennae and maxilliped) (Table S4). Morphological phylogenetic analyses were carried out with Maximum Parsimony with Tree analysis using New Technology (TNT) (Goloboff and Catalano, 2016) and compared with those results obtained through Bayesian estimation by sampling trees in BEAST2. For the TNT analyses the script a.quickie was employed but changing the number of parsimonious trees to 1,000 and setting “resample replications 200” for two hundred bootstrap replicates.

For the BEAST morphological analyses, we included the data as Markov k (Mk) data. Each partition was assigned a site model with the appropriate Lewis Mk substitution model with the package bModelTest. Gamma category count and Proportion Invariant were fixed to zero. MCMC were run for 2×10^6 generations sampling every 2,000.

2.5 Morphological and molecular change correlation with depth

We estimated phenotypic similarity among species using a morphological distance matrix. We only compared taxa from which we were able to obtain molecular data (47 species). Correlation between molecular and morphological differentiation was performed using comparisons between morphological and molecular divergences measured as p-distances computed with MEGA X (Kumar et al., 2018) and PAUP (142 *Phylladiorhynchus* specimens, Table S2). As a proxy of molecular change among species, we employed the gene marker COI since (a) it is the general marker used for species delimitation, showing increasing values of percentage divergences among different taxa at different hierarchical levels (saturation above genus level) and (b) it is also used for molecular divergence estimates with an assigned clock rate (Knowlton and Weigt, 1998); therefore, the marker p-distances could be also considered as

a measure of time of divergence. We test the following hypotheses: 0) there is no difference of morphological and molecular divergence with depth, 1) there is a correlation between morphological and molecular change in species from shelf depth compared to species from deeper slopes, 2) in shallow environments there is a predominance of cryptic species indicating a slowdown in the morphological rate of change compared to species from deeper (slope) depths. Therefore, we modeled the relationship between morphological and genetic distances in *Phylladorhynchus* using linear regressions among species from shelf/slope (18 species) and species from shallow waters (29 species) in R Core Team (2020) with the function `lm` (R Core Team, 2020). To avoid a confounding effect resulting in high morphological and molecular differences by comparisons of unrelated groups, we also compared the correlation among species within monophyletic lineages from shelf/slope and shallow waters. Graphics were plotted using the package `ggplot2` (Wickham 2011).

2.6. Species tree and divergence time estimation

We built a species tree with all six concatenated genes using StarBEAST2 (Heled and Drummond, 2010) in BEAST2, in order to obtain divergence time estimation and a single branch per species which presents all the biological and evolutionary information. Unfortunately, there are no known fossil *Phylladorhynchus* to calibrate the molecular clock. Therefore, we calibrated the molecular clock by including a complete taxon sampling of all galatheoid lineages, which allowed several points of calibration. The most ancient point was the crown age of the Galatheoidea squat lobsters, which is dated in the Bathonian, Middle Jurassic, with the first appearance of a squat lobsters: *Palaeomunidopsis moutieri* Van Straelen, 1925 (Robins et al., 2013, Van Straelen, 1925). The second point of calibration was the age of the crown group of Munididae *sensu stricto*, this is the age at the first appearance of fossils of Munididae sharing the Recent synapomorphies: *Cretagalathea exigua* Garassino, De Angeli & Pasini, 2008 from the Upper Cretaceous of southeastern Morocco (Garassino et al., 2008) with carapace ornamentation and cheliped morphology as in extant munidid species. The most recent point was a secondary calibration obtained from previous studies which estimate the split of *Hendersonida granulata* (Henderson, 1885) from the *Paramunida* species during the Oligocene (Cabezas et al., 2012) (Table S5).

The species tree was obtained following the methodology of Rodríguez-Flores et al. (2020). Before estimating divergence times, we first estimated the best partition scheme fitting the data with PartitionFinder v1.1.0 (Lanfear et al., 2012). We selected the prior ‘Analytical

population size integration' for the population model due to there was no need to estimate the population sizes for each species because our study was focused on species level. We selected bModelTest using 'TransitionTransversionSplit' and an uncorrelated relaxed log normal clock model for each partition. We also used a birth-death model for the tree prior. Mean substitution rates were estimated for each gene, for which we assigned non-informative priors for the substitution rates (gamma distribution setting values for alpha and beta parameters as 0.01 and 100, respectively). Log-normal distributions were chosen as temporal priors for the calibration points (mean=20, stdv=1, offset = 170) for the root of the tree; mean=10, stdv=1, offset = 92 for the MRCA of the Munididae *sensu stricto* group, and mean=1, stdv=1, offset = 30 for the MRCA *Paramunida-Hendersonida*. The Markov Chains Monte Carlo (MCMC) were run for 6×10^8 generations per run, and parameters were logged every 6×10^4 generations. BEAST2 analyses were run in the Cipres Science Gateway at <http://www.phylo.org> (Miller et al., 2011).

Convergence of the chains (trace and effective sample sizes, ESSs) was assessed in Tracer v1.7. The results were summarized and annotated in an MCC tree generated with Tree Annotator v2.5.1 after discarding the first 25% of the trees as burn-in. Species tree was plotted using the R packages ggtree (Yu et al., 2017; Yu, 2020), geoscale and strap (Bell, 2015; Bell and Lloyd, 2015).

2.7. Phylogenetic signal and ancestral character reconstruction

To investigate the habitat colonization of *Phylladiorhynchus*, we measured the phylogenetic signal of the continuous character "depth" with the R package *picante* to calculate K statistics, p -value and plot the phylogenetic signal (Blomberg et al., 2003; Kembel et al., 2010).

Blomberg's K statistic measures the phylogenetic trait signal after comparing the expected signal on a tree (considering both topology and branch lengths) with the signal under a Brownian motion model character evolution. When K is less than one, there is a tendency for less signal than expected (under Brownian motion) ($K \sim 0$, random or convergent pattern of evolution; $K = 1$ correspond to a Brownian motion process, $K > 1$, strong phylogenetic signal, and conservatism of traits) (Blomberg et al., 2003). The mapping of the continuous trait evolution for the character "depth" (the median depth of the trawl where the sequenced specimens were collected, coded in meters) was performed using the R package *phytools* and the plotting function *contMap* (Revell, 2012) with a previous tree pruning to remove the outgroups using the function *drop.tip* of the R package *ape* (Paradis et al., 2004).

We also treated the character “depth” as a discrete character (different habitat colonization), by converting it into a binary categorical trait with only two states (0, 1) corresponding to shallow waters or deep waters using a threshold in the bathymetric range set at 100 m depth. The selection of this depth threshold value generally corresponds on average to the limit between the photic/aphotic zones and agrees with several studies on marine invertebrates, such as gastropods (Modica et al., 2020 and references therein). The 100 m depth threshold is congruent with sampling strategy and gear/sampling method selectivity during Survey and deep sea cruises (Richer de Forges et al., 2013). Moreover, many of these squat lobsters are associated with coral reefs, which only occur down to ~100 m (Huston, 1985). For *Phylladiorhynchus* this depth marks the general boundary between shallow water taxa, which usually do not surpass this boundary, and outer shelf/slope taxa, which are always below this depth (Schnabel and Ahyong, 2019; Rodríguez-Flores et al., 2021).

The estimation of ancestral character states for the habitat colonization (depth) traits was carried out using a continuous-time Markov chain model (Mk). We performed ancestral character reconstruction analyses (ACR) on the calibrated ultrametric tree generated with BEAST2 using the R package phytools (Revell, 2012). The analysis was performed by fitting a single-rate model (model = ER, nsim = 1000, Q = mcmc) (Revell, 2012). We obtained the marginal ancestral states, called as 'empirical Bayesian posterior probabilities' and join these posterior probabilities on the ultrametric tree obtained with BEAST2 using the element lik.anc. We graphically compared the ancestral character reconstruction in the tree with the substitution rate obtained with BEAST2, to detect changes in the substitution rate associated with changes in the habitat colonization.

