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Convergent adaptation of true crabs (Decapoda: Brachyura) to a gradient of terrestrial environments

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Abstract: For much of terrestrial biodiversity, the evolutionary pathways of adaptation from marine ancestors are poorly understood, and have usually been viewed as a binary trait. True crabs, the decapod crustacean infraorder Brachyura, comprise over 7,600 species representing a striking diversity of morphology and ecology, including repeated adaptation to non-marine habitats. Here, we reconstruct the evolutionary history of Brachyura using new and published sequences of 10 genes for 344 species spanning 88 of 104 families. Using 36 newly vetted fossil calibrations, we infer that brachyurans most likely diverged in the Triassic, with family-level splits in the late Cretaceous and early Paleogene. By contrast, the root age is underestimated with automated sampling of 328 fossil occurrences explicitly incorporated into the tree prior, suggesting such models are a poor fit under heterogeneous fossil preservation. We apply recently defined trait-by-environment associations to classify a gradient of transitions from marine to terrestrial lifestyles. We estimate that crabs left the marine environment at least five and up to 15 times convergently, and returned to the sea from non-marine environments three or four times. Although the most highly terrestrial- and many freshwater-adapted crabs are concentrated in Thoracotremata, Bayesian threshold models of ancestral state reconstruction fail to identify shifts to higher terrestrial grades due to the degree of underlying change required. Lineages throughout our tree inhabit intertidal and marginal marine environments, corroborating the inference that the early stages of terrestrial adaptation have a lower threshold to evolve. Our framework and newly compiled fossil and natural history datasets will enable future comparisons of non-marine adaptation at the morphological and molecular level. Crabs provide an important window into the early processes of adaptation to novel environments, and different degrees of evolutionary constraint that might help predict these pathways.

Keywords: Brachyura, crustaceans, convergent evolution, terrestrialization, molecular phylogeny, divergence times, fossil calibration, threshold model

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Introduction

Over 80% of estimated species comprising extant multicellular life inhabit terrestrial and freshwater ("non-marine") settings (Román-Palacios et al. 2022). Microbial life began to populate terrestrial habitats in the Precambrian, with eukaryotes potentially originating in non-marine settings around 1.6 Ga (Jamy et al. 2022), although major multicellular groups such as animals and plants were ancestrally marine. Their terrestrialization followed in the early Paleozoic (approximately 538–444 Ma), led by arthropods entering coastal and marginal marine settings (e.g., estuaries, lagoons), and plants that transformed the land and its sediments (Buatois et al. 2022). Although molecular divergence time estimates infer early Paleozoic ages for terrestrial arthropod crown groups (e.g., Bernot et al. 2022; Benavides et al. 2023), recognizable body fossils of millipedes, arachnids, and hexapods have recorded their presence on land by the onset of the Silurian–Devonian (443–359 Ma). Subsequently, these groups radiated to become prominent components of terrestrial biodiversity. Fossil evidence suggests potential transitions through marginal marine settings (Edgecombe et al. 2020; Lamsdell et al. 2020), but transitions for many modern groups lack such clues (e.g., the remipede sister group is now predominantly restricted to marine layers within anchialine caves), hinting at complex ecological pathways. Here, we examine the evolutionary history of a clade, the true crabs (Decapoda: Brachyura), that might provide insights into the early phases of adaptation from marine to non-marine environments, now obscured by extinction.

As with life in general, crabs have an unequivocally marine ancestor. The largest group of Brachyura, called Eubrachyura, which contains all non-marine members, could be as old as the mid-Jurassic (183–161 Ma) based on phylogenomic divergence time estimates (Wolfe et al. 2019). During the "Cretaceous Crab Revolution" (145–66 Ma), many now-extinct lineages appeared briefly, accompanied by the divergence of many extant superfamilies (Wolfe et al. 2019; Luque et al. 2019b; Wolfe et al. 2021). Although the direct record of fossil crabs from non-marine sediments is depauperate, one well-preserved example of a completely extinct non-marine eubrachyuran lineage is known from around 100 Ma (Luque et al. 2021), and chelipeds of uncertain affinity from non-marine sediments around 74 Ma (Robin et al. 2019). Together, these fossils suggest that crabs have been entering non-marine habitats for the majority of their evolutionary history.

Complementary to direct fossil evidence, dated phylogenies and character mapping have recently been applied (Davis et al. 2022; Tsang et al. 2022). Eubrachyura has been previously divided into two presumed clades based on the position of the male gonopores: "Heterotremata" and Thoracotremata. In a 10-gene molecular study focused on the relationships of the clade Thoracotremata, the common ancestor of this clade was found to be "semi-terrestrial" (in Tsang et al. [2022], this referred to intertidal habitats) and Cretaceous in origin, with at least four transitions to terrestrial and two or three transitions to freshwater lifestyles, all within the Cenozoic (Tsang et al. 2022). In one instance, sesarmid crabs (*Geosesarma*, vampire crabs) transitioned from terrestrial to freshwater habitats. At least six returns to subtidal marine habitats were estimated (Tsang et al. 2022). A separate supertree-based study across Decapoda inferred three transitions to terrestriality and three to freshwater within all of Brachyura (Davis et al. 2022). One reversal from terrestrial to marine habitats was estimated. The oldest event, encompassing the freshwater heterotreme groups Potamoidea, Gecarcinucoidea, and

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Pseudothelphusoidea, occurred in the upper Cretaceous, with others in the Cenozoic. Additionally, Davis et al. (2022) inferred higher rates of speciation in non-marine crabs, but habitat shifts were not found to be a significant causal factor driving crab diversity.

The aforementioned phylogenetic studies, however, treated marine, terrestrial, and freshwater lifestyles as largely discrete ecologies for crabs. Indeed, previous studies have described a gradient of terrestrial change based on independence from standing water (e.g., Bliss 1968; Powers and Bliss 1983; Hartnoll 1988). Others (e.g., Yeo et al. 2008; Cumberlidge and Ng 2009; Cumberlidge et al. 2009) focused on the seven exclusively ("primary") freshwater crab families and their vicariant biogeography leading to high endemicity and risks of extinction, but rarely drew comparisons with terrestrial crabs. Recently, Watson-Zink (2021) unified the conceptualization of the terrestrial and freshwater crab lifestyles as a series of ecological, morphological, and physiological traits describing grades of terrestriality. Crabs can transition from fully marine lifestyles (**Figure 1A-E**) along either of two transition pathways: through marine-associated environments (e.g., the "direct" pathway of Tsang et al. [2022], via intertidal, mangroves, beaches: **Figure 1F-J**) or through freshwater environments (e.g., the "indirect" pathway via estuaries, rivers: **Figure 1K-O**). Each grade of terrestriality is loosely associated with habitats: lower intertidal and estuaries (grade 1), upper intertidal and freshwater (grade 2), beaches and riverbanks (grade 3), and coastal forests and jungles, including tree climbing (grades 4-5; Watson-Zink 2021). Less terrestrial crabs (grades 1 and 2) in either pathway can tolerate fluctuating environments, with osmoregulatory ability likely playing a major role in these lifestyles (Watson-Zink 2021). Crabs of higher terrestriality (grades 3-5) develop further morphological and developmental adaptations, such as branchiostegal lungs and water-wicking setae to prevent desiccation, and increasingly abbreviated larval development and parental care (Watson-Zink 2021). It is evident that multiple brachyuran families have repeatedly evolved members of both transition pathways and various grades, but their distribution across crab phylogeny (within and beyond Thoracotremata) over time remains unclear.

To resolve the convergent evolution and timing of terrestriality, we present the most robust molecular taxon sampling to date for Brachyura, representing 344 species and 88 of 104 families. As our data represent only Sanger sequences of 10 loci, revision of brachyuran systematics is beyond the scope of the current study (Timm and Bracken-Grissom 2015), and efforts are currently underway to clarify deep relationships using phylogenomics. Furthermore, to partially ameliorate false confidence in the topology, we provide additional metrics describing the degree of nodal uncertainty. Using these data, we contrast divergence times inferred using 36 newly vetted calibrations with traditional node dating, and 328 calibrations sampled from the Paleobiology Database under the fossilized birth-death (FBD) and skyline models of tree evolution, one of only a few empirical comparisons of its type. Finally, we summarize the natural history traits of each sampled crab to assign each along a gradient of transitions from marine to terrestrial lifestyles (Watson-Zink 2021), and use Bayesian threshold models of ancestral state reconstruction to estimate convergent events.

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Figure 1. Representative brachyurans displaying different lifestyles and grades of terrestriality. (**A-E**) Fully marine lifestyle, grade 0; (**F-J**) direct marine transition pathway, grades 1-5 bottom to top; (**K-O**) indirect freshwater transition pathway, grades 1-5 bottom to top. (**A**) Portunidae: *Portunus sayi* (Bermuda); (**B**) Calappidae: *Calappa calappa* (Kwajalein Atoll, Marshall Islands); (**C**) Epialtidae: *Cyclocoeloma tuberculatum* (Anilao, Philippines); (**D**) Raninidae: *Ranina ranina* (Oahu, Hawaii, USA); (**E**) Homolidae: *Paromola cuvieri* (Gorringe Ridge, Portugal); (**F**) Gecarcinidae: *Gecarcoidea natalis* (Christmas Island, Australia); (**G**) Gecarcinidae: *Cardisoma guanhumi* (Fort Lauderdale, Florida, USA); (**H**) Ocypodidae: *Uca heteropleura* (Pacific coast, Panama); (**I**) Grapsidae: *Leptograpsus variegatus* (Tasmania, Australia); (**J**) Eriphiidae: *Eriphia sebana* (Heron Island, Queensland, Australia); (**K**) Sesarmidae: *Geosesarma dennerle* (aquarium specimen); (**L**) Deckeniidae: *Madagapotamon humberti* (Montagne de Français Reserve, Madagascar); (**M**) Gecarcinucidae: *Ghatiana botti* (Sindhudurg, India); (**N**) Pseudothelphusidae indet. (Santander, Colombia); (**O**) Hymenosomatidae: *Hymenosoma orbiculare* (Langebaan Lagoon, South Africa). Photo credits: (A) Jessica Riederer; (B, C) Jeanette and Scott Johnson; (D) John Hoover; (E) © OCEANA; (F) John Tann, license CC-BY; (G) Tom Friedel, license CC-BY 3.0; (H) Kecia Kerr and Javier Luque; (I) Joanna Wolfe; (J,N) Javier Luque; (K) Henry Wong; (L) Sara Ruane; (M) Tejas Thackeray; (O) Charles Griffiths.

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Materials and Methods

Taxon sampling

This dataset represents over 15 years of sampling crabs in the field or from museum collections (**Table S1**). The final dataset includes 88 families, 267 genera, 336 species and 344 individuals within the infraorder Brachyura, 42% representing new sequence data, with the remainder obtained directly from GenBank (**Table S1**). All taxonomy was checked against expert compilations (Ng et al. 2008; Poore and Ahyong 2023; WoRMS 2022).

Gene selection

A total of 10 genes were selected based on previous phylogenetic research of decapods (Spears and Abele 1998; Schubart et al. 2000; Tsang et al. 2008; Bracken-Grissom et al. 2013; Tsang et al. 2014). These included two mitochondrial ribosomal RNA (rRNA) coding genes, 12S (small ribosomal subunit) and 16S (large ribosomal subunit) as well as two nuclear rRNA genes, 18S (small ribosomal subunit) and 28S (large ribosomal subunit). The six nuclear protein-coding genes NaK (sodium–potassium ATPase α-subunit), PEPCK (phosphoenolpyruvate carboxykinase), GADPH (glyceraldehyde 3-phosphate dehydrogenase), H3 (histone 3), enolase (phosphopyruvate hydratase), and AK (arginine kinase) were also included. A minimum of two genes were required for each taxon included in the analysis.

DNA extraction, PCR, and sequencing

Genomic DNA was extracted from the gills, abdomen, pereopod, or pleopod, using the Qiagen DNeasy® Blood and Tissue Kit (Cat. No. 69582), QIAamp DNA Mini Kit (Cat. No. 51304) or QIAamp DNA Micro Kit (Cat. No. 56304). Gene regions were amplified with polymerase chain reaction (PCR) using one or more sets of primers. Annealing temperatures and primer sequences are as follows: 12S rRNA (325 bp, Buhay et al. 2007), 16S rRNA (339 bp, Simon et al. 1994; Crandall and Fitzpatrick 1996; Schubart et al. 2002), 18S rRNA (1798 bp, Medlin et al. 1988; Whiting et al. 1997; Whiting 2002; Bracken et al. 2009), 28S rRNA (1892 bp, Whiting et al. 1997; Whiting 2002; Palero et al. 2008), histone 3 (H3) (336 bp, Colgan et al. 1998), NaK (606 bp, Tsang et al. 2008), PEPCK (582 bp, Tsang et al. 2008), GADPH (609 bp, Tsang et al. 2011), enolase (399 bp, Tsang et al. 2011), and AK (630 bp, Tsang et al. 2011).

PCR amplifications were performed in 25–50 µl volumes containing 1 U of Taq polymerase (HotMaster, AccuPrime or REDTaq), PCR Buffer, 2.5 mM of deoxyribonucleotide triphosphate mix (dNTPs), 0.5 µM forward and reverse primer, and 30–100 ng extracted DNA. The thermal profile used an initial denaturation for 1 min at 94ºC followed by 30–40 cycles of 30 sec-1 min at 94ºC, 45 sec-1 min at 46-58ºC (depending on gene region), 1 min at 72ºC and a final extension of 7 min at 72ºC. PCR products were purified using filters (PrepEase™ PCR Purification 96-well Plate Kit, USB Corporation) and sequenced with ABI BigDye® terminator mix (Applied Biosystems, Foster City, CA, USA). Cycle Sequencing reactions were performed in an Applied Biosystems 9800 Fast Thermal Cycler (Applied Biosystems, Foster City, CA, USA), and sequencing products were run (forward and reverse) on an ABI 3730xl DNA Analyzer 96-capillary automated sequencer.

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Phylogenetic analysis

Sequences (n = 2251) were assembled and trimmed within Geneious Prime (Kearse et al. 2012). All protein coding genes (AK, enolase, GADPH, H3, NaK, PEPCK) were checked for pseudogenes following Song et al. (2008). Ribosomal RNA genes (12S, 16S, 18S, 28S), were individually aligned using the MAFFT via local iterative refinement algorithms in Geneious v.2021.0.1 (Kearse et al. 2012; Katoh and Standley 2013). Protein-coding genes were individually aligned in Geneious using the MAFFT global iterative refinement algorithm. To remove regions of questionable homology, rRNA alignments were masked in GBlocks v.0.91b (Castresana 2000) under "less stringent" parameters.

Alignments were concatenated in Geneious Prime. Best-fitting partitions were selected by an edge-linked proportional model (Chernomor et al. 2016) and substitution models with ModelFinder (Kalyaanamoorthy et al. 2017) in IQ-TREE v.2.1.2 (Minh et al. 2020b). The best-fitting scheme was used to estimate the concatenated maximum likelihood (ML) phylogeny, also in IQ-TREE, using 10 independent runs with perturbation strength 0.2 and stopping at 500 iterations, selecting the best topology by the highest log likelihood (Zhou et al. 2018). Ultrafast (UF) bootstrap values were calculated from 1000 replicates using the -bnni flag (Hoang et al. 2018). Gene and site concordance factors (gCF and sCF, respectively) were calculated in IQ-TREE v.2.2.2 (Minh et al. 2020a; Mo et al. 2022), simultaneously generating individual gene trees using ML. We further explored the resolution of individual loci evolving at different rates by using a metric for per-site phylogenetic informativeness (Townsend 2007) estimated by the online PhyDesign program (http://phydesign.townsend.yale.edu/; López-Giráldez and Townsend 2011) using the DNArates substitution model.

We conducted a Bayesian inference (BI) analysis of the concatenated loci using MrBayes v.3.2.7 (Ronquist et al. 2012). Two runs and four chains were run for 35 million generations with 25% burnin. Convergence was assessed by reaching effective sample size >200 for every parameter, and by evaluating posterior distributions in Tracer v.1.7.1 (Rambaut et al. 2018).

Fossil calibration and divergence time inference

We compared two strategies for fossil calibration: (1) 36 newly vetted node calibrations, and (2) 328 fossil occurrences from the Paleobiology Database (PBDB; http://paleobiodb.org/). For node calibration, all calibrations followed best practices regarding specimen data, morphological diagnosis, and stratigraphy (Parham et al. 2012; Wolfe et al. 2016; details in **Text S1, Table S2**), and were assigned to a crown group node at the family level or higher. All internal calibration age distributions were uniform. We applied a root prior with a fossil-informed lognormal distribution (mean = 282 Ma, standard deviation = 0.25, offset = 25; based on the same node in Wolfe et al. [2019]). This node dating strategy used a birth-death tree prior.

We downloaded fossil occurrences from the PBDB on March 23, 2022, for Brachyura at family-level taxonomic resolution, excluding uncertain genera and species, with accepted names only, from Jurassic to Pleistocene. Although issues are known with the entry of decapod fossil taxonomy in the PBDB, higher levels are somewhat adequate (M. Uhen and M. Clapham, pers. comm.). We spot checked occurrences for accuracy, updated PBDB taxonomy where we found errors, and manually removed from our downloads 30 families that could not be placed in our tree (extant families without molecular data, or extinct families with no known phylogenetic

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context). We randomly subsampled 10% of the 3,276 remaining occurrences, resulting in 328 occurrences. All fossil occurrences were assigned age ranges from the PBDB, each with a uniform distribution (Barido-Sottani et al. 2019, 2020). To incorporate these fossil samples as part of the inferred evolutionary process, we used the unresolved time-homogeneous fossilized birth-death (FBD) tree prior (Stadler 2010; Heath et al. 2014; O'Reilly and Donoghue 2020), conditioned on the same root prior as above. The diversification rate was assigned a uniform prior (0, infinity) to reflect the unknown proportion of extinct relative to extant species, and an initial rate of 0.01. The turnover rate and sampling proportion were both assigned uniform priors with distribution (0, 1). For rho, the proportion of living species sampled, the value was fixed at 0.04 based on 7,636 valid brachyuran species in WoRMS (WoRMS 2021).