2.8. Trait dependent diversification analyses

The analyses of diversification estimates [rate of speciation equals speciation rate minus extinction rate ($r = \lambda - \mu$) and the extinction fraction or turnover ($\varepsilon = \mu/\lambda$)] were performed using the MCC species tree obtained with StarBEAST2 after pruning outgroups. To study the mode and tempo of diversification of *Phylladiorhynchus* we first use the R package TreePar (Stadler, 2011) following the procedure and criteria of López-Estrada et al. (2019). Since this method considers the effect of the incomplete taxon sampling on the tree topology and diversification, we used a factor of correction of the incomplete taxonomic sampling (85% of all species in the genus *Phylladiorhynchus*) considering the number of species for which we have no molecular information (eight of 55 species). In TreePar we used the function

bd.shifts.optim to identify shifts or changes in the rate of diversification at particular points in time. We estimated the *Phylladorhynchus* overall diversification rate under a simple Birth-Death model (BD), a Pure-Birth or Yule model (PB), and PB and BD models including variations/shifts in the diversification rate in one and two discrete points in time: yule 1-rate, yule 2-rate, birth-death 1-rate, birth-death 2-rate (Y1r, Y2r and B1r, B2r respectively). We also tested another model that predicts slowdowns in the tempo and mode of diversification, density-dependent model (DDD). We also used the function fitdAICrc of the package LASER (Rabosky, 2006) to compare the results obtained with TreePar and compared here also density-dependent exponential and density-dependent logistic models (DDX and DDL).

We conducted hypothesis-testing by the Likelihood Ratio Test (LRT) to estimate if the diversification rates are dependent on a particular trait (depth) using the Binary State Speciation and Extinction model (BiSSE model, Maddison et al., 2007) in the R package diversitree (FitzJohn, 2012). We aimed to test whether depth was associated with higher speciation rates by constraining a model to have equal speciation rates ($\lambda_1 = \lambda_0$) and to enforce equal speciation rates to be equal across character states ($q_{10} = q_{01}$). We first specified the sampling fraction for each character state (0.9 for shallow species and 0.7 for deeper species). Constrained and full unconstrained models were compared based on their fit to the data (as indicated by the AIC values) using the function anova in diversitree, which also indicates whether the difference in fit is significant or not. The analysis was run with MCMC for 10,000 generations for the unconstrained model. The probability density distribution of each character dependent parameter were obtained with the function profiles.plot.

Last, we reconstructed Lineage Through Time plots (LTT) from the MCC species tree to observe the pattern of diversification and the null model assuming constant speciation (pure birth). We then simulated 1000 trees under a pure birth model with the pbtree function in phytools and plotted the LTT of the simulated trees joined with the LTT of the MCC tree. The estimation of speciation and extinction rates with birth-death models were performed by using the function bd also with phytools.

3. RESULTS

3.1. Phylogeny of *Phylladorhynchus* and its placement in *Galattheoidea*

All phylogenetic analyses recovered families Galatheidae and Munididae as polyphyletic groups (Fig. 2, Fig. S6). *Phylladorhynchus* + *Coralliogalatea* are united in a well-supported

clade at the crown of the tree. Presumed galatheid genera were recovered in three highly divergent well-supported lineages and with no common ancestor: *Phylladorhynchus* + *Coralliogalatea*, *Alainius* lineage, and the clade constituted by the other genera (i.e., *Galatea*, *Fennerogalatea*, *Allogalatea*).

Therefore, the supported relationships at galatheoid lineage level were the following: 1) Munidopsidae was recovered as sister group of all the rest of galatheoids, excluding Porcellanidae 2) the *Alainius* clade formed the basal lineage of a clade including most galatheid genera (except for *Coralliogalatea* and *Phylladorhynchus*) which was sister to a munidid clade, in turn sister to *Phylladorhynchus* + *Coralliogalatea* + *Anomoeomunida*. These relationships were all supported by posterior probabilities (pP) > 0.95 and bootstrap support (bs) >70.

Our results also revealed *Phylladorhynchus* as monophyletic with consistent support across all analyses, and *Coralliogalatea* as its sister group with high support. Bayesian probability and bootstrap support were generally high (pP > 0.9, bs > 70) for both deep and recent nodes. The deletion of distant outgroups did not change the overall topology for the ingroup, but the simplest analysis (including *Coralliogalatea* as the only outgroup) showed higher bootstrap support (Fig. S7). A total of 47 highly supported molecular lineages and 55 morphological lineages were recovered, corresponding to species of *Phylladorhynchus* delimited in Schnabel and Ahyong (2019) and Rodríguez-Flores et al. (2021) (Fig. 2). Diversity of *Phylladorhynchus* appeared structured in 10 different clades (Groups I–X) all highly supported for all performed phylogenetic analyses (Fig. 2). Morphological and molecular relationships mainly presented congruence at clade level, although differed in deep relationships (among clade relationships) and within clade relationships. These 10 clades were all highly genetically divergent, even showing greater distances than those found between families the Galatheidae and Munididae. All shared a particular combination of synapomorphies that are clade-specific, listed below.

Clade I (Fig. 2A) consisted of a group of species belonging to the *ikedai*-group, with morphology close to *P. ikedai* (Miyake and Baba, 1965): having the epigastric ridge usually armed with 4–5 epigastric spines, a triangular rostrum with smooth margins usually lacking subapical spines, a carapace dorsally flattened or slightly convex without intermediary ridges and two spines on flexor margin of third maxilliped merus. It constituted several subclades, the first one comprised *P. acastus*, *P. argus*, *P. paula*, *P. kermadecensis* and *P. punctatus*. The second subclade is constituted by *Phylladorhynchus cepheus* + *P. maestrati* with *P. butes* as

sister. *Phylladorhynchus erebus* and *P. boucheti* were clustered together as sister group of the previous subclades. The latter species were characterized by the number of spines on the branchial margin of the carapace. Moreover, the clade I *ikedai* included a subclade (called *ikedai-2*) containing species with five epigastric spines, globose carapace, and upraised ridges on carapace: the small pair of species *P. koumac* + *P. pulchrus* sister to the pair of species *P. eneus* + *P. heptacanthus*. The sister group of this clade was a lineage constituted by a rare species: *P. iphichus*, the only species of the group having 2 epigastric spines. Due to these differences in morphological characters, the morphological phylogenetic inferences did not recover the clade *ikedai-2* as a subclade of the *ikedai*-group but resolved it as an independent lineage. Species lacking molecular data (*P. ikedai*, *P. idas* and *P. bengalensis*) were clustered with the remaining clade I *ikedai* species, sharing the synapomorphies of the rest of the species of the group (Fig. 2B).

Clade II (*integrivostris*-group 2) contained a group of species with two epigastric spines, leaf-like rostrum with small to obsolescent subapical spines, a minute hepatic spine, three spines on anterior branchial margin, metagastric ridge in dorsal carapace surface scale-like and one spine on flexor margin of third maxilliped merus. Two pairs of sibling species comprised the clade: *P. janiqueae* + *P. medea* (with poor support) clustered to the well-supported subclade *P. zetes* + *P. tiphys* (Fig. 2A). These relationships were mirrored in the morphological tree clade, considering the low support clustering *P. medea* + *P. janiqueae* (Fig. 2B).

Clade III (*integrivostris*-group 3) contained three species having a leaf-like tridentiform rostrum, with subapical spines well developed, rostrum margins serrated, hepatic spine present and three spines on anterior branchial margin and one spine on flexor margin of third maxilliped merus (Fig. 2A). Morphological analyses did not support the inclusion of *P. talaus*. In turn, it united *P. serrivostris* Melin, 1939 as species belonging to the clade, supported by the presence of strongly serrated rostrum and well-developed subapical spines (Fig. 2B). We were not able to obtain molecular data for *P. serrivostris*.

Clade IV consisted of a group of species belonging to the *integrivostris*-4 group, characterized by having a leaf-like rostrum with subapical spines obsolescent or absent, usually two epigastric spines, two spines on anterior branchial margin, plumose setae on pereopods and one spine on the flexor margin of the third maxilliped merus (Fig. 2).

Clade V (*pusillus*-group) included the genus type species *P. pusillus* (Henderson, 1885) and its sister species *P. poeas*, both species considered as pseudocryptic species (Fig. 2A).

Morphological analyses also included other species in this cluster that we were not able to amplify but present morphological affinities to *P. pusillus*: *P. porteri*, *P. lenzi* and *P. triginta* united these species with this group (Fig. 2B). The *pusillus*-group is characterized by the typical presence of a leaf-like rostrum with small subapical spines, usually four spines in the epigastric ridge (except for *P. triginta*) and three spines on the anterior carapace margin. However, among the species within the clade, allometric variation in the epigastric spines exists (from two to six spines).