To reflect the complete absence of brachyuran fossils from earlier than the Jurassic, which represents a known ghost lineage when compared to the diversity and abundance of anomuran fossils, thus earlier diversification of the sister group (Hegna et al. 2020; Wolfe et al. 2021), we also analyzed the fossil occurrence calibration set using a birth-death skyline tree prior with sequential sampling (BDSS; Stadler et al. 2013; Culshaw et al. 2019). Fossil sampling proportion was modeled as time-heterogeneous with time slices before and after the oldest fossil sample (initial values of 0 and 0.1, respectively), and a uniform prior distribution (0, 1). This was done using the TreeSlicer function from the skylinetools package (https://github.com/laduplessis/skylinetools). While we used the same root prior, the origin time was estimated with a uniform prior (182, 372) and an initial value of 325 Ma (**Text S1**; Wolfe et al. 2019). The reproductive number R0 (i.e., birth rate/total death rate) had a dimension of 5; this parameter and the total death rate were both assigned lognormal prior distributions.

All divergence time analyses were conducted in BEAST2 v.2.6.4 (Bouckaert et al. 2019) using a fixed starting tree derived from our ML concatenated results. When using fossil occurrences (FBD and BDSS analyses only), these were added to the starting tree as "rogues" (able to move within pre-assigned family level constraints following Barido-Sottani et al. [2022], as most decapod fossils are fragmentary and cannot be confidently assigned). All analyses linked the substitution models selected by ModelFinder, and the clock models of those partitions (4 categories total). For each calibration strategy and tree prior, we compared two clock models: relaxed lognormal (Drummond et al. 2006) and random local (Drummond and Suchard 2010), using lognormal priors on the mean branch rates (lower and upper values of 0.001 and 1, respectively). Analyses used four to six independent runs for at least 450 million generations with 25% burnin, visualized as a maximum clade credibility tree. Convergence was assessed as above. Having explored a total of six divergence time analyses, we visualized the results from different parameter sets using *chronospace* scripts (Mongiardino Koch et al. 2022; *development version, will provide scripts for final paper*).

Ancestral state reconstruction

To code character states representing a gradient of terrestriality, we used a modified version of the trait-by-environment associations defined by Watson-Zink (2021). Distinct transition pathways were defined for marine and freshwater routes. For each pathway, we used five of the six grades of increasing terrestriality; the highest level does not appear in our data (Watson-Zink 2021). We added a grade 0, to indicate that the ancestral state for all crabs is fully marine (**Figure 1A-E**). Using this framework, we coded discrete grades of terrestriality

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following two schemes. The first scheme coded the taxa that were sequenced in our molecular phylogeny and required detailed justification from natural history literature (**Table S3**, **Text S2**). Justifications accounted for available data on adult habitat, osmoregulatory status, larval developmental strategy, primary respiratory structure, water-wicking setae, burrow type, and diurnal activity period (Watson-Zink 2021). As our phylogeny sampled 4% of brachyuran species as tips, we also constructed a scheme to estimate grades for unsampled species for which the phylogenetic positions are unknown. For this scheme, we downloaded all taxonomic data, including non-marine taxa, from WoRMS as of June 8, 2021. For families sampled in our tree, we used the WoRMS data to estimate the number of species that fall into each grade (without detailed literature survey per species) and accordingly assigned prior distributions to each tip on the molecular phylogeny (**Table S4**).

First, we used stochastic character mapping (Bollback 2006; Revell 2012) to infer ancestral states at each node on the chronogram with vetted calibrations. For this we used a single dataset, where the natural history codings were simplified to marine, and marine/direct and freshwater/indirect transition paths (i.e., three unordered states of a single character), with the posterior distribution simulated 500 times. Next, we used Bayesian threshold models (Revell 2014) to account for gradients of change. A character coded with discrete ordered states (i.e., our grades) was assumed to evolve according to an unobserved continuous trait called "liability" (here representing the coded natural history traits combined with additional unobserved factors). Following Sallan et al. (2018), we assume thresholds represent the amount of change in terrestriality traits that allows a habitat shift. As there are two independent transition pathways with their own gradients, these were analyzed separately for each direction of change (and on subclades for transitions between direct and indirect pathways). Threshold models for ancestral state reconstruction were implemented as the *ancThresh* function in *phytools* (Revell 2012). Each *ancThresh* model (Brownian Motion: BM, Ornstein-Uhlenbeck: OU, and Pagel's Lambda) was run for 50 million generations (5 million for subclades) with 20% burnin (Revell 2014; Sallan et al. 2018).

Results

Phylogenetic relationships

The concatenated alignment length comprised 7,516 bp in total from two mitochondrial rRNA, two nuclear rRNA, and six nuclear protein-coding genes (gene trees visualized in **Figures S1-10**). Results using ML and BI were similar, with some deeper nodes (higher than family level) maintaining low to moderate support (UF bootstrap = 50-94; **Figures 2, S11**) with ML and generally stronger support (most posterior probabilities ≥ 0.98; **Figure S12**) with BI. For each node of the ML tree, gCF reflects the percentage of loci containing all the descendant taxa, and sCF the percentage of sites supporting the node (Minh et al. 2020b). Both concordance factors illustrate a spectrum of support across nodes that are fully supported with UF bootstraps (**Figure S13**). The average gCF was 32.73 (**Figures S11, S13**), indicating one third of loci support the average node. However, nearly half of sites support the average node (average sCF = 45.64), demonstrating the benefit of concatenation for small numbers of loci.

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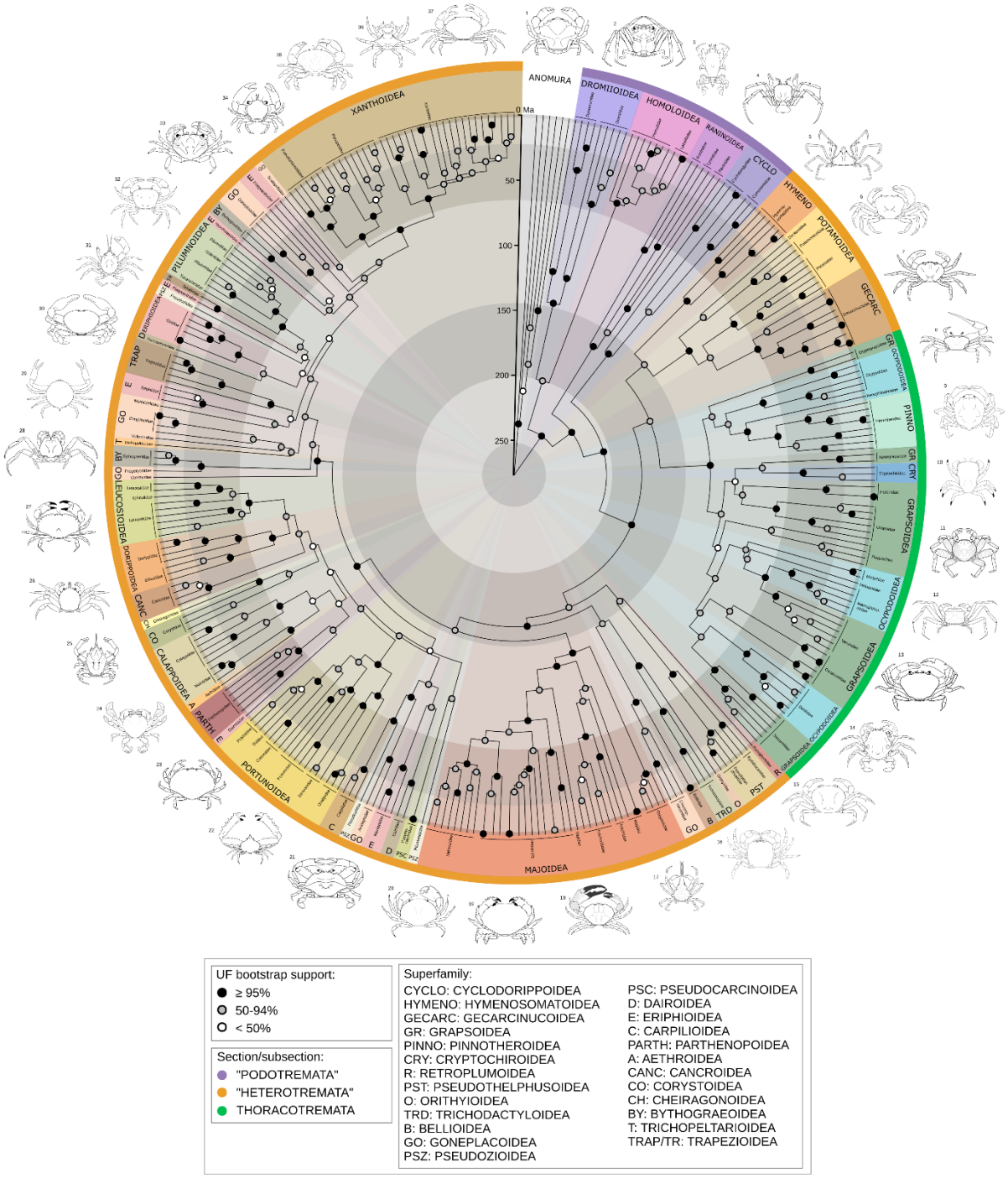

Figure 2. Summary of phylogeny and divergence time estimates for Brachyura. Posterior ages were estimated in BEAST2 using a fixed topology resulting from the concatenated ML analysis in IQ-TREE, 36 vetted node calibrations, a birth-death tree prior, and relaxed lognormal clock model. Shaded circles at nodes represent ultrafast bootstraps. Pie slices are colored by superfamily, with the outermost ring colored by taxonomic section. Line drawings, one representative per superfamily (numbers corresponding to taxa in Table S5), by Javier Luque and Harrison Mancke.

Revision of brachyuran systematics at nodes above the family level would best be undertaken with phylogenomic scale data (Wolfe et al. 2019 and phylogenetic informativeness

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profiles, **Figure S14**), therefore we only briefly summarize the topology results here and in **Figure 2**. Podotremes are paraphyletic with respect to Eubrachyura, forming the following successive clades: Dromioidea + Homoloidea (this pairing has low support from ML, but strong from BI), Raninoidea, and Cyclodorippoidea (latter two clades with full support). Within Eubrachyura, subsection Heterotremata is paraphyletic with respect to monophyletic Thoracotremata. The so-called primary freshwater crabs are polyphyletic. The African and Eurasian groups (Potamoidea and Gecarcinucoidea) form a clade (UF bootstrap = 95, posterior probability = 0.89), and are themselves the sister clade of the Gondwanan Hymenosomatoidea (UF bootstrap = 92, posterior probability = 1). Together, this group comprises the sister group of Thoracotremata, with moderate support from ML (albeit with low concordance factors) and full support from BI. Within Thoracotremata, some higher-level relationships are weakly supported by ML (UF bootstraps < 75%, low gCF), but most nodes are similar to BI (where they have moderate to high support). Both Grapsoidea and Ocypodoidea are polyphyletic.

Meanwhile, the Neotropical freshwater groups branch off within clades including the deepest (Pseudothelphusoidea) and second deepest (Trichodactyloidea) divergences within the main heterotreme group, although these nodes are not strongly supported by traditional metrics in either analysis (concordance factors for both are > 60, some of the highest in our data). The remaining heterotremes are subdivided into Majoidea, and two large supported clades containing 24 and 23 families, respectively. Within these latter clades, the superfamilies Eriphioidea and Goneplacoidea are strongly polyphyletic. Some deep splits within both clades are poorly supported (some nodes UF bootstrap < 50, concordance factors = 0, posterior probability < 0.8).

We find that 76 of all sequenced families are monophyletic, with the same exceptions in both ML and BI trees. Paraphyletic families are: the podotremes Homolidae (containing Latreillidae), Raninidae (containing Lyreididae), and Cyclodorippidae (containing Cymonomidae), and the heterotremes Epialtidae (containing Mithracidae), Carcinidae (containing Thiidae and Polybiidae), Corystidae (containing Cheiragonidae), Leucosiidae (containing Iphiculidae), and Pilumnidae (containing Galenidae). Polyphyletic families, all within heterotremes, are: Majidae, Bythograeidae, Platyxanthidae, and Pseudoziidae.

Divergence times

Results of divergence time inference vary depending on parameters used, with results of the vetted calibration strategy distinct on the major axis (**Figure 3A**), and the FBD and BDSS results being similar to one another. Although none of the random local clock analyses converged after extensive runtime, we plotted samples from their individual chains with burnin of 50% to reduce the effect of poor mixing; when included, the choice of clock model also differs significantly (**Figure 3B**), but mostly in the same direction at the same nodes as the calibration strategy (**Figure 3C**). In case the unconverged analyses were skewing the results, we plotted results from relaxed lognormal clocks alone (**Figure S15**), finding the groupings by calibration strategy were upheld.

Similar to Wolfe et al. (2019), using the vetted node calibrations, the divergence of Meiura (i.e., the root node) is inferred in the Permian (mean age at 277 Ma), while crown group Brachyura diverged in the Triassic (mean age 241 Ma), and crown group Eubrachyura in the

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Jurassic (mean age 179 Ma). Superfamily level divergences were inferred in the Jurassic for podotremes, and almost entirely within the Cretaceous within Eubrachyura (**Figure S16**).

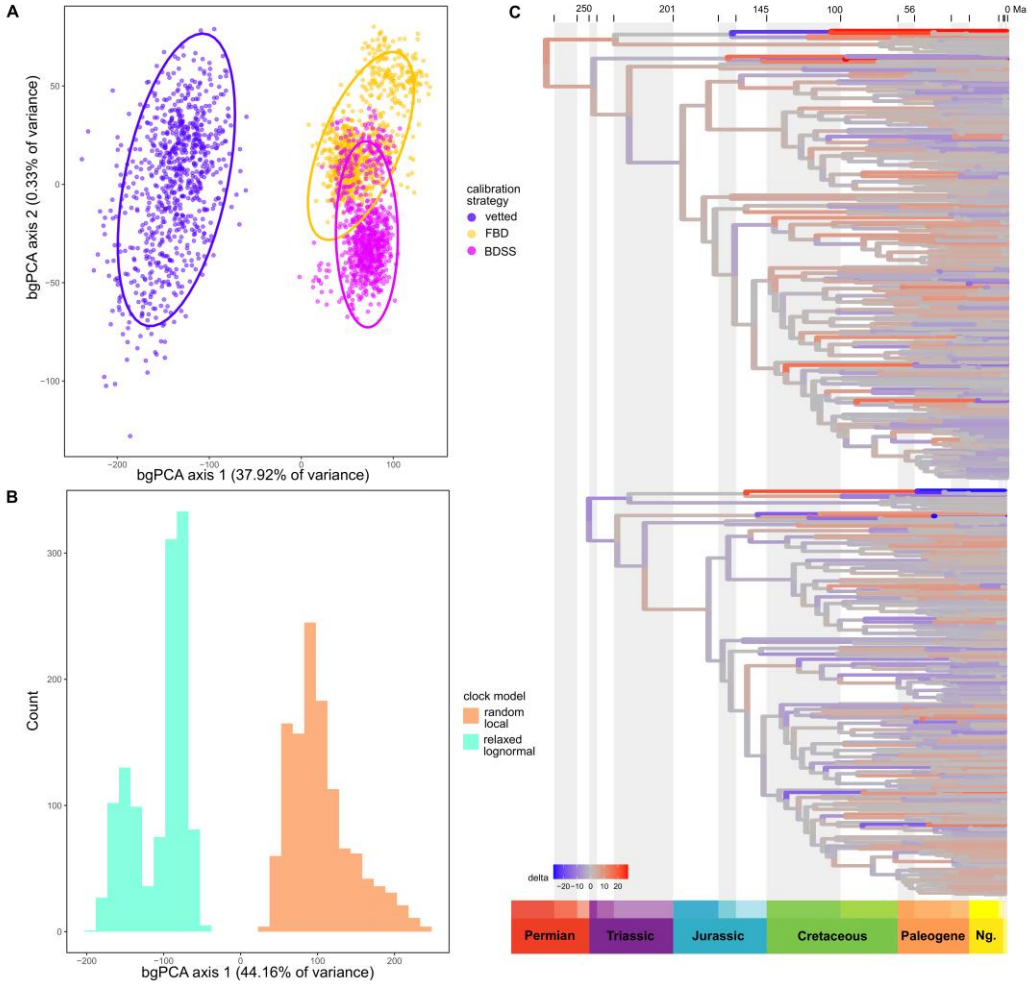

Figure 3. Sensitivity of divergence time estimates to inference strategy plotted with *chronospace*, with outgroup taxa removed from these analyses. (**A**) Between--group principal component analysis (bgPCA) separating chronograms by calibration strategy and (**B**) by clock model (note: analyses with the random local clock model did not converge, so individual chains are sampled here with 50% burnin). (**C**) Change in branch lengths along the major bgPCA axis, discriminating based on calibration strategy. Negative extreme above, positive extreme below.