Clade VI or true *integrivostris*-group contained a group of four species that included *P. integrivostris* (Dana, 1852) and related species characterized by the presence of a leaf-like rostrum with small subapical spines, margin serrated, hepatic spine absent, two spines on anterior branchial margin, usually iridescent setae on carapace like and one spine on flexor margin of third maxilliped merus (Fig. 2A). Identical relationships were recovered in the morphological tree (Fig. 2B).

Clade VII or *nudus*-group consisted of small species characterized by having the epigastric ridge on the carapace unarmed, usually a leaf-like rostrum, carapace globose with uplifted ridges, dactylar spines on walking legs, sexual dimorphism with females more robust than males and two spines on flexor margin of third maxilliped merus. The group contains cryptic species, with a clade that included sibling species, *P. phanus* and *P. marina*, and with *P. jeffkinchi* as sister of this species pair. *Phylladorhynchus phlias* was recovered as sister of this subclade and with *P. nudus* Macpherson, 2008 as the sister lineage of the rest of the species (Fig. 2A). These relationships were recovered in the morphological tree (Fig. 2B).

Clade VIII, the *spinosus*-group, consisted of four species having a dagger-like rostrum, carapace with secondary ridges, third sternite with a blunted median projection, dactylar spines on walking legs, and one spine on flexor margin of the third maxilliped merus (Fig. 2A). The morphological tree supported the relationships between *P. spinosus* Schnabel & Ahyong, 2019 + *P. asclepius* as sister to the pair *P. lini* + *P. euryalus* (Fig. 2B).

Clade IX (*integra*-group) comprised medium-sized species: *P. integrus* (Benedict, 1902), *P. australis* and *P. nui* (both Schnabel & Ahyong, 2019). This group was characterized by having leaf-like or dagger-like rostrum, four epigastric spines, biconcave third sternite and one spine on flexor margin of the third maxilliped merus. Internal relationships were not clear or poorly unsupported by the molecular data (Fig. 2A), and internal relationships between species varied slightly in the proposed morphological tree (Fig. 2B).

Clade X (*integrastrostris*-group 5) included two sibling species (*P. joannotae* and *P. amphion*) characterized by having an unarmed epigastric ridge on the carapace, a leaf-like rostrum with small subapical spines, carapace globose with uplifted ridges, dactylar spines on walking legs, sexual dimorphism with females more robust than males and one spine on flexor margin of third maxilliped merus. The morphology tree identified this clade with strong support (Fig. 2B).

Concerning the molecular relationships among these clades, group I was recovered as sister of the other clades, clades II–VI formed a group, which was sister lineage to the group containing clades VII–X, each with high support. Whereas internal phylogenetic relationships among the cluster containing clades II–VI were mostly unresolved, relationships among clades VII–X were well supported: the clade VII (*nudus*-group) and clade VIII (*spinosus*-group) were clustered together, the *integra*-group (clade IX) was sister to this group and the clade X or *integrastrostris*-5 was recovered as sister of the others.

3.2. Morphological and molecular change correlation with depth

Our results of the simple linear regression among morphological and molecular evolution in *Phylladiorhynchus* indicated correlation in species from both deep vs. shallow waters: p -values $2.779 \cdot 10^{-13}$ and 0.01933 ; slope (b) 0.35951 and 0.08935 respectively (Fig. 3). However, the regression slope became much steeper in *Phylladiorhynchus* from the continental shelf and slope than in shallow species, showing a more positive correlation. When considering only comparisons among species within clades, this correlation became more significant in species from shelf/slope (p -value = $6.55 \cdot 10^{-16}$, $b = 0.39615$) and not significant in shallow species (p -value = 0.05896 , $b = 0.49264$). Average values of morphological distances were higher in deep sea species whereas average genetic distances were higher in shallow water species, also in the cases comparing species within lineages (Fig. 3).

3.3. Species tree and time divergence estimation

Each gene partition was treated separately to build the species tree according to the results of the PartitionFinder. The time to the most recent common ancestor (tMRCA) of *Coralliothaltea* and *Phylladiorhynchus* was at 183.27 million years ago (Ma) during the Toarcian, Lower Jurassic (95% HPD: 212.68–159.61). The origin of the genus *Phylladiorhynchus* was estimated at 157.96 Ma (95% HPD: 185.43–134.26), at the transition of the Oxfordian and the Kimmeridgian during the Upper Jurassic. The origin of the genus

preceded the origin of a clade including all the other galatheid lineages (143.72 Ma; 95% HPD: 176.18–113.20) and the origin of all galatheid genera analyzed (Fig. 4). The split of the *ikedai*-group from other lineages of *Phylladorhynchus* was estimated in the Lower Cretaceous at 130.28 Ma (95% HPD: 156.13–106.59). Subsequently, the *nudus* clade started diversifying in the Turonian (Upper Cretaceous), placed at 90.95 Ma (95% HPD: 112.42–69.32). The tMRCA of the true-*integrivostris* was placed at the end of the Campanian (Upper Cretaceous), 74.82 Ma (95% HPD: 102.62–52.08). Clade III (*integrivostris*-3) has an origin of diversification dated back to the Paleocene at 64.87 Ma (95% HPD: 86.09–42.51), with a subsequent split of the lineage to form *P. pollux* and *P. peneleos* at 58.63 Ma (95% HPD: 80.66–33.32). The tMRCA of several of the *Phylladorhynchus* lineages were placed at the Oligocene, in the Chattian: *integrivostris*-2 (clade II), 27.11 Ma (95% HPD: 38.42–16.92), *spinusus*-group (clade VIII), 26.70 Ma (95% HPD: 40.38–15.65); *integrivostris*-5 group (clade X) 26.67 Ma (95% HPD: 44.24–11.13); followed by the diversification of the *integra*-group (clade IX) (17.36 Ma, 95% HPD: 24.16–10.51), and the most recent split of the *P. pusillus* + *P. poeas* (clade V) at the Miocene, Tortonian, with an estimate age of 8.40 Ma (95% HPD: 15.88–1.75) (Fig. 4).

3.4. Phylogenetic signal of the habitat, molecular substitution rate and ancestral reconstruction of the depth

We obtained a Blomberg's K statistic = 0.7 for the bathymetry in *Phylladorhynchus*, indicating that the observed signal in the depth can be fit in a Brownian motion model of trait evolution on the phylogeny but have a certain convergent pattern of evolution. We also obtained a PIC.variance.P (p -value of observed vs. random variance of phylogenetic independent contrasts) = 0.001, which means the bathymetry has nonrandom phylogenetic signal in the phylogeny of *Phylladorhynchus*.

According to the results obtained with BEAST and Tracer, best clock model and best tree prior of our data were an uncorrelated lognormal clock and a Birth-Death model. The ultrametric tree obtained with the COI + 16S + H3 dataset recovered a similar topology compared to the other phylogenetic results and overall high support for the different ten lineages recovered by BI an ML analyses, with some of the deep nodes unsupported and some changes in the species relationships within the clade I *ikedai*-group (Fig. 5). Clustering of clades II–VI and clades VII–IX were also supported.

Median substitution rate was mapped out along the ultrametric tree based on COI + 16S + H3 partitions, to detect accelerations and slowdowns along the branches and nodes allowed by the uncorrelated lognormal clock (Fig. 5). The results of the ancestral state reconstruction indicated that colonization of deeper waters from shallow water ancestors occurred independently at least three times during the evolution of *Phylladiorhynchus* (Fig. 5). The root ancestral state of the genus was most likely a shallow water ancestor. The first deep sea colonization event occurred in the *ikedai*-group (clade I) ancestor, a group mainly found on the continental shelf and slope, with a reversion to the ancestral habitat in the clade containing the species *P. pulchrus* and *P. koumac*, both *ikedai* species from shallow water reefs. The second event took place in the ancestral lineage of the *integra*-group (clade IX) and the third and last event was in the *pusillus*-group (clade V), which includes also *P. lenzi* (Rathbun, 1907) and *P. porteri* according to morphological relationships (Fig 2B). Acceleration in the median substitution rate was shown in several branches along the phylogeny; most of them coincided with a change of habitat between deep and shallow waters occurred; on the branch preceding the ancestor of *P. pulchrus* and *P. koumac* being more than twice that of the rate of the sister group (*ikedai*-group deep species), and those preceding the ancestor of the *spinosus*-group (clade VIII) and *nudus*-group (clade VII), being twice compared with the rate of the branching of *integra*-group. Interestingly, a slowdown was detected in the branch preceding the *pusillus*-group ancestor, where a habitat colonization changes from shallow to deep-environment occurred (Fig. 5). This evidence suggests a bathymetric effect in the molecular substitution rate in *Phylladiorhynchus*, although change of rate was also seen in the branching of *P. orpheus* with respect to other species of the true *integrivostris*-group (clade VI).