Divergence estimates using fossil occurrence sampling were both considerably younger than with the vetted calibrations, with the root estimate in the Jurassic in both cases (mean ages at 180 Ma for FBD, and 191 Ma for BDSS; **Figures S17-18**). The PBDB calibrated analyses are relatively immune to the root prior (**Figure S19A**). Most other nodes were similarly compressed, with crown group Brachyura in the Jurassic and superfamily level divergences pushed to the Upper Cretaceous and Paleogene, although the posterior did not follow the marginal prior at some nodes with BDSS (**Figure S19B**). These analyses often inferred the placement of "rogue" fossils within the stem groups of their families. Consequently, a number of family level crown group ages were underestimated relative to their known vetted calibrations (e.g., Dromiidae, Dynomenidae, Raninidae, Percnidae, Varunidae, Euryplacidae, and Panopeidae; **Table S2**).

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Evolution of terrestriality

In the summary of stochastic character mapping, six total shifts from marine to non-marine were inferred (**Figure S20**). These were at the base of Pseudothelphusoidea, Trichodactylidae, Menippidae, Eriphiidae, and Oziidae, and at the base of the clade of (Thoracotremata, Hymenosomatidae, Potamoidea, Gecarcinucidae). The latter node was split, with slightly higher posterior probability of being freshwater than terrestrial or marine, leading to a freshwater node for the base of (Hymenosomatidae, Potamoidea, Gecarcinucidae) and a terrestrial common ancestor of Thoracotremata. As individual stochastic character maps inferred shifts on branches leading to a single coded tip (e.g., *Carcinus maenas*), the median number of shifts to non-marine was 12. One shift from the freshwater to terrestrial pathway was found in Hymenosomatidae (note, all non-zero grades were collapsed, so the "terrestrial" members here are intertidal). Two shifts from terrestrial to freshwater were found in Glyptograpsidae and Varunidae, respectively. Two reversals to marine were inferred at the clades of Xenophthalmidae and Pinnotheridae, and Cryptochiridae.

Using threshold models for both transition pathways, the best-fitting model was OU based on the lowest output Deviance Information Criterion (DIC) (**Table S6**). For the direct pathway, two shifts to non-marine grades were inferred at nodes: one at the base of Thoracotremata, and one in Menippidae (**Figures 4, S21**). If we consider grades 1 and 2 to be semi-terrestrial (similar to a character state from Tsang et al. [2022] referring to intertidal habitats), then the number of node origins for grades 3–5 is three: one each at the base of Ocypodidae, the clade formed by (Gecarcinidae, Sesarmidae, and Dotillidae), and the clade formed by (Mictyridae, Heloeciidae, Macrophthalmidae, and Varunidae). The last clade features a return to grade 2 at the base of the clade of Macrophthalmidae and Varunidae. Based on the estimated liabilities (i.e., thresholds of change required to transition to a different grade), it is 8–34 times easier to move to grades 1 and 2 than to grades 3 and above (**Table S6**, **Figure S22A-B**). Six reversals to not being terrestrial via this pathway (i.e., scored as grade 0) are inferred in: Glyptograpsidae, the clade of Xenophthalmidae and Pinnotheridae, Xenograpsidae, Cryptochiridae, Plagusiidae, and Varunidae. In the case of Glyptograpsidae and Varunidae, these shifts are to the indirect freshwater pathway (**Figure 4**). Some tips that were coded with a majority of the prior probability failed to infer a shift at any nodes, such as Hymenosomatidae, Eriphiidae, and Oziidae (60% grade 1 for the former, 100% for the latter two), and Gecarcinidae (entirely grades 3–5, with 70% at grades 4 and 5).

For the indirect pathway, four shifts to non-marine grades were inferred at nodes: one at the base of the clades Potamoidea + Gecarcinucidae, and one each for Glyptograpsidae, Pseudothelphusoidea, and Trichodactylidae (**Figures 4, S23**). If we consider grades 1 and 2 to be semi-terrestrial, then only Pseudothelphusoidea and Potamidae + Gecarcinucidae are inferred (each with nodes at grade 3). The liabilities indicate that it is extremely easy to move to grade 1, but 10 times harder to move to grade 2, and over 100 times harder to move to grade 3 (**Table S6**, **Figure S22C-D**). Hymenosomatidae has 25% tip prior probabilities at grade 1, but no shifts were inferred. When analyzed as subclades, a transition was inferred from ancestrally freshwater to non-freshwater in Hymenosomatidae (**Figure S24**), but we could not infer a transition from ancestrally terrestrial (direct pathway) to freshwater for Sesarmidae (**Figure S25**).

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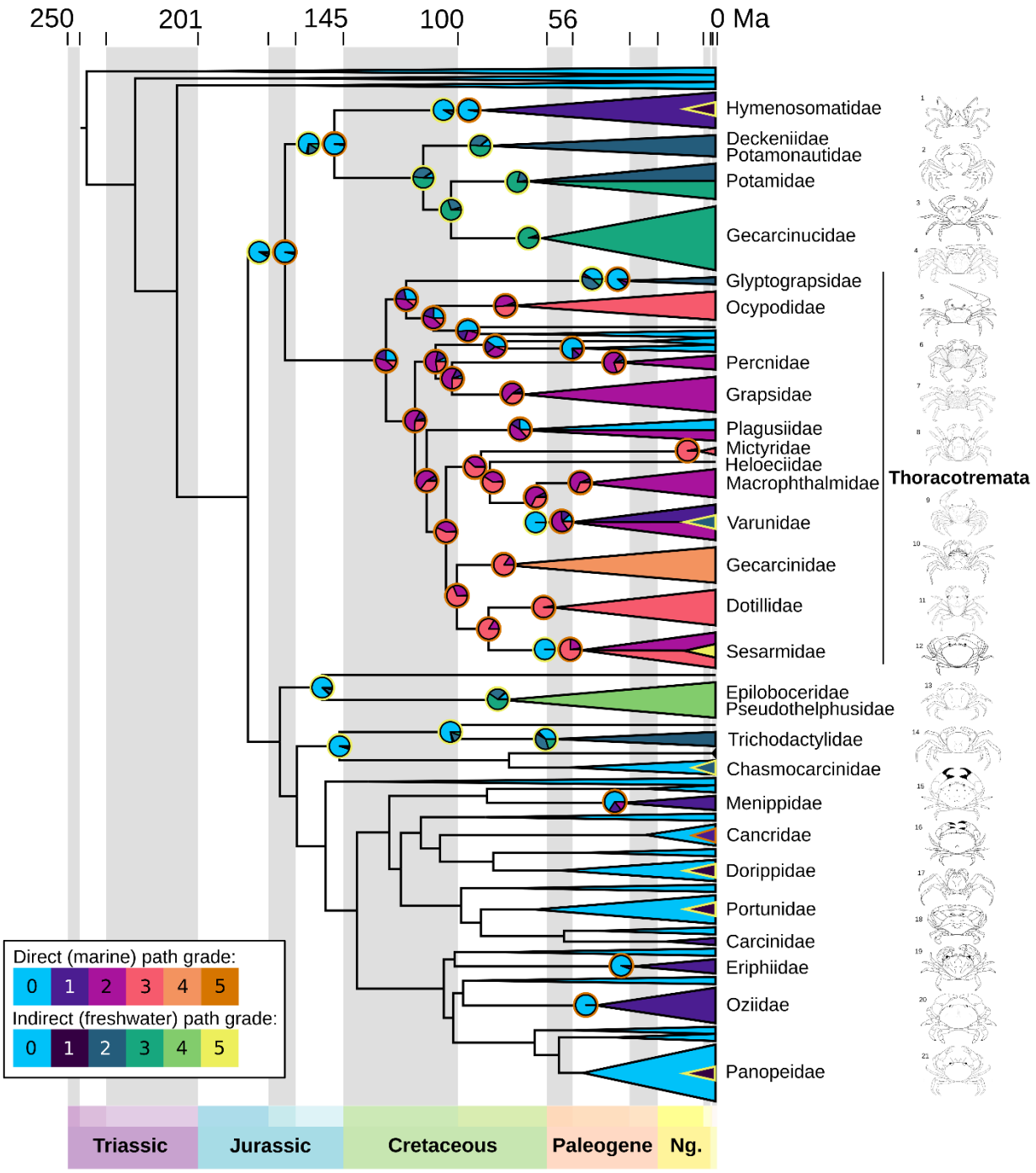

Figure 4. Composite of ancestral state reconstructions for the two transition pathways under best-fitting OU models in *ancThresh*, with fully marine clades (all families that are not labeled) reduced for clarity and outgroups removed. Legend for grades and colors representing each pathway at bottom left: fully marine crabs (grade 0), lower intertidal and estuaries (grade 1), upper intertidal and freshwater (grade 2), beaches and riverbanks (grade 3), and coastal forests and jungles (grades 4-5). Pies at nodes represent the estimated ancestral state with the outer ring indicating the pathway (at some nodes, both pathways are shown; when node is inferred marine, none are shown). Tip codings are based on estimates by family (Table S4), with the collapsed clades showing the color that represents the largest slice of their prior probabilities (split in the case of equal probabilities for two grades). For clades that have a small number of taxa in a grade from the opposite pathway, a small triangle is added. Line drawings at right (numbers corresponding to taxa in Table S5), by Javier Luque and Harrison Mancke.

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Discussion

Relationships and divergence of true crabs

Previous molecular phylogenies of Brachyura have been constructed from eight to 10 Sanger loci (Tsang et al. 2014, 2022), mitochondrial genomes (Tang et al. 2017; Tan et al. 2019; Wang et al. 2021; Jennings et al. 2021; Lau et al. 2021; Sun et al. 2022; Zhang et al. 2022), transcriptomics (Ma et al. 2019) and genomic target capture (Wolfe et al. 2019). However, the deep relationships among families and superfamilies remain uncertain, as the most extensive study (Tsang et al. 2014) sampled only 58 of 104 families with eight genes and low support at deep nodes, and more extensive gene sampling was coupled with even lower taxon sampling (Timm and Bracken-Grissom 2015; Wolfe et al. 2019). Although it is evident that the genes we and others have used are insufficient to resolve deep relationships even with current taxon sampling (**Figure S14**), many regions of the tree are strongly supported. For example, the broadest strokes of our topological results (**Figure 2**) contribute to the chorus of molecular and morphological analyses rejecting the monophyly of podotremes (e.g., Ahyong et al. 2007; Tsang et al. 2014, 2022; Luque et al. 2019a, 2019b; Tan et al. 2019) and heterotremes (e.g., Scholtz and Richter 1995; von Sternberg and Cumberlidge 2001; Tsang et al. 2014; Ma et al. 2019; Tan et al. 2019). Our divergence time estimates exceed most previous publications, except the deeper ages inferred by Wolfe et al. (2019) and the hypotheses of Guinot et al. (2019), but see below for evaluation.

The relationships among thoracotremes were recently examined by Tsang et al. (2022). As in their study, we find polyphyly of Ocypodoidea (fiddler, ghost crabs, and relatives), although our Grapsoidea (shore crabs, land crabs, and relatives) are separated into five clades, as opposed to four in Tsang et al. (2022). The main nodes where our results differ are: (1) the derived position of Dotillidae (sand bubbler crabs), (2) separation of the symbiotic groups Cryptochiridae (coral gall crabs) and Pinnotheridae (pea crabs), and (3) the position of Plagusiidae (different between ML and BI in our data: see **Figure S12**). For points (2) and (3), we do recover weak support using all metrics. Ultimately, both studies use eight of the same loci. Our data incorporates the nuclear rRNA genes, with relatively low phylogenetic informativeness above the family level (**Figure S14**), yet both studies produce strong support at the base of thoracotreme families (note that Tsang et al. [2022] designated UF bootstraps > 90% as strong, which would add several nodes to our "strongly supported" category in **Figure 2**). Finally, the backbone of thoracotreme phylogeny has been briefly addressed in two phylogenomic studies (Ma et al. 2019; Wolfe et al. 2019), and our results are similar to both, including the position of Sesarmidae (e.g., mangrove and vampire crabs) under models analyzing nucleotide data. A more robust understanding of internal thoracotreme relationships may be derived with additional phylogenomic data, but our results are sufficient to infer ancestral states, with the caveat of lower confidence at the abovementioned nodes.

Polyphyly of the "primary" freshwater crab families (Deckeniidae, Epiloboceridae, Gecarcinucidae, Potamidae, Potamonautidae, Pseudothelphusidae, Trichodactylidae) has been found previously (e.g., von Sternberg and Cumberlidge 2001; Tsang et al. 2022). The inclusion of Hymenosomatidae (pillbox crabs) with the African and Eurasian freshwater groups in our results is novel, as it is the first analysis to incorporate this family in a larger tree. The grouping of African and Eurasian freshwater crabs with thoracotremes is otherwise fairly well supported

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in previous studies (e.g., Tang et al. 2017; Ma et al. 2019; Tan et al. 2019; Jennings et al. 2021; Zhang et al. 2022). We contradict previous analyses, where the Neotropical Pseudothelphusoidea were closely related to the freshwater group (Tsang et al. 2014) and share a number of morphological synapomorphies (Cumberlidge et al. 2021). The Neotropical Trichodactylidae were more closely related to other heterotremes. Our results weakly support convergent origins of Pseudothelphusoidea (**Figure 2**), leading to subsequent inference of separate transitions to freshwater. Divergence time estimates under all models push the origin of all primary freshwater groups older than 66 Ma, with the African and Eurasian group over 100 Ma, consistent with a deeper cryptic history (Wolfe et al. 2019), particularly in non-marine environments (Tsang et al. 2014; Luque et al. 2021). Nevertheless, our mean divergence time estimates post-date the complete breakup of Pangaea (approximately 175 Ma), and do not support the Gondwanan origin of freshwater crabs (Klaus et al. 2011; Tsang et al. 2014) with these data.

Many of the relationships among families and superfamilies of the remaining heterotremes are not critical for the question of terrestriality. However, most of the deep relationships that we do observe, even with poor nodal support from ML, are congruent with the broad results retrieved from target capture of over 400 loci (Wolfe et al. 2019), except for the position of Menippidae (stone crabs). Our topologies for the relationships within superfamilies are largely congruent with previous Sanger data (Tsang et al. 2014), with some families exchanging places (e.g., Evans 2018; Mendoza et al. 2022) and some other groups with previous conflict still unresolved (Hultgren and Stachowicz 2008; Lai et al. 2014; Windsor and Felder 2014). The position of Dorippoidea nested well within heterotremes is consistent with previous molecular analysis (Tsang et al. 2014), but may confound hypotheses of early fossils that assume dorippoids are the earliest eubrachyuran branch (e.g., Guinot et al. 2019). One potentially novel result is the polyphyly of Bythograeoidea (hydrothermal vent crabs), that had not previously been included in a global analysis with as many genera (absent from Tsang et al. [2014]; no outgroups in concatenated analyses of Mateos et al. [2012]). Several non-monophyletic families were broken up by the insertion of closely related families, perhaps representing morphological groups that could be redefined as subfamilies (e.g., Lyreididae, Iphiculidae, potentially the cylodorippid genus *Tymolus*). In summary, we observe many similarities with previous analyses, and some new hypotheses that await improved molecular sampling before suggesting new systematic changes.

Which divergence time estimates are reliable?

The factors that we investigated for different methodological choices were the calibration strategy and the clock model. Although divergence time estimates have only been visualized previously for only one dataset of echinoids with *chronospace* (Mongiardino Koch et al. 2022), we see significant differences in our data. Our results were impacted by the tested methods even more substantially than in the echinoid data, for which the results were sensitive to clock model choice, but not to substitution model or subsets of loci (Mongiardino Koch et al. 2022). In our data, a strong separation of variance of both clock model and calibration strategy were observed (**Figure 3A, B**), with a similar pattern of posterior ages from both factors (**Figure 3C**). However, the random local clock model, which accounts for the evolution of evolutionary rates in a clade-specific manner (Drummond and Suchard 2010; Ho and Duchêne 2014), failed to converge after months of runtime, so we cannot be certain of the ultimate effect on divergence time estimates.

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We were initially interested in using FBD and BDSS because these tree models describe the processes of speciation, extinction, and fossil sampling that led to the true tree, and could be more accurate (Wright et al. 2022). A precursor method that incorporates fossil counts, but not directly into the tree model, has been previously used for lobsters (Bracken-Grissom et al. 2014). Although the gold standard for improved age accuracy is to couple process-based tree models with total evidence tip dating (i.e., morphological character data from all incorporated fossils), it was not possible to include over 300 extant taxa, plus numerous fossils. Brachyura have a somewhat good fossil record: they preserve abundant biomineralized hard parts, but the majority are dorsal carapaces and cheliped fragments. It is challenging to identify phylogenetically diagnostic characters in fragmented fossils due to substantial convergence in carapace and cheliped morphology (Guinot 2019; Luque et al. 2019b, 2021; Wolfe et al. 2021), and extensive missing data that could compromise their placement within crown groups. Nevertheless, our evaluation of the brachyuran fossil record in the context of vetted crown and stem groups identified many calibration fossils that were much older than previously appreciated. Most crown group families have exemplars preserved in the Eocene and Paleogene (66–34 Ma), as well as an increasing number of well-preserved Cretaceous fossils (Ossó 2016; Luque et al. 2017, 2021).

Although records are abundant in the PBDB, brachyuran fossil sampling is not as evenly distributed as in many clades used as test cases for the performance of FBD and skyline models (e.g., Gavryushkina et al. 2014; Heath et al. 2014; Renner et al. 2016; Barido-Sottani et al. 2019; O'Reilly and Donoghue 2020). Subsampling a fossil record using the unresolved FBD can be accurate with an evenly sampled clade such as cetaceans (Barido-Sottani et al. 2019), but can be highly inaccurate if the fossils have limited phylogenetic information (O'Reilly and Donoghue 2020). A recent analysis of mammals (Luo et al. 2021), however, found that fossil sampling density does not have linear effects on divergence time estimates. Altogether, it is difficult to generalize about the best models, unless prior knowledge is contradicted.

A major issue was estimating the root age of Meiura. Brachyura have a known ghost lineage, with stem group members *Eocarcinus* and *Eoprosopon* from the early Jurassic (approximately 190 Ma; Haug and Haug 2014; Hegna et al. 2020; Scholtz 2020; Wolfe et al. 2021). The oldest crown group brachyuran fossil occurrences in PBDB were also from the early Jurassic, representing less than 1% of total occurrences. Meanwhile, multiple modern anomuran families were already present in the late Jurassic (164–145 Ma; e.g., Fraaije et al. 2019, 2022; Robins and Klompmaker 2019), when their divergence likely took place (Bracken-Grissom et al. 2013; Wolfe et al. 2019), strongly suggesting the divergence of the common ancestor of Meiura, and probably Brachyura, happened in the very earliest, or more likely prior to, the Jurassic. Yet, the FBD and BDSS analyses, despite incorporating a small number of Jurassic occurrences, inferred impossibly young ages, as observed by O'Reilly and Donoghue (2020). Even the BDSS analysis including a time slice with no fossil sampling before the oldest occurrence (allowing a ghost lineage: Culshaw et al. 2019; O'Reilly and Donoghue 2020) seemed to be a poor fit, and could not avoid estimating an unreasonably young root age. As such, given the data currently available for brachyurans, we recommend the use of vetted calibrations and a simple model over process-based tree models subsampling the entire record. We recommend caution if using FBD models (and their extensions) to estimate divergences when a morphological matrix is unavailable.

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How many times and when did crabs terrestrialize?

The number of estimated shifts to terrestriality changes when considering additional crabs with known tip states in our data. We inferred five or six shifts to non-marine lifestyles at nodes, fewer than Tsang et al. (2022) within Thoracotremata alone. All shifts occur at well-supported nodes (**Figures 2, 4**), although the common ancestor of (Thoracotremata, Hymenosomatidae, Potamoidea, Gecarcinucidae) has only moderate support, perhaps contributing to the uncertainty at this node with stochastic mapping (**Figure S20**). However, at least nine additional families have some proportion of their prior probability in grades 1–2 (some all the way up to 100%, but most with lower probabilities), nested among marine sisters (**Figure 4**). Adding these brings the number of transitions to 14, distributed from Cretaceous to the last 10 million years. Although it is not included in the molecular phylogeny, there was likely another convergent transition to non-marine lifestyle in the Cretaceous fossil *Cretapsara* (Luque et al. 2021), resulting in a total of at least 15 terrestrialization events across at least 30 families.

The three to four losses of terrestriality that we estimate include some nodes with poor support (the Cretaceous Xenograpsidae and Cryptochiridae, and the Eocene Plagusiidae). Character sequence reversals are not often favored by threshold models (Revell 2014), so it is intriguing that we find these nodes. Across the tree of eukaryotic life, reversals to marine from non-marine lifestyles are more common than expected (Jamy et al. 2022), and more have been found in Thoracotremata (Tsang et al. 2022), so we could indeed be underestimating the phenomenon of returning to a marine environment.

Across plants and animals, more terrestrial species come from freshwater ancestors (Román-Palacios et al. 2022), a pathway we only observe potentially once, in Hymenosomatidae. We estimate two instances of freshwater crabs evolving from terrestrial ancestors, in Glyptograpsidae and Varunidae. Owing to the ordering of grades through the transition pathways, and the implementation of *ancThresh*, it is very challenging to infer these changes. The estimated liabilities are too high to infer freshwater Sesarmidae from a terrestrial ancestor, although this is further complicated by a higher base grade (i.e., starting at grade 2–3) within the two transition pathways, and possibly by the number of species that have convergently evolved arboreal lifestyles in mangroves (Fratini et al. 2005; Naruse and Ng 2020) and in freshwater derived habitats (Diesel 1989). These four clades are, however, the only brachyuran groups where the data suggest transitions between the main pathways, so the overall number of convergent events is not affected.

Implications for early phases of arthropod terrestrialization

An outstanding question is the lifestyle of the common ancestor of the clade containing the majority of non-marine crabs: Thoracotremata, Hymenosomatoidea, Potamoidea, Gecarcinucoidea. Stochastic character mapping suggests the state of this node is uncertain (**Figure S20**), although the common ancestor may have been estuarine and likely lived in the Jurassic. It is also quite possible that the common ancestor was marine (**Figure 4**), and direct and indirect pathways were established independently in the thoracotreme and freshwater clades. If the ancestor was estuarine, the Early Cretaceous common ancestor of Thoracotremata transitioned from the indirect pathway to a likely intertidal grade on the direct pathway. Crabs in low grades of both transition pathways have different osmoregulatory adaptations (Watson-Zink 2021), so perhaps this common ancestor ecologically resembled some modern

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Hymenosomatidae (**Table S3**), or resembled a hypothesis based on the only non-marine Cretaceous body fossil (Luque et al. 2021). The common ancestor could have had some degree of osmoregulatory ability, perhaps experiencing early development in marine or estuarine environments (Watson-Zink 2021).

The hypothetical common ancestor of many terrestrialized crabs, developed above, offers some lessons for understanding the Paleozoic terrestrialization of other arthropod groups. Despite a discrepancy of 100–150 Ma between divergence time estimates and body fossils, there are examples of Cambrian and Ordovician trace fossils that reveal limited excursions into non-marine environments, and perhaps more extensive life in marginal marine settings (e.g., Collette et al. 2010; Mángano et al. 2021; Buatois et al. 2022). Therefore, the fluidity of crab transitions into lower grades of terrestriality could hint at the types of adaptations other arthropods experienced in these early periods: osmoregulation and abbreviated and/or migratory larval development (Watson-Zink 2021). Other ecologies may resemble fiddler crabs that have adapted to coastal hypersaline environments, building their burrows well inland (Thurman 1984).

Additional instances of small numbers of taxa entering grades 1–2 through either pathway (e.g., Carcinidae, Panopeidae, freshwater Varunidae in **Figure 4**) could provide some insights on the early stages of terrestrial adaptation. In particular, the above examples harbor some of the most invasive crab taxa: *Carcinus maenas* (European green crab), *Hemigrapsus sanguineus* (Asian shore crab), and *Rhithropanopeus harrisii*. These species are notable for tolerating exceptionally wide-ranging salinities as larvae, and have wide and migratory habitat preferences as adults (e.g., Young and Elliott 2020). The invasive *Eriocheir sinensis* (Chinese mitten crab) can tolerate estuarine to full freshwater (Zhang et al. 2019). Another example is the hymenosomatid *Halicarcinus planatus*, with a wide salinity tolerance that could help this species adapt to, and invade, warming Antarctic waters (López-Farrán et al. 2021). Many other hymenosomatid genera have members in both freshwater and low salinity estuarine/mangrove habitats, and many have plastic osmoregulatory capabilities (Chuang and Ng 1994). Perhaps the ancestors of diverse non-marine groups originated with lifestyles similar to successful invaders.

Groups sharing convergent morphological adaptations to higher grades of terrestriality, such as branchiostegal lungs in Gecarcinucidae, Gecarcinidae, Ocypodidae, and Pseudothelphusidae, or water-wicking setae in Gecarcinidae and Sesarmidae (Watson-Zink 2021 and **Table S3**), are deeply separated by over 150 Ma of evolution. Convergent terrestrial morphology in crabs, with likely pathways through a habitat gradient, perhaps with some traits of invasive taxa, could illuminate the hypothesis that arachnids convergently transitioned to terrestriality (Ballesteros et al. 2022). However, it is possible that horseshoe crabs (chelicerates, not decapods) returned to marine habitats even if they are phylogenetically nested within arachnids, as our crab analyses have inferred at least two Cretaceous reversals that involved likely intertidal (grade 2) ancestors.

Conclusions

Herein, we inferred a large molecular phylogeny of true crabs, estimated divergence times that were older than previously thought, and estimated the number of transitions from marine to non-marine lifestyles. We found up to 15 convergent transitions through direct and

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indirect pathways, with at least three climbing to higher degrees of terrestrial adaptation. The most highly terrestrial clades were some of the oldest non-marine inferences in our data, with their common ancestors having diverged over 66 Ma. At least nine more recent events throughout the Cenozoic led to crabs living in intertidal and marginal marine environments, a shift that is estimated to be much easier based on lower threshold liability and likely fewer traits required. As instances of convergent evolution provide emerging models in the form of "natural experiments", the framework we have developed to compare the gradient of adaptations will enable future research that aims to "predict" the constraints leading to repeated trait evolution and better understand the drivers of biodiversity across related groups.

Author Contributions

JMW, KAC, DLF, HDBG conceived the project; STA, TYC, KHC, KAC, SRD, DLF, JWM, PKLN, EPT, NDP, RR, BPT, LMT, RW, AMW, HDBG provided samples; HDBG, EPT, RR, BPT, LMT, AMW extracted DNA and conducted sequencing; LB, HDBG curated sequence data; LB conducted phylogenetic analysis; JL vetted fossil calibrations; JMW, JBS developed and performed divergence time analysis; JMW, VMWZ coded natural history; JMW performed comparative methods and wrote the manuscript with input from all authors.

Supplementary Material

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.tmpg4f52z

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Figure 1. Representative brachyurans displaying different lifestyles and grades of terrestriality. (**A-E**) Fully marine lifestyle, grade 0; (**F-J**) direct marine transition pathway, grades 1-5 bottom to top; (**K-O**) indirect freshwater transition pathway, grades 1-5 bottom to top. (**A**) Portunidae: *Portunus sayi* (Bermuda); (**B**) Calappidae: *Calappa calappa* (Kwajalein Atoll, Marshall Islands); (**C**) Epialtidae: *Cyclocoeloma tuberculatum* (Anilao, Philippines); (**D**) Raninidae: *Ranina ranina* (Oahu, Hawaii, USA); (**E**) Homolidae: *Paromola cuvieri* (Gorringe Ridge, Portugal); (**F**) Gecarcinidae: *Gecarcoidea natalis* (Christmas Island, Australia); (**G**) Gecarcinidae: *Cardisoma guanhumi* (Fort Lauderdale, Florida, USA); (**H**) Ocypodidae: *Uca heteropleura* (Pacific coast, Panama); (**I**) Grapsidae: *Leptograpsus variegatus* (Tasmania, Australia); (**J**) Eriphiidae: *Eriphia sebana* (Heron Island, Queensland, Australia); (**K**) Sesarmidae: *Geosesarma dennerle* (aquarium specimen); (**L**) Deckeniidae: *Madagapotamon humberti* (Montagne de Français Reserve, Madagascar); (**M**) Gecarcinucidae: *Ghatiana botti* (Sindhudurg, India); (**N**) Pseudothelphusidae indet. (Santander, Colombia); (**O**) Hymenosomatidae: *Hymenosoma orbiculare* (Langebaan Lagoon, South Africa). Photo credits: (A) Jessica Riederer; (B, C) Jeanette and Scott Johnson; (D) John Hoover; (E) © OCEANA; (F) John Tann, license CC-BY; (G) Tom Friedel, license CC-BY 3.0; (H) Kecia Kerr and Javier Luque; (I) Joanna Wolfe; (J,N) Javier Luque; (K) Henry Wong; (L) Sara Ruane; (M) Tejas Thackeray; (O) Charles Griffiths.

Figure 2. Summary of phylogeny and divergence time estimates for Brachyura. Posterior ages were estimated in BEAST2 using a fixed topology resulting from the concatenated ML analysis in IQ-TREE, 36 vetted node calibrations, a birth-death tree prior, and relaxed lognormal clock model. Shaded circles at nodes represent ultrafast bootstraps. Pie slices are colored by superfamily, with the outermost ring colored by taxonomic section. Line drawings, one representative per superfamily (numbers corresponding to taxa in Table S5), by Javier Luque and Harrison Mancke.

Figure 3. Sensitivity of divergence time estimates to inference strategy plotted with *chronospace*, with outgroup taxa removed from these analyses. (**A**) Between--group principal component analysis (bgPCA) separating chronograms by calibration strategy and (**B**) by clock model (note: analyses with the random local clock model did not converge, so individual chains are sampled here with 50% burnin). (**C**) Change in branch lengths along the major bgPCA axis, discriminating based on calibration strategy. Negative extreme above, positive extreme below.

Figure 4. Composite of ancestral state reconstructions for the two transition pathways under best-fitting OU models in *ancThresh*, with fully marine clades (all families that are not labeled) reduced for clarity and outgroups removed. Legend for grades and colors representing each pathway at bottom left: fully marine crabs (grade 0), lower intertidal and estuaries (grade 1), upper intertidal and freshwater (grade 2), beaches and riverbanks (grade 3), and coastal forests and jungles (grades 4-5). Pies at nodes represent the estimated ancestral state with the outer ring indicating the pathway (at some nodes, both pathways are shown; when node is inferred marine, none are shown). Tip codings are based on estimates by family (Table S4), with the collapsed clades showing the color that represents the largest slice of their prior probabilities (split in the case of equal probabilities for two grades). For clades that have a small number of taxa in a grade from the opposite pathway, a small triangle is added. Line drawings at right (numbers corresponding to taxa in Table S5), by Javier Luque and Harrison Mancke.

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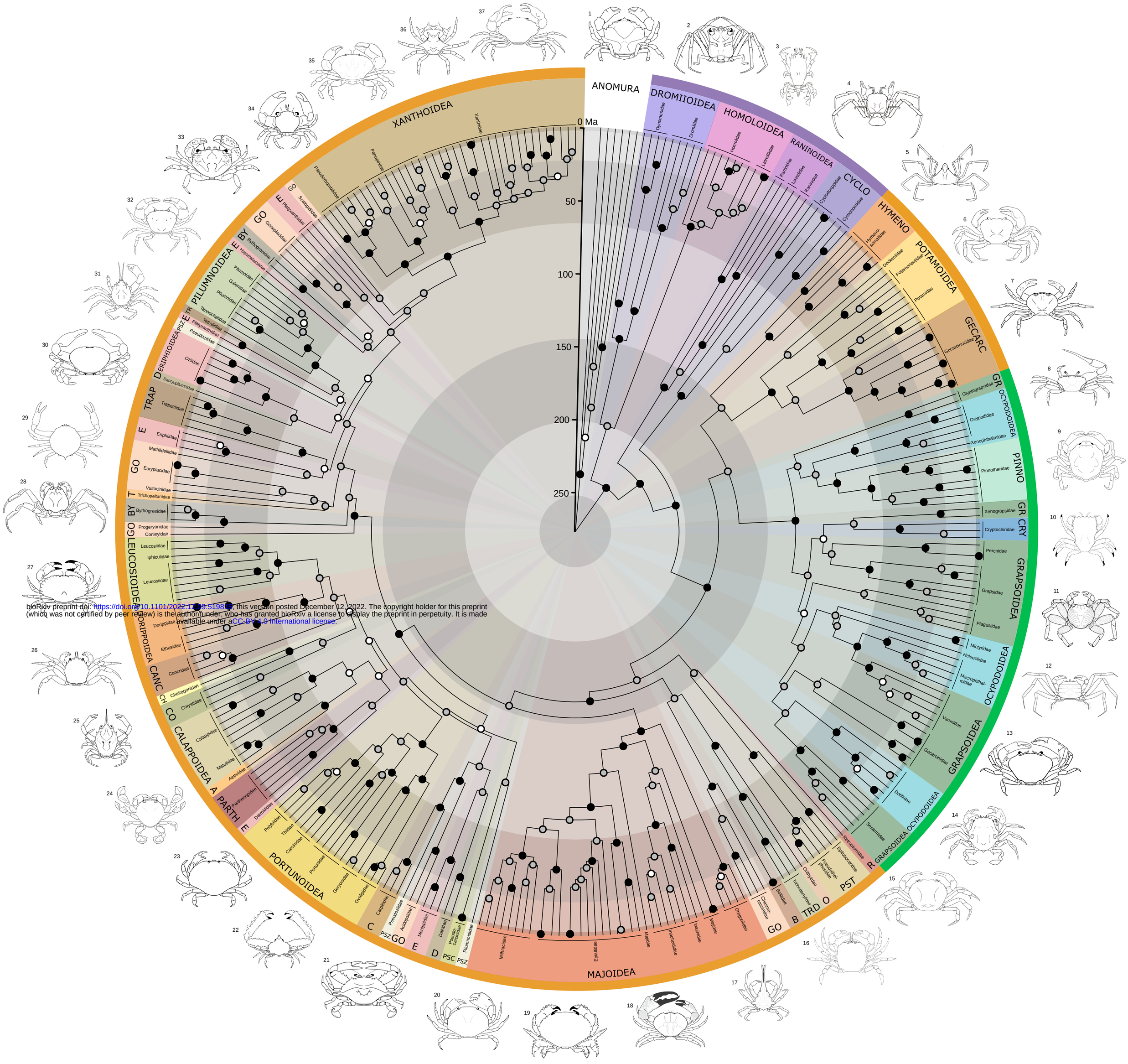