The continuous mapping analysis performed on the MCC species tree obtained with starBEAST2 also determined a shallow water root as the ancestral state, supporting the ancestral reconstruction of discrete characters (Figs. 5, 6). The first colonization of deeper waters from shallow dwelling ancestors was estimated to occur during the Lower Cretaceous, with the origin of diversification of the *ikedai*-group, which includes mostly species from the continental shelf and slope, with a median estimated between the Upper Jurassic and the Lower Cretaceous (~140 Ma). The reversion within this group to shallower waters was estimated to be at the Lower Miocene 20.29 Ma (HPD: 33.23–17.79) in *P. koumac* + *pulchrus*. The second event was along the branch leading to the clade *integra*-group clade in the 133.20–17.36 Ma interval, with a median in the Campanian (Upper Cretaceous). It contains *P. nui*, which colonized deeper water than its congeners (exceeding 1200 m depth); lastly, the most recent

event occurred on the branch leading to the *pusillus*-clade, in which species are typically from around 100 m depth usually not surpassing 200 m, in the 75.8–8.4 Ma interval, with a median in the Bartonian (Middle Eocene) (Fig. 6).

3.3. Tempo and mode of diversification of *Phylladorhynchus*

According to our results with LASER and TreePar we cannot reject a pure-birth diversification model with zero extinction (parameter $\mu = 0$) (Table S8). The PB model was selected as the best model fitting our data in TreePar. We recovered from the analyses with LASER also a PB as best constant rate model and a Y2r as best rate variable model. In conclusion, we cannot reject the null hypothesis of cladogenesis under constant rates for the diversification of *Phylladorhynchus*. We recovered slight differences in the rate of speciation among character states according to the BiSSE models (Fig. 7), but these differences were not significant when comparing full and constrained models, and the model that fitted our data best was that with equal speciation rates across character states. Moreover, there were no differences in the diversification between deep and shallow dwelling *Phylladorhynchus* (Fig. 7) leading to the conclusion that bathymetry does not have a significant effect on the diversification of the genus, given our data.

On the other hand, LTT plots showed different diversification trends for each shallow and deep lineage (considering the *ikedai*-lineage, being the most diverse lineage with most species from shelves and slope) (Fig. 8), although again not differences in the speciation parameter (*ikedai*-group $\lambda = 0.0143263$, shallow water *Phylladorhynchus* $\lambda = 0.0140435$), and we gathered the same result as previous analyses for the extinction parameter ($\mu = 0$). The LTT analyses of *Phylladorhynchus* (Fig. 8 first panel) showed a trend of constant diversification even above a pure birth model, with an initial radiation followed by a slowdown or stasis during time span 120 to 80 Ma (Cretaceous), then a recovery of the accumulation of lineages followed by other stasis during the Paleocene (ca. 45–20 Ma) and a final acceleration since the last 15 Ma. The lineage accumulation trends differ slightly among the predominant deep sea *Phylladorhynchus* (*ikedai*-group) and the shallow water counter parts, showing both groups an initial radiation, two events of slowdown or diversification stasis with a recover in the between and an acceleration to the present. These events were longer in time, steeper (considering the diversification curve), even under the constant diversification model, and more recent in the *ikedai*-group (first event ca. 85–45 Ma, second ca. 38–7 Ma) compared to the shallow

Phylladorhynchus (first event in the Cretaceous, ca. 120–80 Ma, second event in the Paleogene, ca. 50–30) (Fig. 8).

4. DISCUSSION

4.1. Systematics and phylogenetic relationships of *Phylladorhynchus* within Galatheoidea

The generally accepted relationships among galatheoid families and the monophyly of Galatheidae and Munididae (Ahyong et al., 2010, 2011a; Schnabel et al., 2011b; Bracken-Grissom et al., 2013; Palero et al., 2019; Rodríguez-Flores et al., 2018) were not recovered in our analyses (Fig. 2, Fig. 4). This is not surprising since previous studies have pointed out the polyphyly of the more diverse genera of each family (e.g., *Munida*: Rodríguez-Flores et al., 2018; *Munidopsis*: Ahyong et al., 2011b). The sister group of *Phylladorhynchus* is *Coralliogalatea*, conforming with the current systematic hypotheses that propose these two groups as closely related lineages (Rodríguez-Flores et al., 2018), with the chief synapomorphy being the presence of gonopods only on the second abdominal somite of males (Tirmizi and Javed, 1980; Macpherson and Baba, 2011). A close relationship between the monospecific genus *Anomoeomunida* (from the Caribbean Sea), and *Coralliogalatea* plus *Phylladorhynchus* is supported in the phylogenetic analyses (Fig. 2). The clade constituted by the three lineages is united by synapomorphies such the presence of an excavated orbit that is delimited by a lateral orbital spine (Macpherson and Baba 2011; Rodríguez-Flores et al., 2018; Schnabel and Ahyong, 2019; Rodríguez-Flores et al 2021). Unfortunately, the calibrated species tree did not support this clade, recovering *Anomoeomunida* as part of the Munididae group (Fig. 4). Therefore, the phylogenetic position of *Anomoeomunida* remains ambiguous until more evidence is gathered. However, our results provide strong support for *Coralliogalatea* + *Phylladorhynchus* as an independent evolutionary lineage separate from Galatheidae s.s., suggesting that the family-level classification should be revised. The cladogenesis in this group appears to have started earlier during the Lower Jurassic with the split of *Coralliogalatea* from *Phylladorhynchus*, followed by an origin of diversification of *Phylladorhynchus*, dated to the Upper Jurassic (Fig. 4), at around the same time as the radiation of the remaining squat lobsters began (Robins et al., 2012, 2013; Robins and Klompmaker, 2019).

Several modern genera of squat lobsters have been recognized in the Cenozoic fossil record or later (e.g., *Sadayoshia*, *Agononida* or *Shinkaia* Baba & Williams, 1988; De Angeli

and Garassino, 2003; Garassino et al., 2008; Schweitzer and Feldmann, 2000; Hyžný and Schlögl, 2011). Other modern squat lobsters are known from the Cretaceous, e.g., *Munida* and *Munidopsis*, or even before, appearing during the Tithonian (Upper Jurassic), e.g., *Galathea* (Schweitzer et al., 2010; Ahyong et al., 2011a). The phylogenetic reconstructions of genera without fossil record has revealed more recent age estimates: Mesozoic (*Lauriea*), Lower Cenozoic (*Coralliogalathea*) and Tertiary (*Leiogalathea* and *Paramunida*) (Cabezas et al., 2012, Palero et al., 2017, Rodríguez-Flores et al., 2019a, 2020). Taking into account all these data, our results indicate that *Phylladiorhynchus* is one of the contemporary genera of squat lobsters with the most ancient origin of diversification. Indeed, the Jurassic squat lobster *Juracrista* Robins, Feldmann & Schweitzer, 2012 and in particular *J. costaspinosa* Robins, Feldmann & Schweitzer, 2012 closely resembles to *Phylladiorhynchus* in the shape of the rostrum and supraorbital spines (Robins et al., 2012; Rodríguez-Flores et al., 2021), and may even be congeneric. The main lineages within *Phylladiorhynchus* (clades I–X) also appear to be surprisingly ancient, with divergence times in the Cretaceous and throughout the Miocene. Cladogenesis events in *Phylladiorhynchus* even precede the origin of diversification of most other galatheoid (Rodríguez-Flores et al., 2019b, 2020).