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UF bootstrap support:

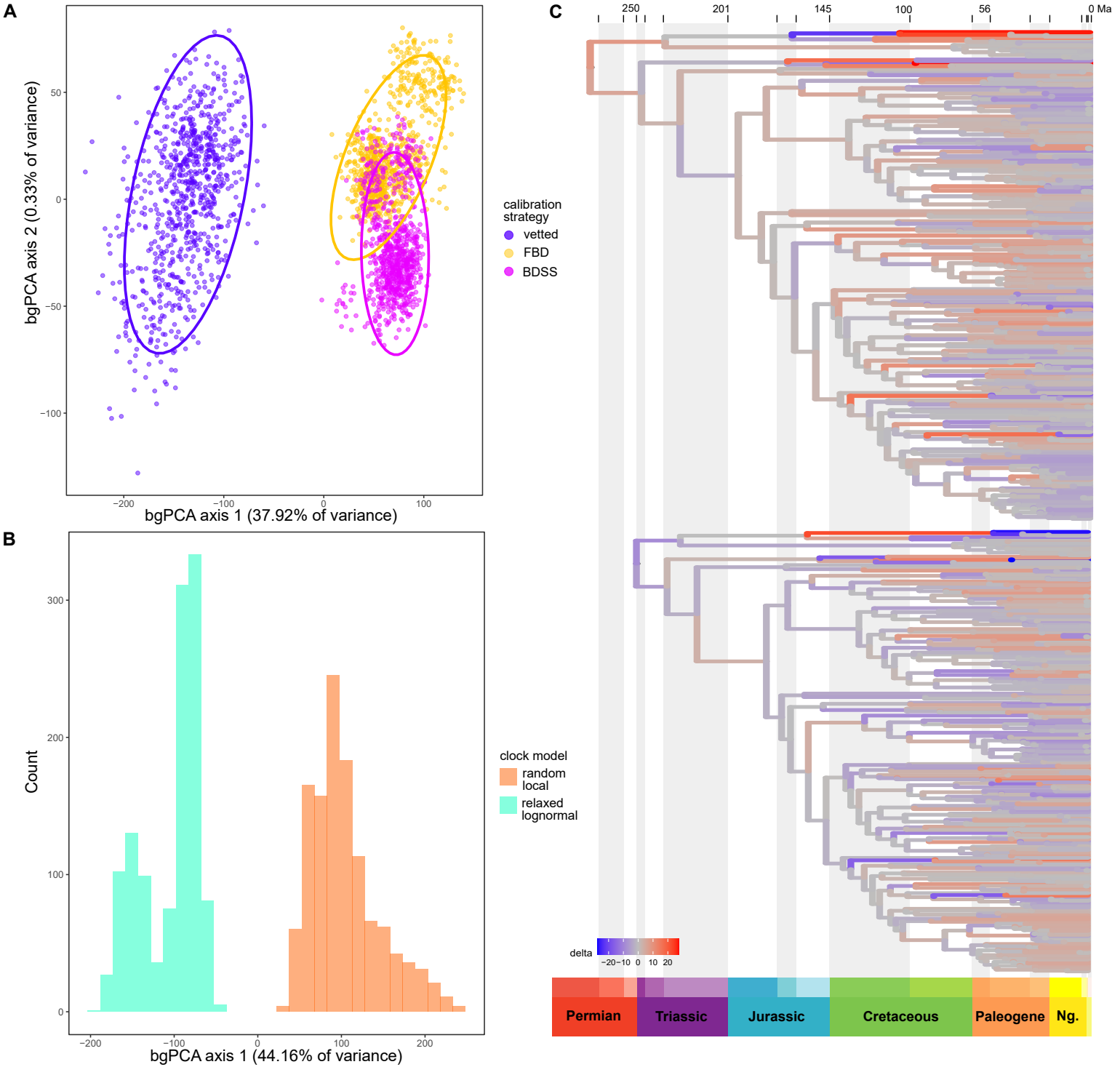
- ● ≥ 95%
- ● 50-94%
- ○ < 50%

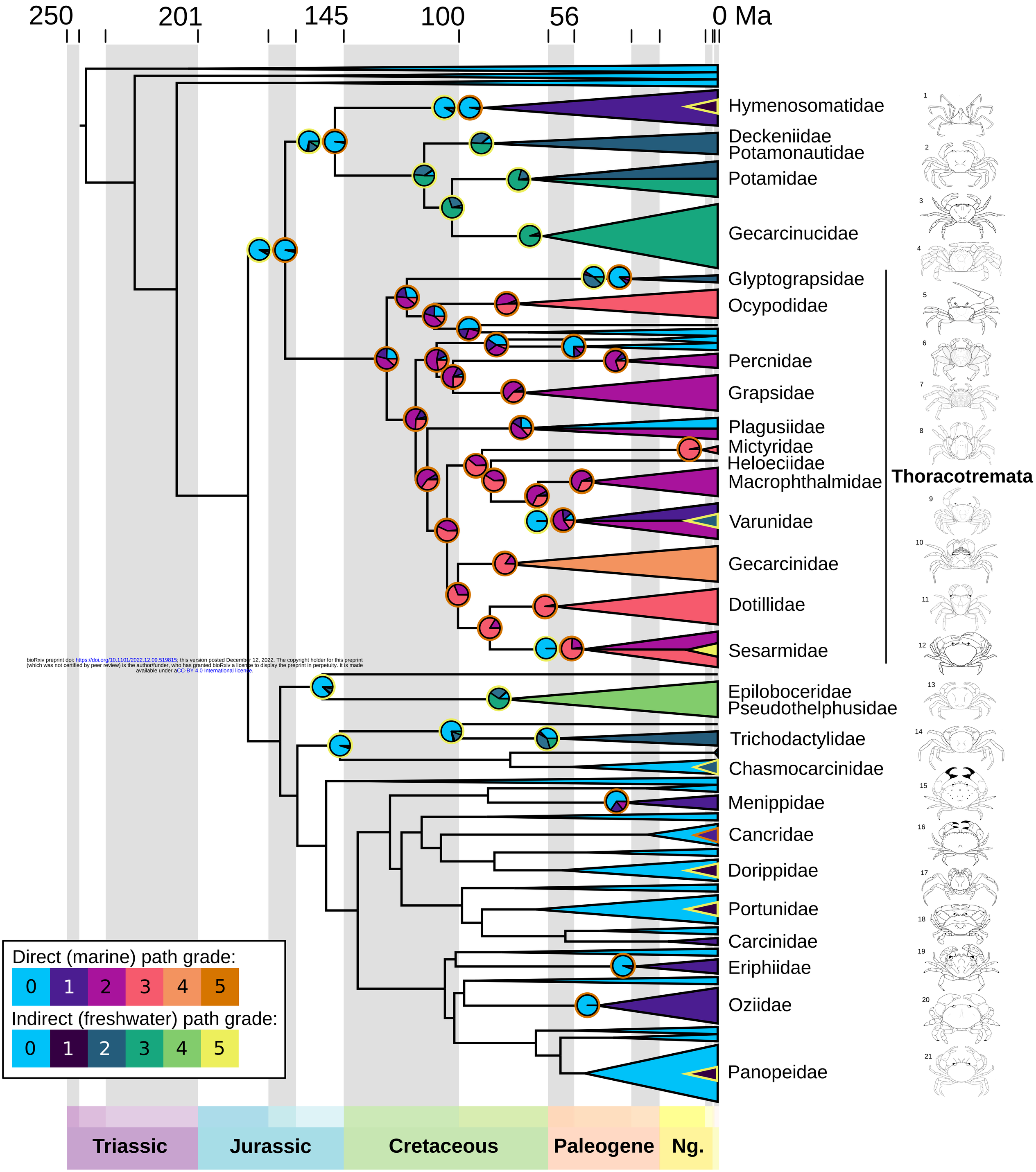
Section/subsection:

- "PODOTREMATA"
- "HETEROTREMATA"
- THORACOTREMATA

Superfamily:

CYCLO: CYCLODORIPPOIDEA
HYMENO: HYMENOSOMATOIDEA
GECARC: GECARCINUCOIDEA
GR: GRAPSOIDEA
PINNO: PINNOTHEROIDEA
CRY: CRYPTOCHIROIDEA
R: RETROPLUMOIDEA
PST: PSEUDOTHELPHUSOIDEA
O: ORITHYIOIDEA
TRD: TRICHODACTYLOIDEA
B: BELLIOIDEA
GO: GONEPLACOIDEA
PSZ: PSEUDOZIOIDEA
PSC: PSEUDOCARCINOIDEA
D: DAIROIDEA
E: ERIPHIOIDEA
C: CARPILIOIDEA
PARTH: PARTHENOPOIDEA
A: AETHROIDEA
CANC: CANCROIDEA
CO: CORYSTOIDEA
CH: CHEIRAGONOIDEA
BY: BYTHOGRAEOIDEA
T: TRICHOPELTARIOIDEA
TRAP/TR: TRAPEZIOIDEA


A
bgPCA axis 2 (0.33% of variance)
bgPCA axis 1 (37.92% of variance)
calibration strategy
vetted
FBD
BDSS
B
Count
bgPCA axis 1 (44.16% of variance)
clock model
random local
relaxed lognormal
C
250
201
145
100
56
0 Ma
delta
−20 −10 0 10 20
Permian
Triassic
Jurassic
Cretaceous
Paleogene
Ng.



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Supplemental Information:

Text S1. Fossil node calibrations with references. The topology defining the nodes is the concatenated ML tree.
Text S2. References associated with natural history codings in Table S3.

Figure S1. Gene tree for 12S. Nodes are unlabeled as gene trees were calculated as part of the concordance factor analysis (labels visualized in Figure S11). Branches colored by superfamily, as for Figure 2.
Figure S2. Gene tree for 16S. Branches colored by superfamily, as for Figure 2.
Figure S3. Gene tree for 18S. Branches colored by superfamily, as for Figure 2.
Figure S4. Gene tree for 28S. Branches colored by superfamily, as for Figure 2.
Figure S5. Gene tree for AK. Branches colored by superfamily, as for Figure 2.
Figure S6. Gene tree for enolase. Branches colored by superfamily, as for Figure 2.
Figure S7. Gene tree for GADPH. Branches colored by superfamily, as for Figure 2.
Figure S8. Gene tree for H3. Branches colored by superfamily, as for Figure 2.
Figure S9. Gene tree for NaK. Branches colored by superfamily, as for Figure 2.
Figure S10. Gene tree for PEPCK. Branches colored by superfamily, as for Figure 2.
Figure S11. Full phylogenetic hypothesis for Brachyura based on the topology from the ML concatenated analysis. Values at nodes represent ultrafast bootstraps / gene concordance factors (gCF) by partition / updated site concordance factors (sCF). Branches colored by superfamily, as for Figure 2.
Figure S12. Full phylogenetic hypothesis for Brachyura based on the topology from the Bayesian concatenated analysis. Values at nodes represent posterior probabilities. Branches colored by superfamily, as for Figure 2.
Figure S13. Plots of concordance factors versus UF bootstrap values for the ML concatenated tree. (**A**) Gene concordance factors by partition. (**B**) Updated site concordance factors.
Figure S14. Results of phylogenetic informativeness profiling for 10 Sanger genes.
Figure S15. Sensitivity of divergence time estimates to inference strategy plotted with *chronospace*, with outgroup taxa removed from these analyses. This plot shows between--group principal component analysis (bgPCA) separating chronograms by calibration strategy, for only relaxed lognormal clock models (all fully converged).
Figure S16. Full divergence time estimates for Brachyura as depicted in Figure 2. Posterior ages were estimated in BEAST2 using 36 vetted node calibrations (represented by numbered circles following the order in Text S1) and the topology fixed from Figure S11, a birth-death tree prior, and relaxed lognormal clock model. Horizontal shaded bars represent 95% HPD intervals. Branches colored by superfamily, as for Figure 2.
Figure S17. Full divergence time estimates for Brachyura using the FBD. Posterior ages were estimated in BEAST2 using 328 calibrations from PBDB added as rogues to the topology fixed from Figure S11, an FBD tree prior, and relaxed lognormal clock model. Horizontal shaded bars represent 95% HPD intervals. Branches colored by superfamily, as for Figure 2.
Figure S18. Full divergence time estimates for Brachyura using BDSS. Posterior ages were estimated in BEAST2 using 328 calibrations from PBDB added as rogues to the topology fixed from Figure S11, a BDSS tree prior, and relaxed lognormal clock model. Horizontal shaded bars represent 95% HPD intervals. Branches colored by superfamily, as for Figure 2.

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Figure S19. Comparison of posterior probability distributions for divergence time analyses under different calibration strategies in BEAST2, and the same analyses under the marginal prior (removing sequence data). The posterior analyses are shaded; marginal priors are superimposed on the same axes with a heavy line of the same color. (**A**) Root; (**B**) 20 most sensitive nodes, calculated based on Figure 3A.
Figure S20. Summary of 500 stochastic character maps coding tips in a simplified form as: fully marine, terrestrial (through direct marine pathway), and freshwater, under the best-fitting all rates different (ARD) model. These codings are based on the transition pathways scored from the literature supported data in Table S3.
Figure S21. Ancestral state reconstruction for the sequence from fully marine to terrestrial through direct marine pathway, under the best-fitting OU model in *ancThresh*. The tip codings are based on estimates by family as coded in Table S4, with their prior probabilities visualized as small pies at tips.
Figure S22. Posterior density of liabilities estimated in *ancThresh*, indicating the thresholds of change required to shift character states. As in Sallan et al. (2018), the threshold for exiting marine (grade 0) is held at 0, and values for exiting grade 5 are infinity as there are no subsequent states to transition into. (**A**) Sequence from fully marine to terrestrial through direct marine pathway, under OU model, and (**B**) with grade 0 removed for clarity. (**C**) Sequence from fully marine to terrestrial through indirect freshwater pathway, under OU model, and (**D**) with grades 0-1 removed for clarity.
Figure S23. Ancestral state reconstruction for the sequence from fully marine to terrestrial through indirect freshwater pathway, under the best-fitting OU model in *ancThresh*. The tip codings are based on estimates by family as coded in Table S4, with their prior probabilities visualized as small pies at tips.
Figure S24. Ancestral state reconstructions for transitions between pathways for subclade Hymenosomatidae, under the OU model in *ancThresh*. (**A**) From ancestrally freshwater to direct pathway. In this case, state 0 reflects fully marine plus terrestrial prior probabilities. (**B**) From terrestrial through the direct pathway, to freshwater. Posterior density of liabilities from (**C**) ancestrally freshwater to direct pathway and (**D**) terrestrial through the direct pathway, to freshwater.
Figure S25. Ancestral state reconstructions for transitions between pathways for subclade Sesarmidae, under the OU model in ancThresh. (**A**) From ancestrally terrestrial to indirect freshwater pathway. In this case, state 0 reflects fully marine plus terrestrial prior probabilities. (**B**) From freshwater through the indirect pathway, to terrestrial. Posterior density of liabilities from (**C**) ancestrally terrestrial to indirect freshwater pathway and (**D**) freshwater through the indirect pathway, to terrestrial.

Table S1. Sample information for new and previous sequence data.
Table S2. Fossil node calibrations with details following Wolfe et al. (2016, 2019). The topology defining the nodes is the concatenated ML tree.
Table S3. Discrete coded terrestriality grades for all sequenced taxa, with evidence for each trait supported by literature. Transition pathway 0 represents fully marine lifestyle, 1 represents transition to terrestriality through marine pathway, 2 represents transition through freshwater pathway. Grades as in Watson-Zink (2021).

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Table S4. Prior probabilities of terrestriality grades estimated for each family, accounting for states from taxa that are not sequenced, based on WoRMS. Transition pathway 0 represents fully marine lifestyle, 1 represents transition to terrestriality through marine pathway, 2 represents transition through freshwater pathway. Grades as in Watson-Zink (2021).
Table S5. Taxonomic key for line drawings in Figures 2 and 4.
Table S6. Model parameters estimated by *ancThresh*. Means reported for best-fitting model only (or OU model only for subclades), after excluding 20% burnin. As in Sallan et al. (2018), the threshold for exiting marine (grade 0) is held at 0, and values for exiting grade 5 are infinity as there are no subsequent states to transition into.

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Text S1. Fossil Calibrations

Placement	Superfamily	Family	Genus & species	Oldest fossil occurrence reported in:
Crown	Galatheoidea	Porcellanidae	*Vibrissalana jurassica* Robins and Klompmaker, 2019	Robins and Klompmaker (2019)
Crown	Dromioidea	Dromiidae	*Dromiopsis gigas* Forir, 1887	Forir (1887)
Crown	Dromioidea	Dynomenidae	*Graptocarcinus muiri* Stenzel, 1944	Stenzel (1944)
Stem	Homoloidea	Homolidae	*Doerflesia omata* Feldmann and Schweitzer, 2009	Feldmann and Schweitzer (2009)
Stem	Palaeocorystoidea	Palaeocorystidae	*Joeranina kerri* Luque et al. 2012	Luque et al. (2012)
Crown	Raninoidea	Lyreididae	*Marylyreidus punctatus* (Rathbun, 1935) (as *Notopocorystes*)	Rathbun (1935)
Crown	Cyclodorippoidea	Cymonomidae	*Cymonomus primitivus* Müller and Collins, 1991	Müller and Collins (1991)
Crown	Potamoidea	Potamidae	*Alontecarcinus buratoi* De Angeli and Caporiondo, 2019	De Angeli and Caporiondo (2019)
Crown	Ocypodoidea	Ocypodidae	*Uca maracoani* (Latreille, 1802)	Brito (1972) (as *Uca antiqua maracoani*)
Crown	Pinnotheroidea	Pinnotheridae	*Pinnixa* sp.	Luque et al. (2017)
Crown	Grapsoidea	Percnidae	*Percnon santurbanensis* Ceccon and De Angeli, 2019	Ceccon and De Angeli (2019)
Crown	Grapsoidea	Grapsidae	*Metopograpsus badenis* Müller, 2006	Müller (2006)
Crown	Grapsoidea	Varunidae	*Brachynotus corallinus* Beschin, Busulini, De Angeli & Tessier, 2007	Beschin et al. (2007)
Crown	Grapsoidea	Gecarcinidae	*Cardisoma guanhumi* Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828	Collins and Donovan (1998)
Crown	Grapsoidea	Sesarmidae	indet.	Serrano-Sánchez et al. (2016)
Crown	Pseudothelphusioidea	Pseudothelphusidae	indet.	Luque et al. (2019)
Crown	Trichodactyloidea	Trichodactylidae	indet.	Klaus et al. (2017)
Crown	Majoidea	Mithracidae	*Micippa antiqua* Beschin, De Angeli, and Checchi, 2001	Beschin et al. (2001)
Stem	Portunoidea	Eogeryonidae	*Eogeryon elegius* Ossó, 2016	Ossó (2016)
Crown	Portunoidea	Geryonidae	*Chaceon helmstedtense* (Bachmayer and Mundlos, 1968) (as *Coeloma* ?)	Bachmayer and Mundlos (1968)
Crown	Portunoidea	Portunidae: Thalamitinae	*Lessinithalamita gioiae* De Angeli and Ceccon, 2015	De Angeli and Ceccon (2015)
Crown	Portunoidea	Polybiidae	*Liocarcinus heintzi* Schweitzer and Feldmann, 2010	Schweitzer and Feldmann (2010)
Crown	Parthenopoidea	Parthenopidae	*Aragolambrus collinsi* Ferratges, Zamora, and Aurell, 2019	Ferratges et al. (2019)
Crown	Calappoidea	Calappidae	*Calappa zinsmeisteri* Feldmann and Wilson, 1988	Feldmann and Wilson (1988)
Crown	Cancroidea	Cancridae	*Anatolikos undecimspinosus* Schweitzer et al. 2006	Schweitzer et al. (2006)
Crown	Dorippoidea	Dorippidae	*Bartethusa hepatica* Quayle and Collins, 1981	Quayle and Collins (1981)
Crown	Leucosioidea	Leucosiidae	*Typilobus alponensis* Beschin, De Angeli, and Zorzin, 2009	Beschin et al. (2009)
Crown	Goneplacoidea	Euryplacidae	*Chirinocarcinus wichmanni* (Feldmann et al., 1995) (as *Glyphithyreus*)	Feldmann et al. (1995)

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Crown	Eriphioidea	Eriphiidae	*Eriphia verrucosa* (Forskål, 1775) (as *Cancer*)	Betancort et al. (2014)
Crown	Trapezioidea	Trapeziidae	*Archaeotetra lessinea* De Angeli and Ceccon, 2013	De Angeli and Ceccon (2013)
Crown	Eriphioidea	Oziidae	*Ozius collinsi* Karasawa, 1992	Karasawa (1992)
Crown	Pilumnoidea	Pilumnidae	*Glabropilumnus trispinosus* Beschin, Busulini, and Tessier *in* Beschin et al., 2016	Beschin et al. (2016)
Crown	Goneplacoidea	Goneplacidae	*Carcinoplax temikoensis* Feldmann and Maxwell, 1990	Feldmann and Maxwell (1990)
Crown	Xanthoidea	Pseudorhombilidae	*Pseudorhombila patagonica* Glaessner, 1933	Glaessner (1933)
Crown	Xanthoidea	Panopeidae	*Panopeus incises* Beschin, Busulini, De Angeli, and Tessier, 2007	Beschin et al. (2007)
Crown	Xanthoidea	Xanthidae	*Phlyctenodes edwardsi* Beschin, Busulini, and Tessier *in* Beschin et al., 2016	Beschin et al. (2016)

Fossil Calibrations References

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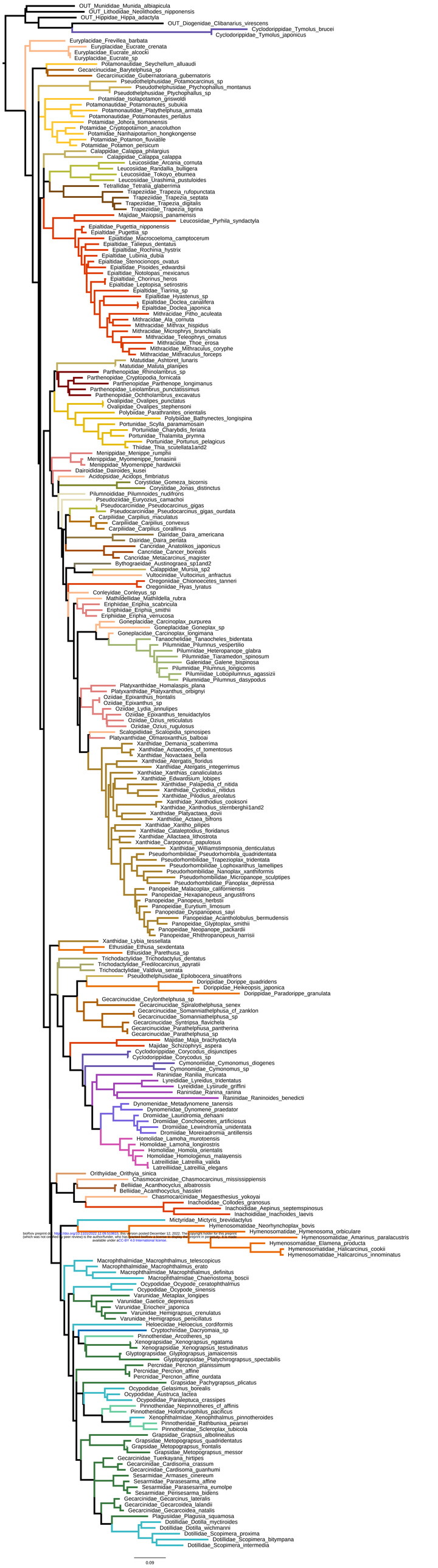

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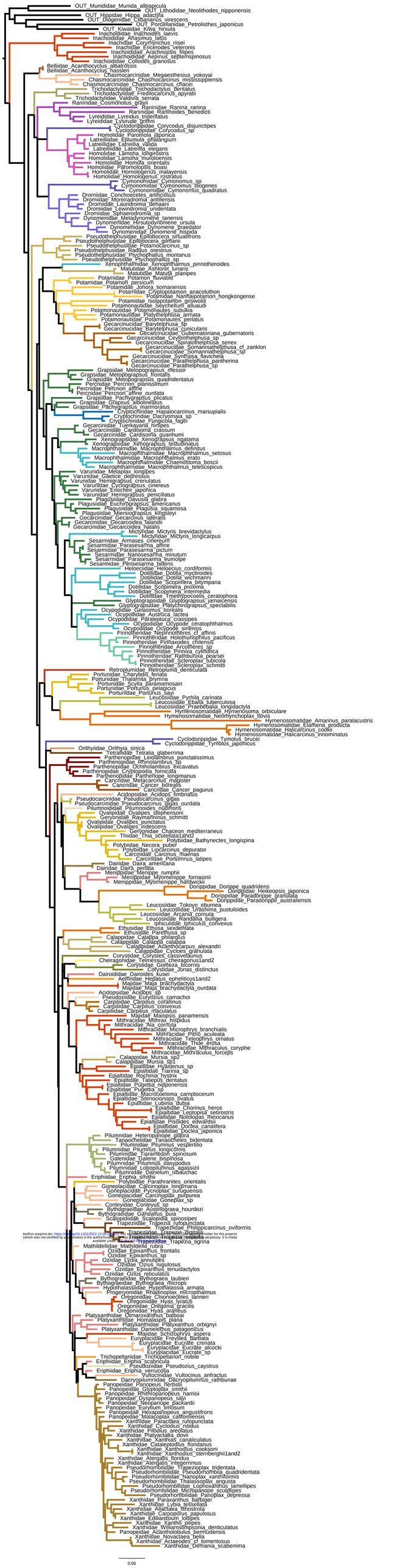

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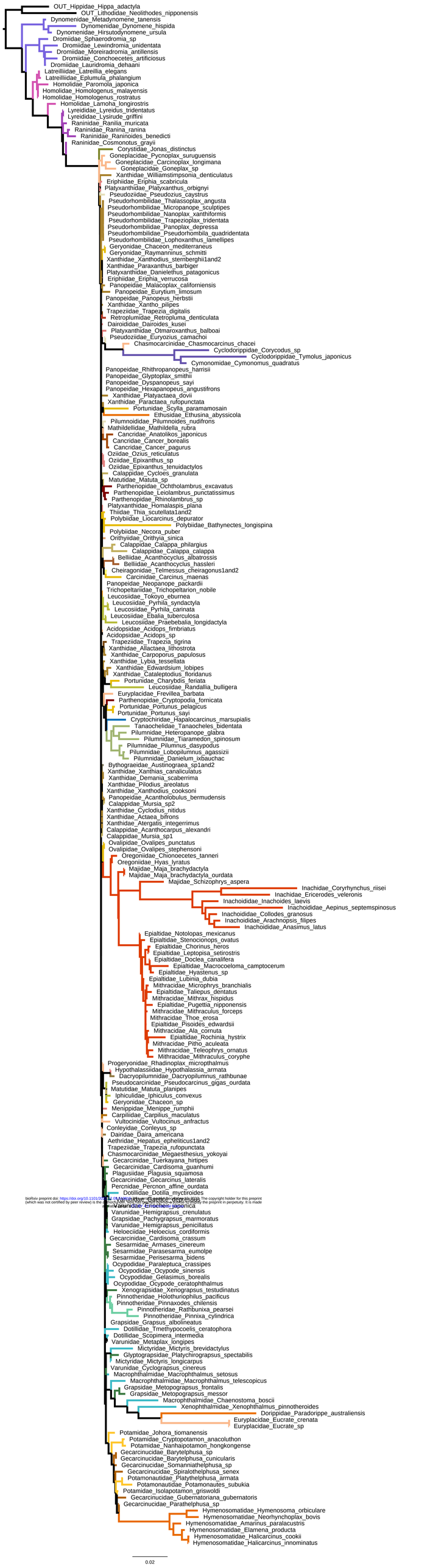

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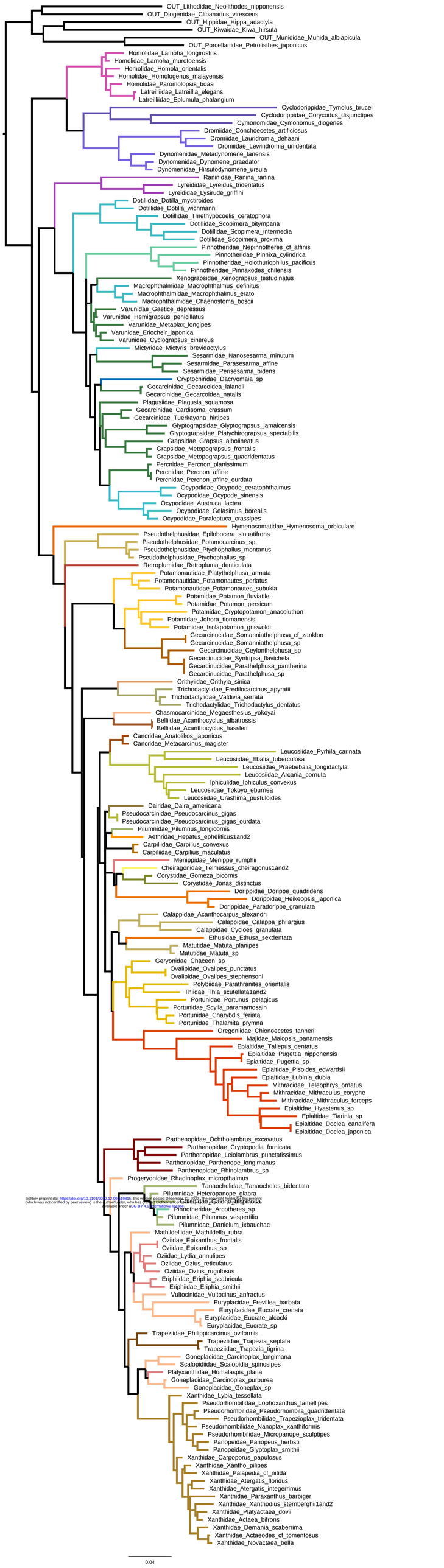

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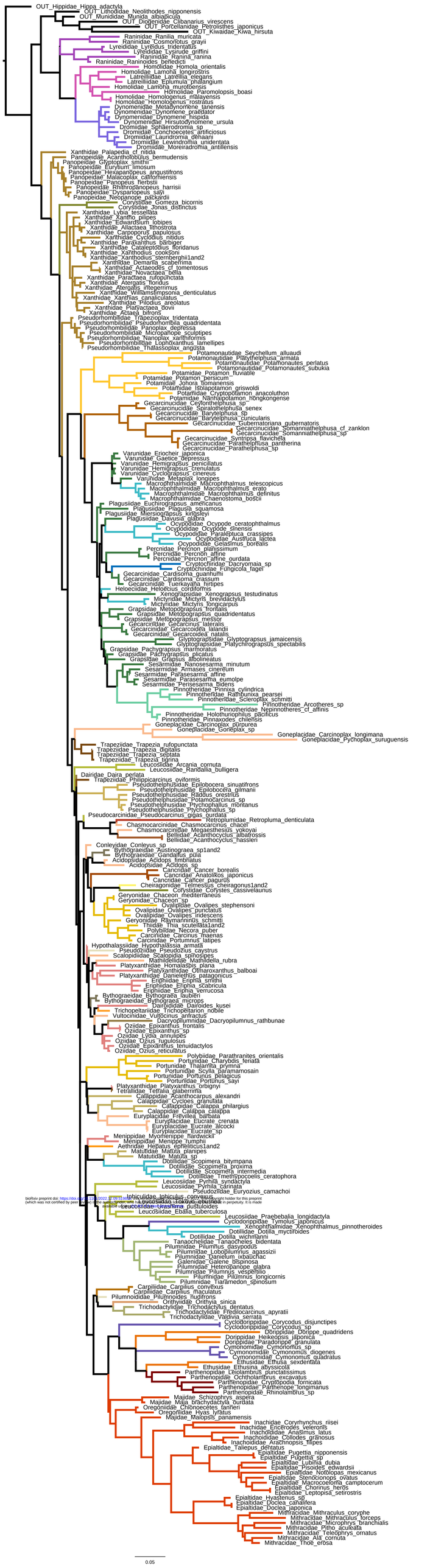

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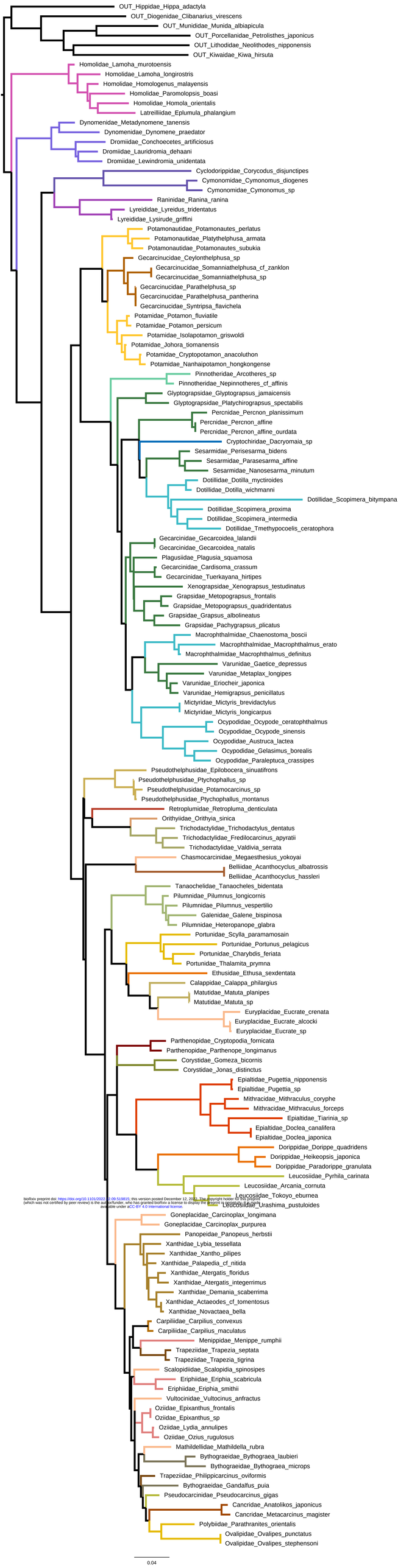