Although all current genus diversity is distributed in the Indo-Pacific region, considering the proposed time of divergence and the existence of related forms, a Tethyan geographic origin appears most likely for *Phylladiorhynchus*. Previous studies have proposed diversification of the main squat lobster lineages in the Central Indo-Pacific (*sensu* Spalding et al., 2007; Ahyong et al., 2011a) with several biogeographical reconstructions of galatheoids highlighting the importance of the southwest Pacific area for diversification. These we proposed to be associated with the geological and ecological changes that took place in this region during the late Paleogene-early Neogene period (Schnabel et al., 2011a; Cabezas et al., 2012; Palero et al., 2017; Rodríguez-Flores et al., 2020). However, the antiquity of the lineages with respect to other squat lobsters, the existence of high diversity in the ancient Tethys Sea during the Jurassic (Robins et al., 2012, 2013) and some fossil species in the area with close morphology (Robins et al., 2012; Beschin et al., 2016) supports a more likely Tethyan origin for *Phylladiorhynchus*.

4.2. Patterns of inshore/offshore colonization during their evolutionary history

Our results indicate some degree of phylogenetic signal related with the bathymetry but also a degree of convergent evolution. This phylogenetic signal is a quantitative measure of the

degree to which phylogeny predicts the ecological similarity of species, which tend to resemble each other more than under a null model (Kembel et al., 2010; Blomberg and Garland, 2002). It seems that independent habitat colonization between deep sea and shallow waters have occurred in the evolutionary history of *Phylladiorhynchus*. Previously, two evolutionary scenarios have been proposed to explain the directionality of environmental colonization: (1) from shallow to deep-waters (inshore–offshore trends), a pattern observed for the majority of marine taxa (Jablonski and Bottjer, 1990; Sepkoski, 1991; Jacobs and Lindberg, 1998; Raupach et al., 2004, 2009; Smith and Stockley, 2005; Priede and Froese, 2013; Lee et al., 2019b) and (2) invasion of shallower waters from the deep sea (offshore–inshore trends), a rarer pattern observed for instance in some groups of corals (Lindner et al., 2008; Hoeksema, 2012).

The most likely explanation for observed patterns of present-day depth distribution is that the genus *Phylladiorhynchus* originated in a shallower environment and colonized deeper waters, consistent with the inshore–offshore hypothesis (Fig. 5 and 6). This inference is congruent with the extant diversity in coral reefs and shallow environments (Rodríguez-Flores et al., 2021) and is also supported by the typical habitat in shallow coral reefs of their sister group (*Coralliogalatea*) (Rodríguez-Flores et al., 2018). Subsequently, radiation towards deeper environments has independently occurred at least twice: (1) in the *integra*-group (clade IX), reaching the deepest records for *Phylladiorhynchus* (*P. nui* and *P. integra* down to >1200 m and (2) in the *ikedai*-group (clade I; Baba et al., 2009; Lee et al., 2019a; Schnabel and Ahyong, 2019), (Figs. 5 and 6). Lastly, the group constituted by the sibling species *P. poeas* and *P. pusillus* seems to prefer shelf habitats, usually appearing below 50 meters and rarely deeper than 300 meters depth (Schnabel and Ahyong, 2019; Rodríguez-Flores et al., 2021). A pattern of multiple lineages independently colonizing the deep sea during the Cenozoic Era have been already shown in several marine taxa, including fishes, crustaceans, mollusks, and echinoderms (Raupach et al., 2004, 2009; Lorion et al., 2010; Lins et al., 2012; Priede and Froese, 2013; Kou et al., 2020).

The timing estimates for these colonization events revealed an interesting pattern in *Phylladiorhynchus*. From shallow water ancestors, a first environmental change towards the deep sea in *Phylladiorhynchus* was estimated to be early during the evolution of the squat lobsters, during the Lower Cretaceous, e.g., *ikedai*-group, followed by two more recent events of deeper water colonization (Fig. 6). Deep sea colonization events by the modern fauna have occurred predominantly during the Cenozoic (McClain and Hardy, 2010 and references

therein), including the colonization of hydrothermal vents (Herrera et al., 2015). Nevertheless, considering the fossil record, the current Paleozoic-origin deep sea fauna constitutes only a very small fraction of the modern taxa (Lipps and Hickman 1982, McClain and Hardy, 2010). Oceanic anoxic events and the increase of the temperature at the Permian–Triassic boundary and from the Mesozoic to the early Cenozoic caused mass extinction events, even leading to the complete loss of some deep sea taxa (Jacobs and Lindberg, 1998). However, some taxa survived and persisted in the deep sea or, alternatively, in oxygenated shallow water refugia with a prior re-colonization of the deep sea or suffered allopatric fragmentation (White, 1988, Wilson, 1999; Lins et al., 2012; Kou et al., 2020; Thuy et al., 2012). Recent studies suggest that some crustaceans colonized the deep sea and persisted there during the Mesozoic Era (Lins et al., 2012; Audo et al., 2021; Kou et al., 2020). This could also be the case for *Phylladorhynchus*, whose bathyal members appear to have persisted in deep waters since the Lower Cretaceous.

4.3. Potential effect of depth in rates of molecular and morphological evolution

We hypothesized that the environmental change from shallow to deep waters or vice versa could leave a footprint in the rates of molecular and morphological evolution. Linear regressions between morphological and molecular divergences overall indicated a strong effect of the habitat with depth, considering the correlation of morphological and molecular evolution of *Phylladorhynchus*, and therefore a general trend of more cryptic/pseudocryptic species in shallow water than in the deep sea (Fig. 3). Species from deeper waters (*ikedai*-, *integra* and *pusillus*-lineages) present greater morphological and lower genetic divergences in comparison to species from shallower water. These positive correlations could be also an effect of comparing ancient lineages with high phylogenetic distances and different evolutionary trajectories. However, most deep sea species belong to the same subclade sharing a common ancestor. On the contrary, shallow water species belong to independent clades not sharing the same common ancestor (Fig. 5). Therefore, we compare these changes among closely related species within lineages (clades I–X) instead among all species from different lineages and obtained the same results. These patterns of morphological evolution in shallow versus deep-waters resembles the proposed scenario for the deep sea under the stability-time hypothesis (McClain and Schlacher, 2015), in which low physiological stress promotes ecological speciation processes through fine niche partitioning (McClain and Schlacher, 2015). Ecological speciation could promote higher levels of morphological diversification among

related species by reducing constraints of phenotypic evolution in species at greater depths (Pfenning et al., 2010; Fitzpatrick, 2012). On the other hand, higher prevalence of shallow water cryptic species of *Phylladiorhynchus* could arise from convergent evolution (independent lineages adopting similar solutions) and stasis (strong stabilizing selection reducing the morphological divergence) (Struck et al., 2019).

The genetic distances among some of these species largely surpass those observed between other squat lobster genera (Machordom and Macpherson, 2004, Cabezas et al., 2008; Macpherson and Robainas-Barcia, 2013, Schnabel and Ahyong, 2019, Rodríguez-Flores et al., 2021). Our BEAST2 analyses with a molecular clock that allows consideration of different rates for each branch, recovered an acceleration in the stem branch of the ancestor of the whole group but also an ancient origin of cladogenesis (Upper Jurassic), so observed high divergences might be explained by a combination of antiquity and acceleration of the molecular substitution rate. On the other hand, our reconstruction suggests that the stem of shallow water ancestors might show an acceleration in the molecular rate of evolution in comparison to deep sea lineages, who appear to undergo a slowdown on such rate (Fig. 5). Life at depth could be associated with a scattered food and oxygen availability, stable but low temperatures, and high hydrostatic pressures (Rex and Etter 2010), which could be linked to a low metabolic rate, long generation time and large body size. This might result in a deceleration in the molecular evolution rate (or an acceleration compared to the shallow water sister taxa). Differences in habitat colonization have a deep impact in the molecular evolution of related crustaceans (Hebert, 2002; Saclier et al., 2018). Therefore, analyzing a proxy of molecular evolution (e.g., transition over transversion, the ratio of non-synonymous over synonymous substitution rates) between shallow and deep squat lobster is an interesting prospect for future studies, of course gathering a larger set of molecular data.