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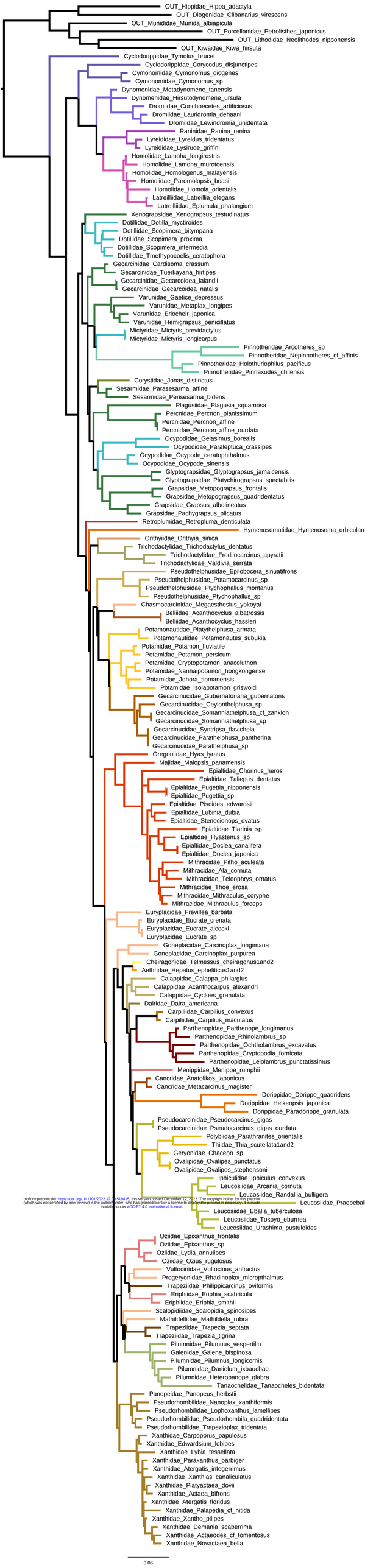

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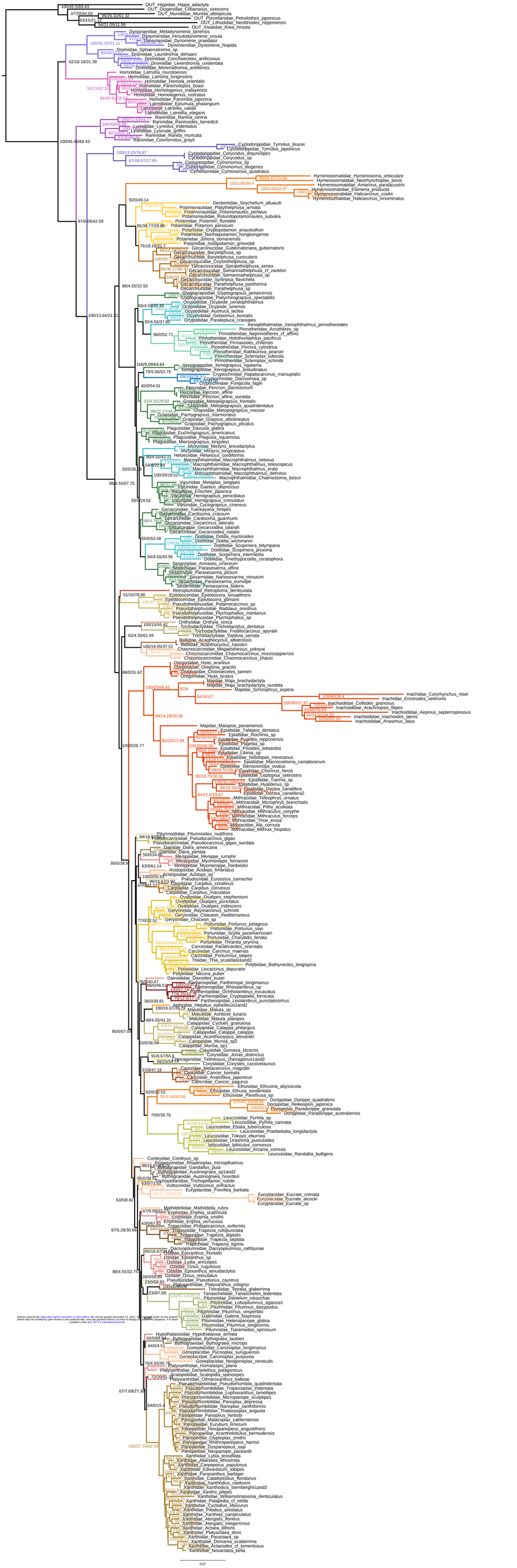

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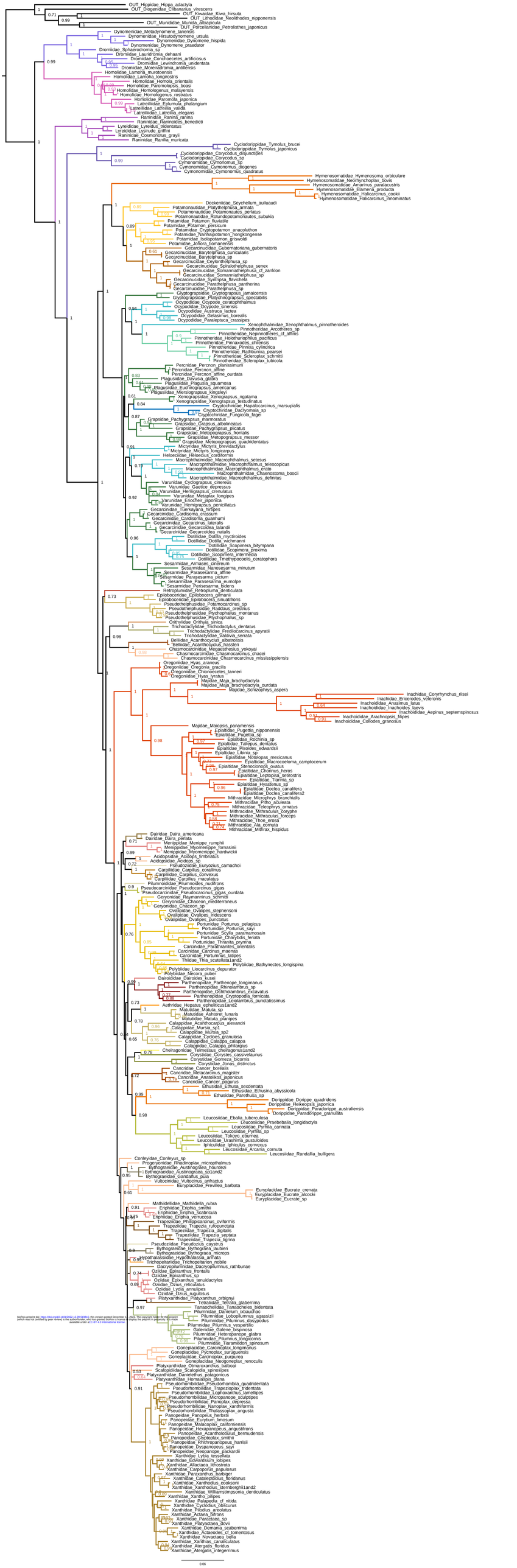

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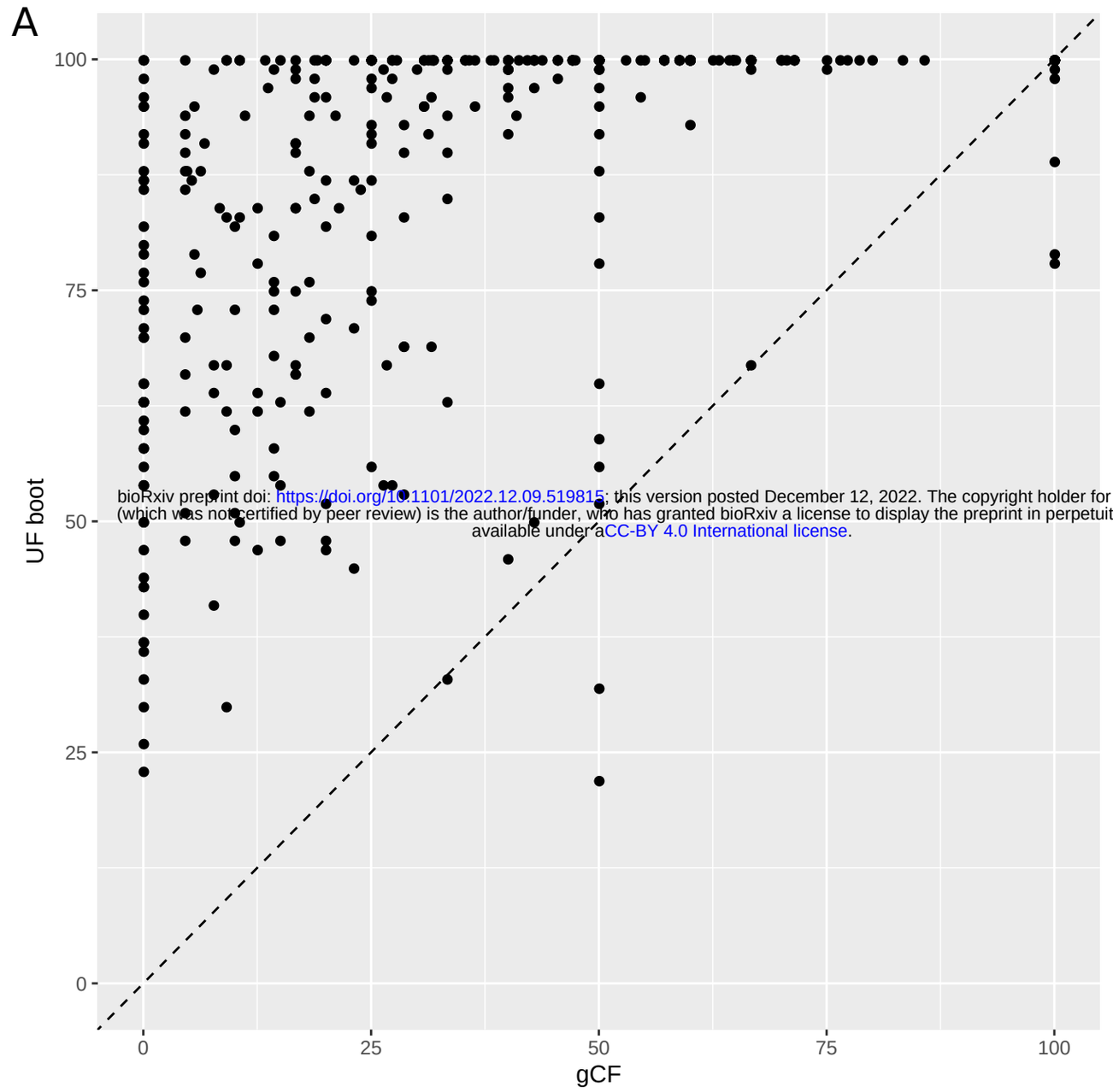

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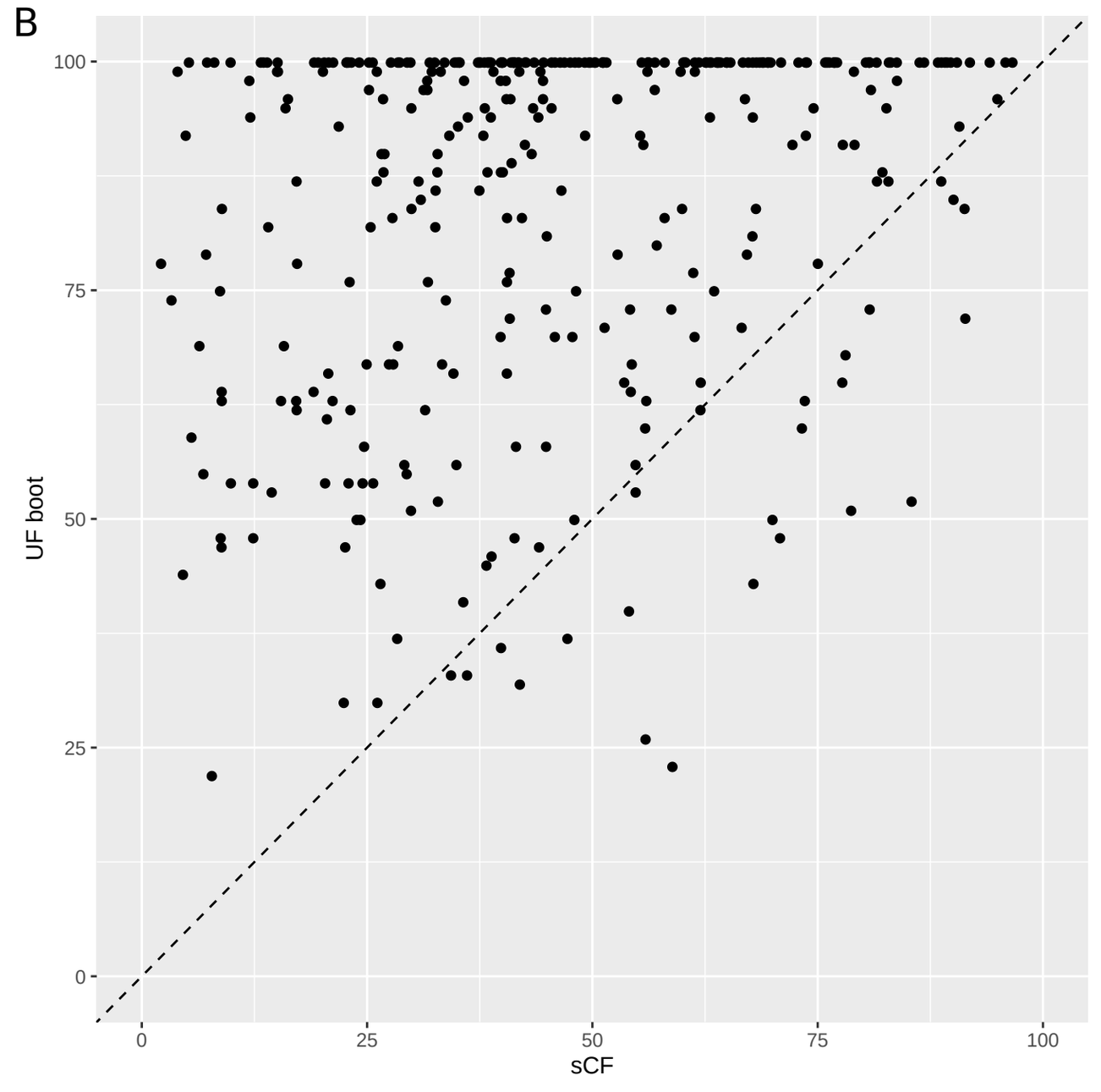