4.4. Potential effect of depth in the diversification/speciation of *Phylladiorhynchus*

We proposed that environmental colonization (shallow versus deep) could affect diversification rate (mode and tempo of cladogenesis). Our results suggest that best model of diversification fitting our *Phylladiorhynchus* dataset is a pure birth model, whereas according to BiSSE analyses, deep sea colonization is not a key innovation that affecting the speciation/net diversification rates (Fig. 7). In this sense, results are surprising that such an ancient group does not exhibit any significant shift on their diversification and that such a lack of extinction rate in the models employed (Table S8), although slight differences were detected in the cladogenetic

trends between shallow and deep clades. The diversification trend dynamics of the whole group is characterized by an early burst of speciation (Fig. 8) followed by decelerated periods of diversification with intermittent diversification recoveries. The slowdowns are more pronounced in the main deep sea clade *ikedai* even under the model that consider constant diversification, whereas the slopes are steeper although, there were not significant differences between the speciation rates in deep and shallow lineages (Fig. 8). The first of these slowdowns in the diversification rate of the deep sea *ikedai* clade spans the Upper Cretaceous-Lower Paleogene, coinciding with the K-Pg transition (Cretaceous-Tertiary extinction), when three-quarters of the life forms on Earth went extinct (Hull, 2015); the second took place during the Oligo-Miocene (*integra* group), where high tectonic activity in the Indo-Pacific might have influenced the dynamics of speciation (Williams and Duda, 2008; Cabezas et al., 2012). On the other hand, shallow water diversification slowdowns coincide with the Cretaceous anoxic periods (Rex and Etter, 2010) and with post Cretaceous extinctions. The higher species diversity in the *ikedai* clade (about 20 species) in comparison to the shallow water clades, characterized by having a poorer species richness (from 2 to 6 species) could be indicative of an effect of the depth in the diversification of the group. This pattern of clade diversity might correspond with McClain and Schlacher's (2015) proposal of decreasing taxonomic distance with increasing depth. According to this hypothesis, in a phylogeny of a group occurring in both shallow and deep waters, it would be likely to find higher ancient lineage diversity in shallow waters than in the deep sea. This is the case of *Phylladiorhynchus*, with seven main lineages found in shallow waters and only three typical of deeper waters. Other authors have found unexpected effects of depth in the diversification rate of marine invertebrates. Modica et al. (2020) found that diversification rate was unaffected by depth in Terebridae but suggested an increase in the rate triggered by the colonization of deep waters. Conversely, O'Hara et al. (2019) pointed out that in Ophiuroidea, deep sea diversity is attended by a low diversification rate, but also strongly influenced by latitude. Therefore, we must avoid generalizations in the diversification trends of marine taxa, since the evolutionary history of each group may have been shaped by distinct factors.

In spite of the diversification trends of the group, our results recover a constant diversification rate in *Phylladiorhynchus*. This result could be an effect of the incomplete and biased taxon sampling of the extant and extinct species, and so the diversification analyses and their fluctuation in relation to environmental factors should be interpreted cautiously. Several authors have proposed that inferring diversification parameters with only extant taxa using

molecular phylogenetics in the absence of the fossil taxa cannot be reliable (Rabosky, 2010; Loucas and Pennell, 2020). The genus *Phylladorhynchus* is characterized by an unexpectedly high diversity, with around 50 species discovered in the last few years (Schnabel and Ahyong, 2019; Rodríguez-Flores et al., 2021). At least 4 of the previously described species include species complexes (Rodríguez-Flores et al., 2021) and some of the records from the East Pacific could represent additional new taxa (e.g., DiSalvo et al., 1988; Retamal & Arana, 2016). Considering that we suspect we only know of one-third of species of galatheoid squat lobsters (Appeltans et al., 2012) and with our limited knowledge of the deep sea floor (Ramirez-Llodra et al., 2010), further sampling and taxonomic identifications are required to better understand the diversification dynamics of squat lobsters and other groups. Nevertheless, given that the recent taxonomic synopses of *Phylladorhynchus* (Schnabel and Ahyong, 2019; Rodríguez-Flores et al., 2021) are based on the results of more than three decades of intensive sampling in the Indo-Pacific, lending confidence to the general robustness of our analyses.

4.5. Relation of depth with geographic lineage range and geographic speciation patterns

We initially hypothesized that deep sea colonization can influence both geographic lineage ranges and geographic speciation patterns. General reviews have demonstrated that shallow water species usually have smaller geographic ranges than species inhabiting deeper areas such as continental shelf, slope, or abyssal plains (Halsband et al., 2020). Therefore, smaller clade ranges are more likely for lineages from shallow than from deep waters. However, throughout the study of *Phylladorhynchus* we did not find any sign that indicates a relationship between the clade range and the bathymetric range (Fig. 6). The genus presents a largely tropical distribution (Fig. 1C) that includes some widely distributed species, a pattern like many other species of Galatheoidea (Macpherson and Baba 2012; Cabezas et al., 2011; Rodríguez-Flores et al., 2018). All clades of shallow water *Phylladorhynchus* included species with allopatric distributions with lack of geographic overlap, for instance the clade III, distributed from Western Australia to French Polynesia, with an absence of species range overlap in its distribution area. Clade VIII has a disjunct distribution from Western Australia to New Caledonia and New Zealand, and in Taiwan, with only two species that overlap in their distribution (Rodríguez-Flores et al., 2021) (Fig. 6). On the other hand, the *ikedai*-group includes several sympatric deep sea species that are closely related (Rodríguez-Flores et al., 2021) (Fig. 6). The overlap of geographic ranges of species of the same clade is more common in continental shelf/slope species than in shallow species, warranting further investigation.

Some species may have formed by allopatric speciation facilitated by bathymetric shifts, for instance, within the *integra*-group, *P. nui* Schnabel & Ahyong, 2019, and *P. australis* Schnabel & Ahyong, 2019 overlap in their geographic range but do not overlap in their bathymetrically. However, the eurybathic *P. integrus* that shares the subclade with the above species does not overlap geographically with the others. Vertical speciation has been previously reported for some species of *Leiogalathea* together with morphological adaptations to deeper environments (Rodríguez-Flores et al., 2020) a pattern repeatedly observed in deep sea invertebrates (e.g., Prada and Hellberg, 2021; Breusing et al., 2020).

Shallow water *Phylladiorhynchus* include often cryptic species (Rodríguez-Flores et al., 2021) (Fig. 3) that are generally allopatric, reducing selective pressures promoting the evolution of morphological differences related to species interactions, whereas sympatric species often accumulate morphological differences that might allow them to avoid competitive exclusion (Chenuil et al., 2019). Sympatric distributions in shallow cryptic species might be explained by ancient divergence and recent secondary contact (see the case of *Coralligalathea* in Rodríguez-Flores et al., 2018), whereas in the deep sea, ecological speciation and morphological divergence might account for overlapping of the distributions in species of the same clade. Ecological divergence and allopatric isolation play a key role in speciation of marine invertebrates, generating allopatric divergence after the generation of horizontal/vertical barriers and ecological isolation due to niche segregation in the deep sea (Prada and Hellberg, 2021; Breusing et al., 2020).

5. CONCLUSIONS

<Reconstructing the evolutionary history of *Phylladiorhynchus* has not only shown that there is still much to uncover about the systematics of squat lobsters, but also that *Phylladiorhynchus* is one of the most ancient lineages of extant squat lobsters, with a complex evolutionary history since the Jurassic, and several independent shallow- to deep-water colonization events. Indeed, this environmental shift has shaped the molecular and morphological diversity in the group and it may be possible for related groups to be differentially affected by habitat change. This line of research should be extended to squat lobsters that are highly diverse and where contrasting evolutionary phenomena, such as adaptive radiation, rapid speciation, cryptic species or high morphological diversification have been previously detected (Machordom and Macpherson, 2004; Rodríguez-Flores et al., 2019a,b; Dong et al., 2019, 2021). However, to better understand

the effects of the depth on evolutionary dynamics, speciation and extinction, increased taxonomic effort is essential for understanding the evolutionary pathways of this and other crustacean groups.

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Figure captions

Figure 1. Selected hypotheses of the evolutionary history of the squat lobsters *Phylladiorhynchus* over time and considering environmental shifts: A. Selective models of molecular evolution in terms of the decoupling of morphological and molecular change, B. Adaptive radiation patterns: Changes in the diversification rates, in terms of speciation (λ) and extinction (μ) rates, appear in phylogram as a result of environmental change (e.g., bathymetric shifts); C. The current distribution of *Phylladiorhynchus* species spans the tropical and subtropical Indo-Pacific region could also have been affected by the colonization of deep versus shallow environments.

Figure 2. Phylogenetic hypotheses of Galatheoidea based on A., concatenated genetic markers (COI, 16S, PEPCK, H3, 28S, 18S) obtained with BI and ML, and based on B., morphological characters obtained with TNT and BEAST. Asterisk above branches in A indicate bootstrap support (2 asterisk = support from BI and ML, one asterisk = support from only one of the treatments. Values of bootstrap lower than 70 and pP lower than 0.80 are not shown. Posterior probability is reflected in each node in B. Species groups are indicated with color squares and roman numeration; species names are indicated at branch tips in both trees. Pictures from the top to the bottom: *P. paula*, *P. koumac*, *P. zetes*, *P. gustavi*, *P. peneleos*, *P. poeas*, *P. orpheus*, *P. phanus*, *P. lini*, *P. nui*, *P. joannotae*. Credit images (MNHN, UF, NIWA): L. Corbari, K. Schnabel, B. Richer de Forges, G. Paulay, TY. Chan, Z. Duris, A. Anker, and P.C. Rodríguez-Flores.

Figure 3. Linear regression results of the relation between molecular (COI) differentiation and morphological differentiation (in terms of uncorrected p-distance) in A) all set of *Phylladiorhynchus* species from shallow waters (left) and comparisons only within *Phylladiorhynchus* shallow clades (II, II, IV, VI, VII, VIII), (right), and B) all set of *Phylladiorhynchus* species from deep waters (left) and comparisons within *Phylladiorhynchus* deep clades I, V and IX (right), p-value of each analysis is indicated on the top right of each graph. Carapaces exemplify the morphological diversity among shallow water clades (A) and deep sea clades (B).

Figure 4. Maximum clade credibility tree for *Phylladiorhynchus* in a Galatheoidea phylogenetic context obtained with StarBEAST2 using 78 species. Calibration points considered in the analysis are highlighted with *. Numbers on nodes indicate posterior probability for the corresponding nodes. Bars represent the 95 % highest posterior density. Yellow circles at nodes indicate tMRCA of *Phylladiorhynchus* genus (most ancient circle) and tMRCA for most other Galatheoidea lineages for comparison of ancestry (circle most recent).

Figure 5. Ultrametric tree obtained from BEAST of the concatenated genes (COI, 16S and H3) after pruning outgroups and ancestral discrete character reconstruction on the tree for the character “depth” codified as shallow and deep. Legend indicates the range of the substitution rate along the branches obtained with the relaxed molecular clock in BEAST, grey color indicates unsupported branches. Circle size on nodes indicate Bayesian posterior probabilities (pP) and marginal the marginal ancestral states for the character depth. Species names are indicated at the branch tips. Roman numbers indicate each reconstructed phylogenetic clade, I: *ikedai*-group, II: *integrastrostris*-

group 2, III: *integrivostris*- group 3, IV: *integrivostris*-group 4, V: *pusillus*-group, VI: true *integrivostris*-group, VII: *nudus*-group, VIII: *spinosus*-group, IX: *integra*-group, X: *integrivostris*-group 5).

Figure 6. Continuous mapping of the species median depth on the calibrated species tree obtained from BEAST after pruning outgroups and clade geographic range for the main phylogenetic lineages of *Phylladorhynchus*, from the top to the bottom: *integrivostris*-5 group and *spinosus*-group, *integra*-group and *nudus*-group, *ikedai*-group and true *integrivostris*-group, *integrivostris*-2 and 3 group; and *integrivostris*-4 and *pusillus*-group. Vertical lines indicate median age of habitat change. Roman numbers indicate each reconstructed phylogenetic clade, I: *ikedai*-group, II: *integrivostris*-group 2, III: *integrivostris*- group 3, IV: *integrivostris*-group 4, V: *pusillus*-group, VI: true *integrivostris*-group, VII: *nudus*-group, VIII: *spinosus*-group, IX: *integra*-group, X: *integrivostris*-group 5.

Figure 7. A. Diversification rate, speciation rate and extinction rate for shallow and deeper *Phylladorhynchus* using BiSSE models via MCMC chain runs for 10000 generations in each case for a full unconstrained model (see text).

Figure 8. Lineages-through-time (LTT) plot based on the MCC species tree (black line) showing the diversification of *Phylladorhynchus* lineages throughout time in million years (X-axis). Background colors represents the expected distribution of 1000 trees under a pure-birth model and assuming constant diversification (red line). The Y-axis is on a logarithmic scale.

Supplementary material

Table S1. List of depths of each lot of specimens analyzed for this study.

Table S2. Primers used for this study and references.

Table S3. Sequenced material including GenBank Accession numbers.

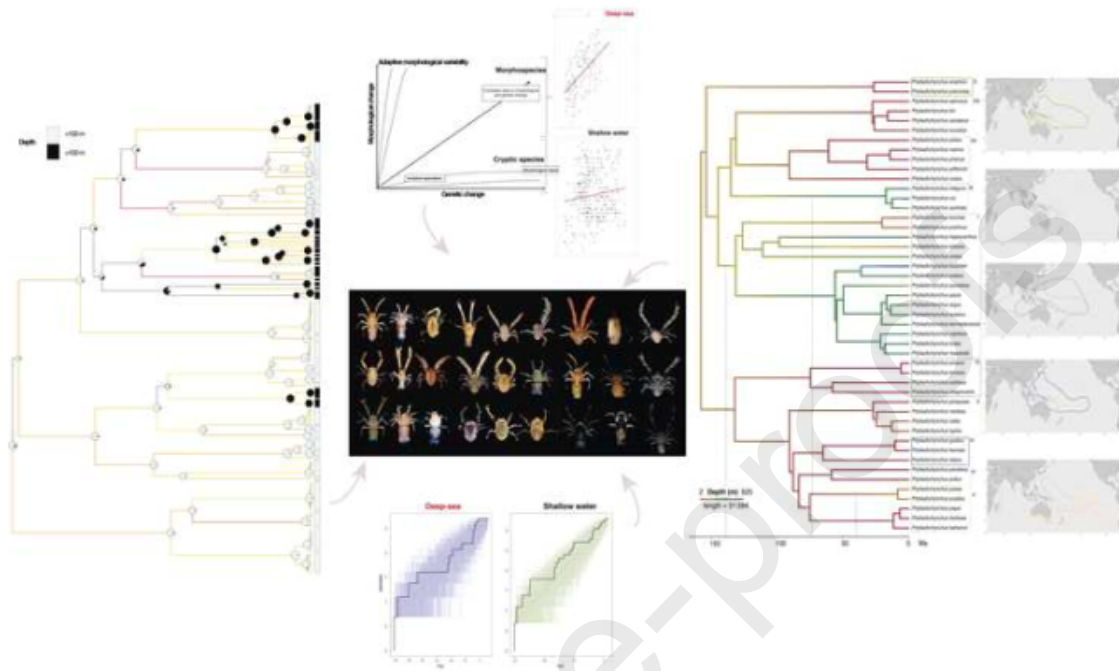
Table S4. Morphological characters analyzed and states for each character.

Table S5. Calibration points for the time divergence estimation analyses and references used for this study,

Figure S6. Phylogenetic trees resulted from ML and BI without collapsing nodes.

Figure S7. Phylogenetic trees resulted after removing outgroups.

Table S8. Results of LR (Likelihood ratio test) of the diversification analyses



Highlights

The known diversity of *Phylladiorhynchus* recently increased from five to 55 species

Multilocus and morphological phylogenies were inferred based on all known *Phylladiorhynchus* diversity to test the effect of depth on the evolution and diversification of the genus.

Our phylogenetic reconstruction showed that the sister group of *Phylladiorhynchus* is *Coralliogalatea* and this clade is not closely related to other Galatheidae

Ten morphologically well-delimited clades are identified within the genus

The ancestor of the genus originated in shallow water during the Upper Jurassic and independently colonized deeper waters during diversification

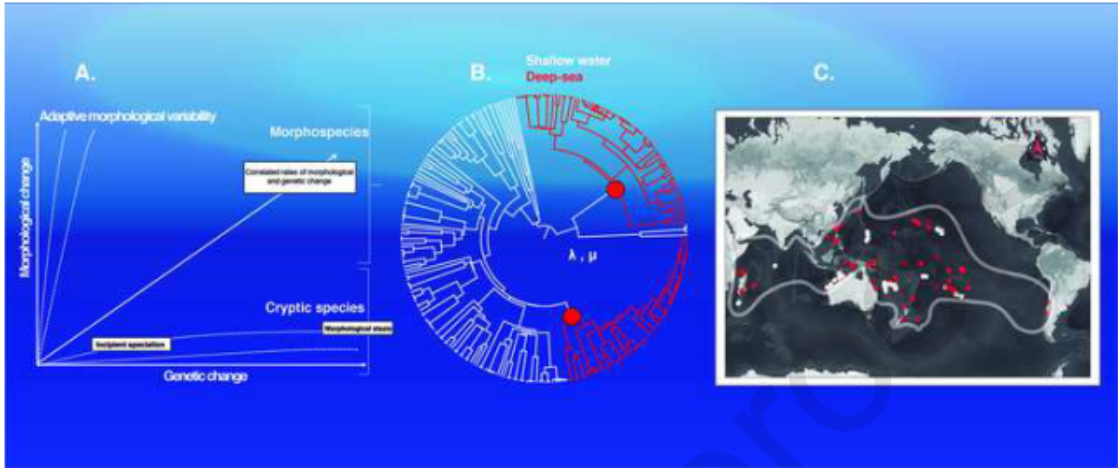
Shallow water species present a slowdown in the morphological evolution and a higher molecular substitution rate in comparison with deep-sea species

Depth does not significantly affect the diversification of *Phylladiorhynchus* in terms of speciation and extinction rates

Deep-sea species of *Phylladiorhynchus* tend to be sympatric whereas shallow water species present allopatric distributions

Author statement

Paula C. Rodríguez-Flores: Conceptualization, Data Curation, Methodology, Formal analysis, Visualization, Writing- Original draft preparation. **Enrique Macpherson:** Funding acquisition, Data Curation, Supervision, Writing - Review & Editing. **Kareen Schnabel:** Resources, Writing - Review & Editing. **Shane Ahyong:** Resources, Writing - Review & Editing. **Laure Corbari:** Funding acquisition, Resources, Writing - Review & Editing. **Annie Machordom:** Funding acquisition, Supervision, Validation, Writing - Review & Editing.



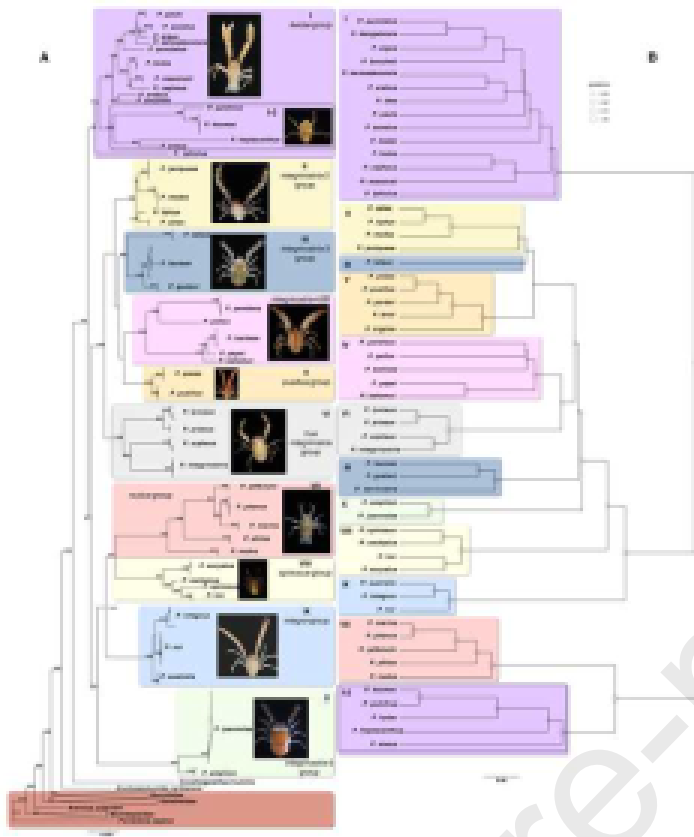


Figure 2

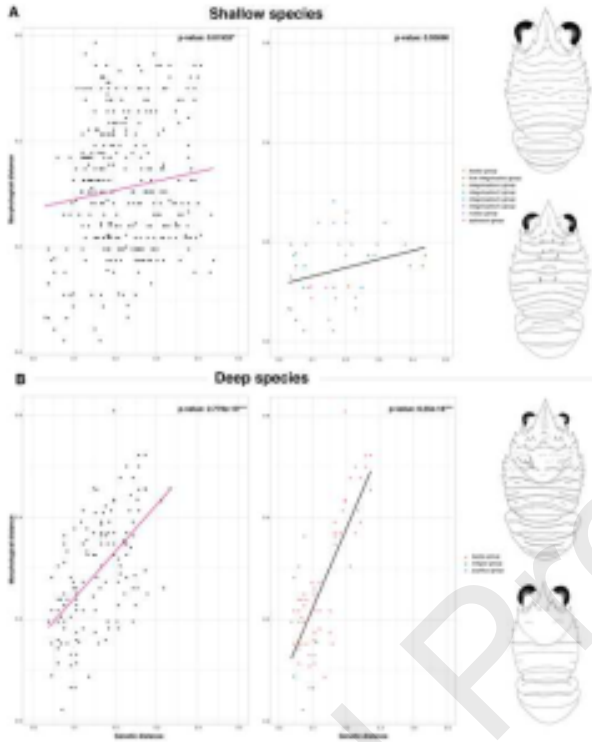
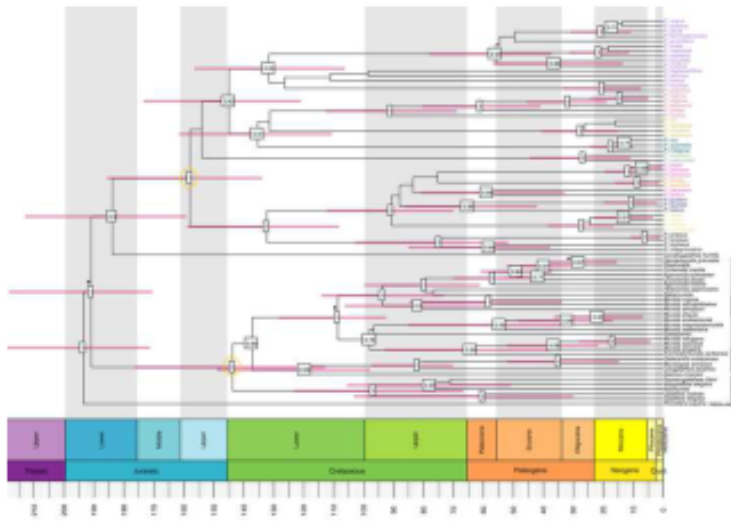
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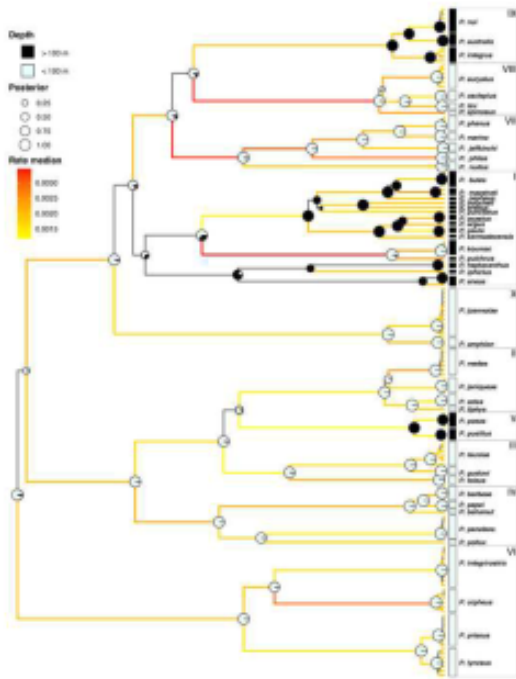
Figure 4

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Figure 1 [Click here to access/download/figure/figure3.png](#)



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Figure 8

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