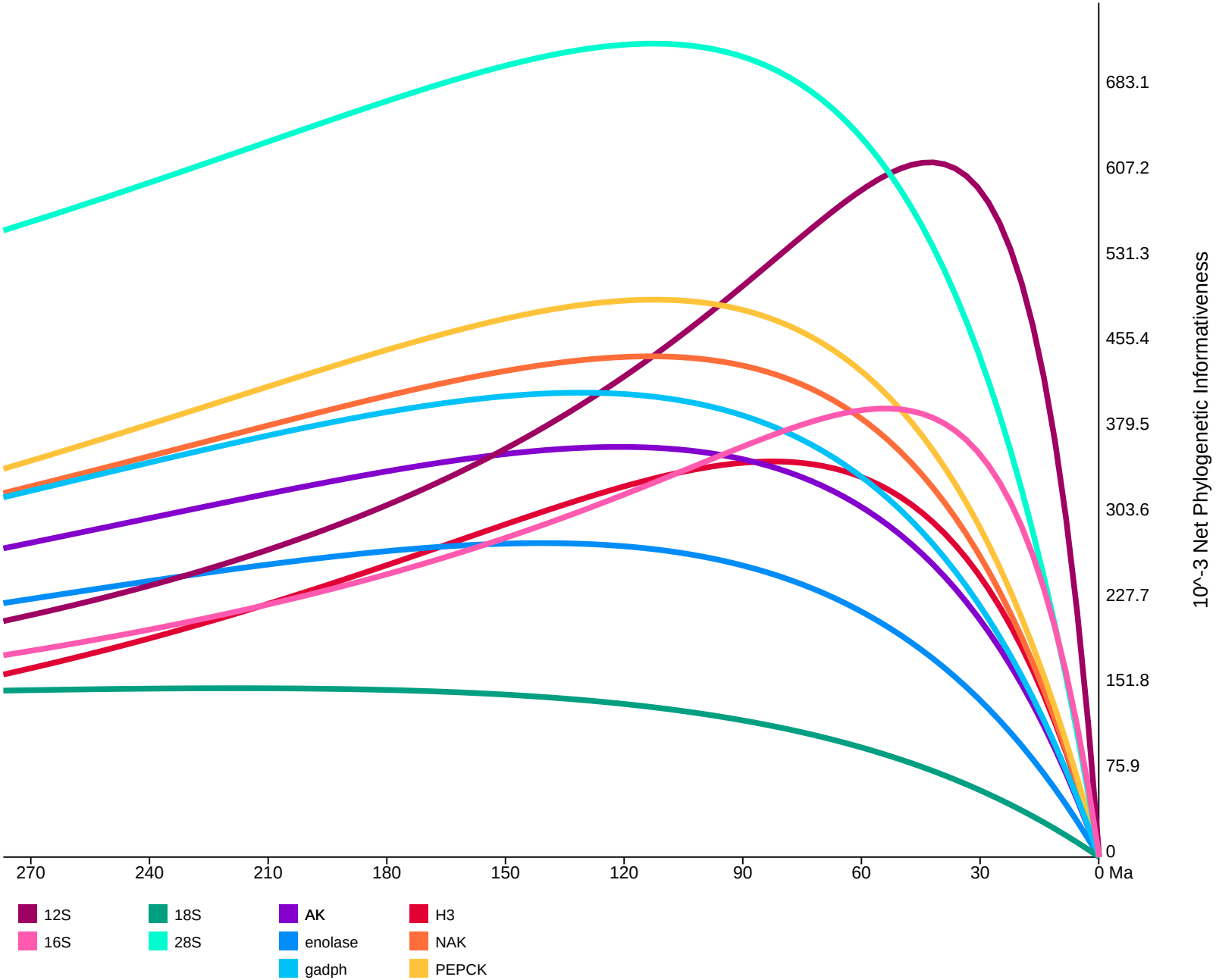
683.1
607.2
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455.4
379.5
303.6
227.7
151.8
75.9
0
10^-3 Net Phylogenetic Informativeness
270
240
210
180
150
120
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30
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12S
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28S
AK
enolase
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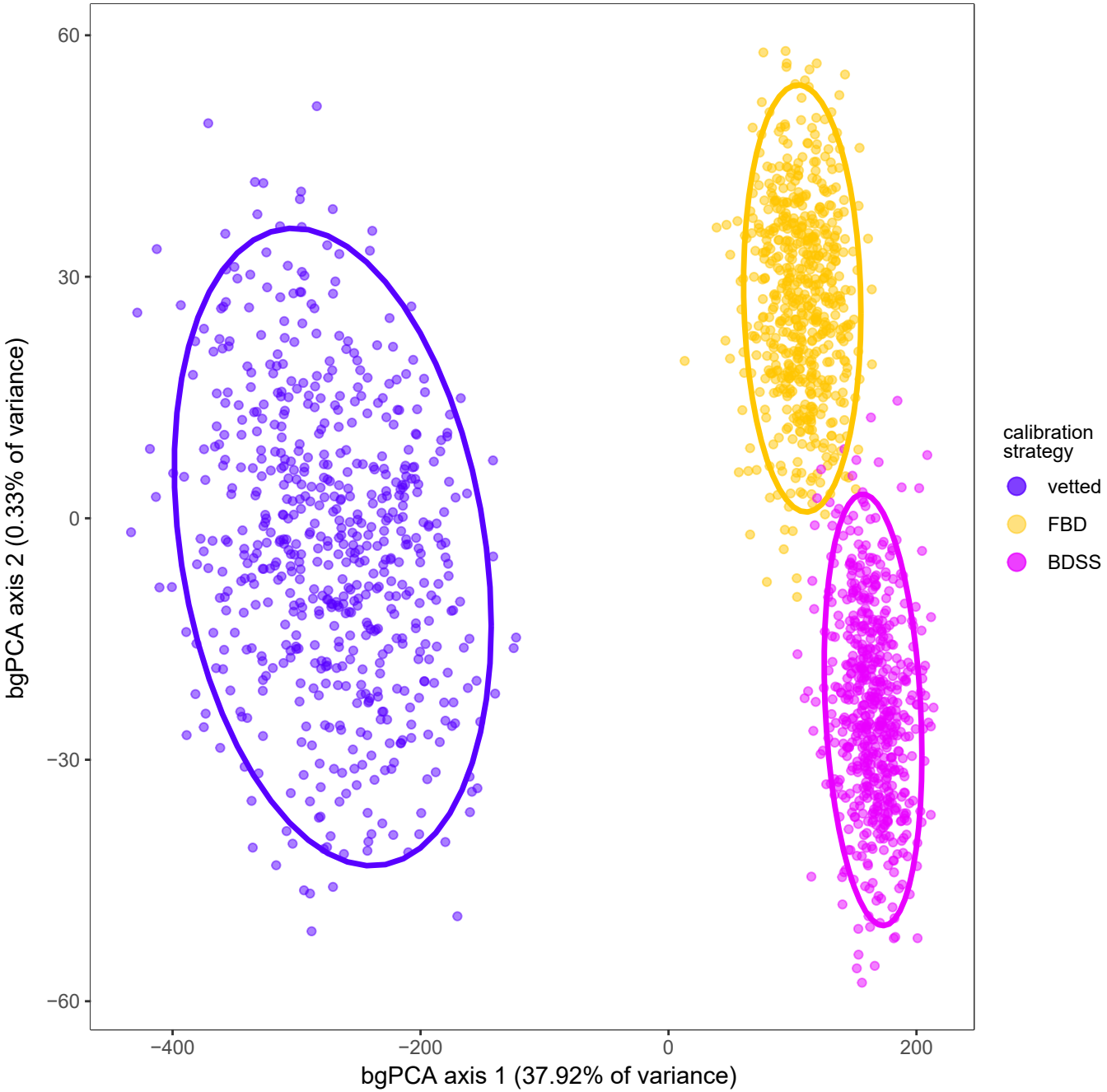
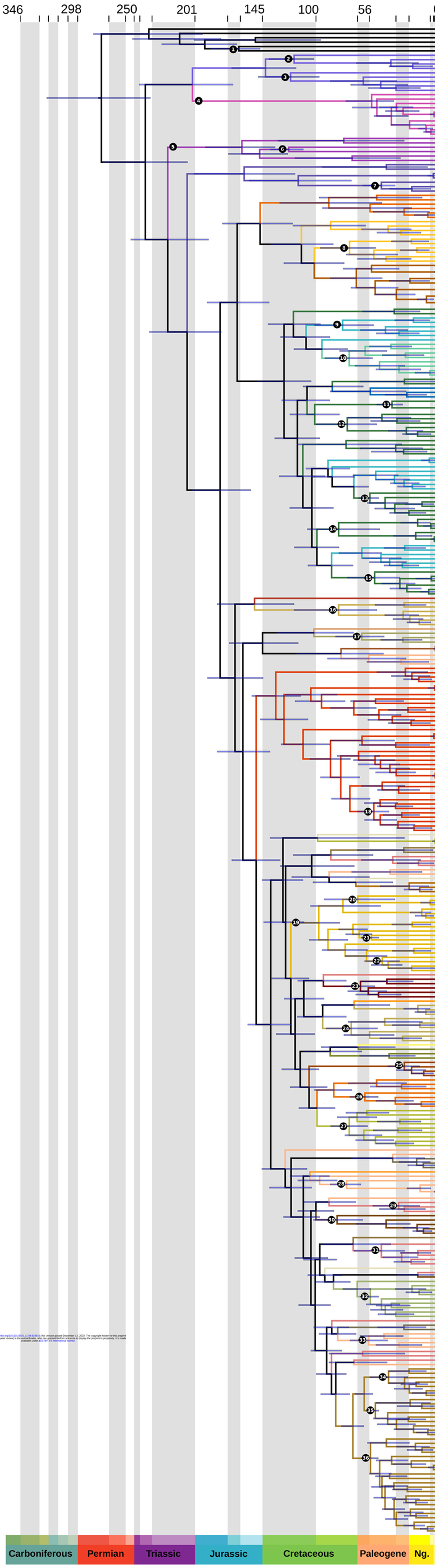
H3
NAK
PEPCK


60
30
0
−30
−60
bgPCA axis 2 (0.33% of variance)
−400
−200
0
200
bgPCA axis 1 (37.92% of variance)
calibration strategy
vetted
FBD
BDSS



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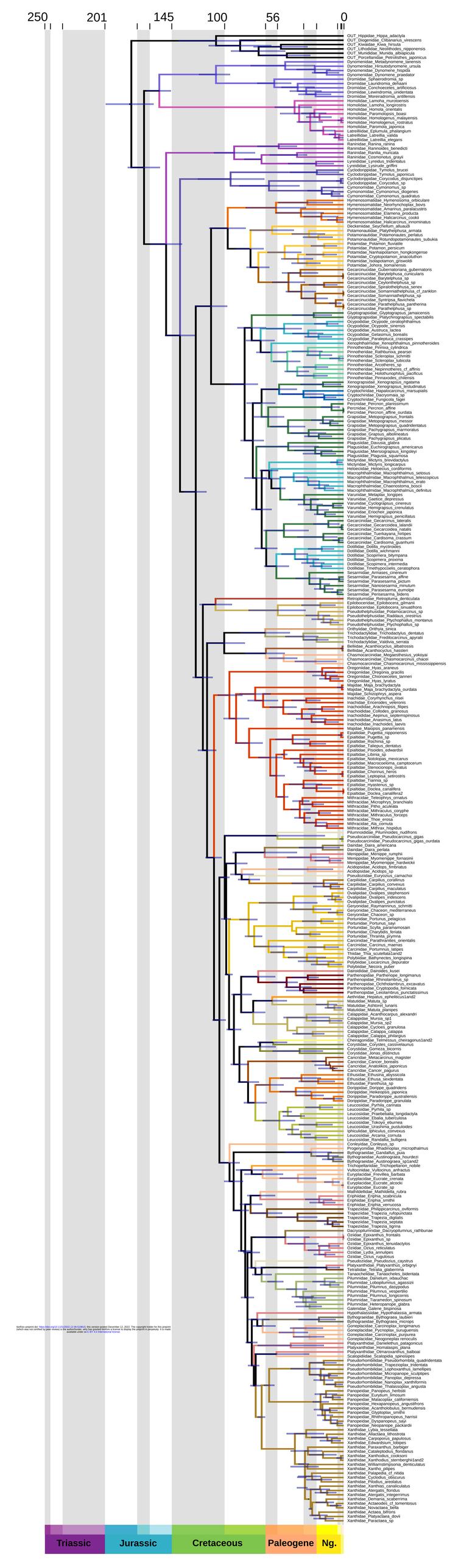

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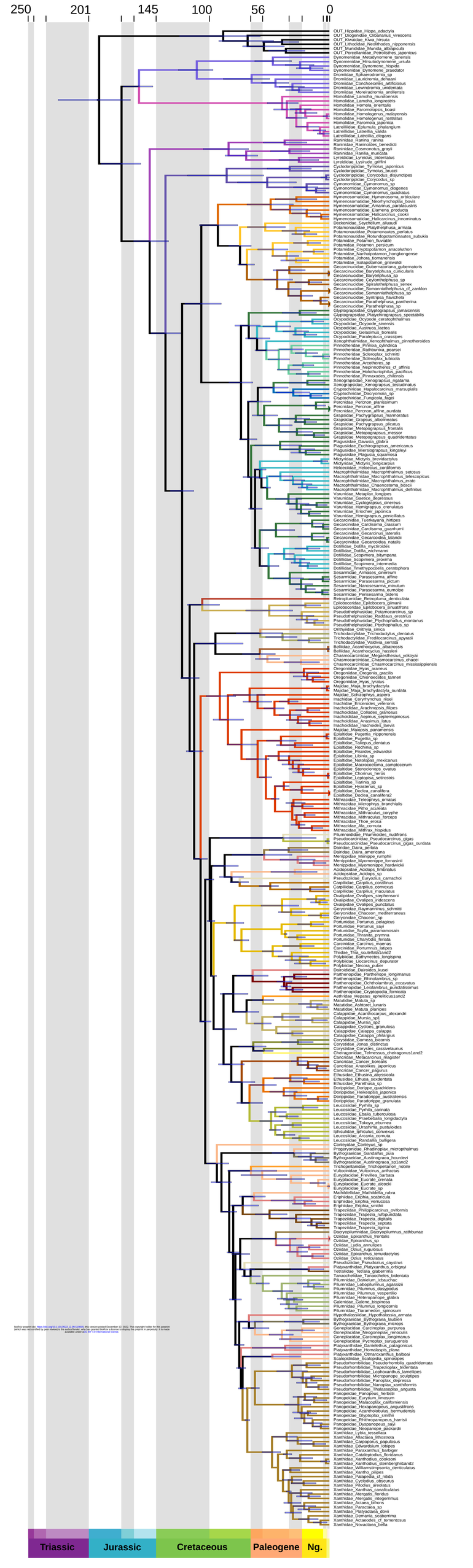

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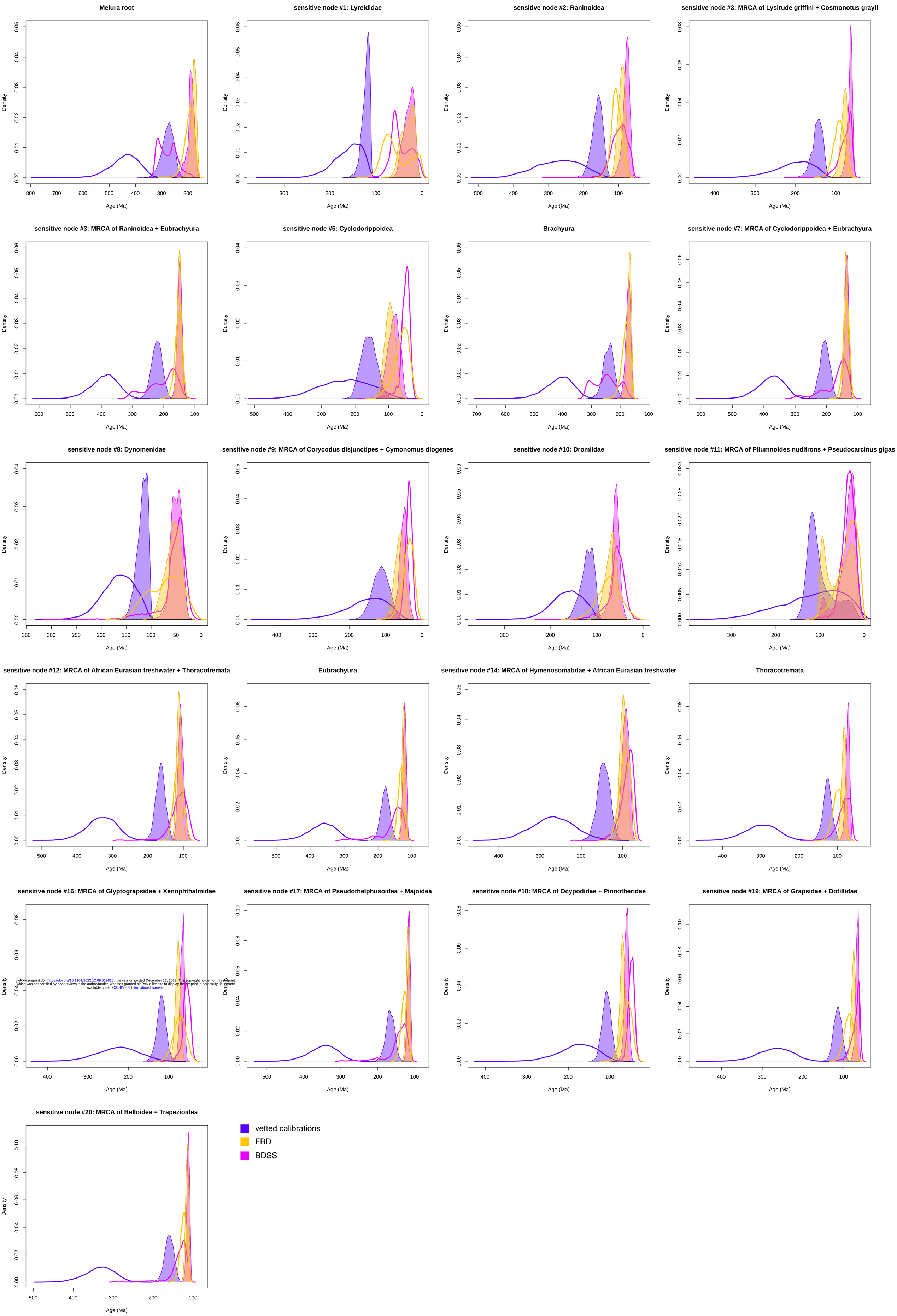

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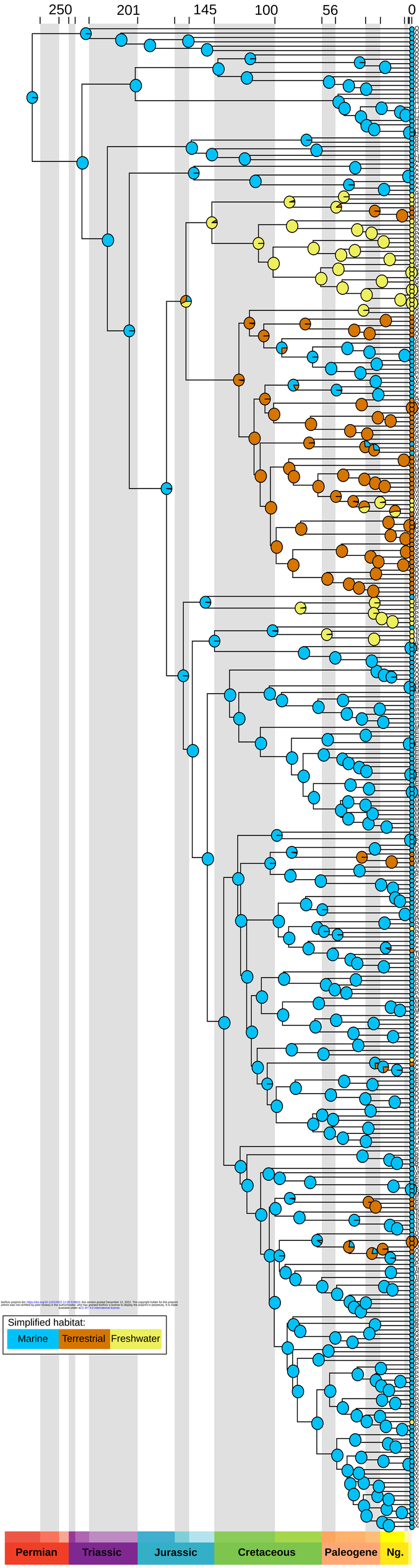
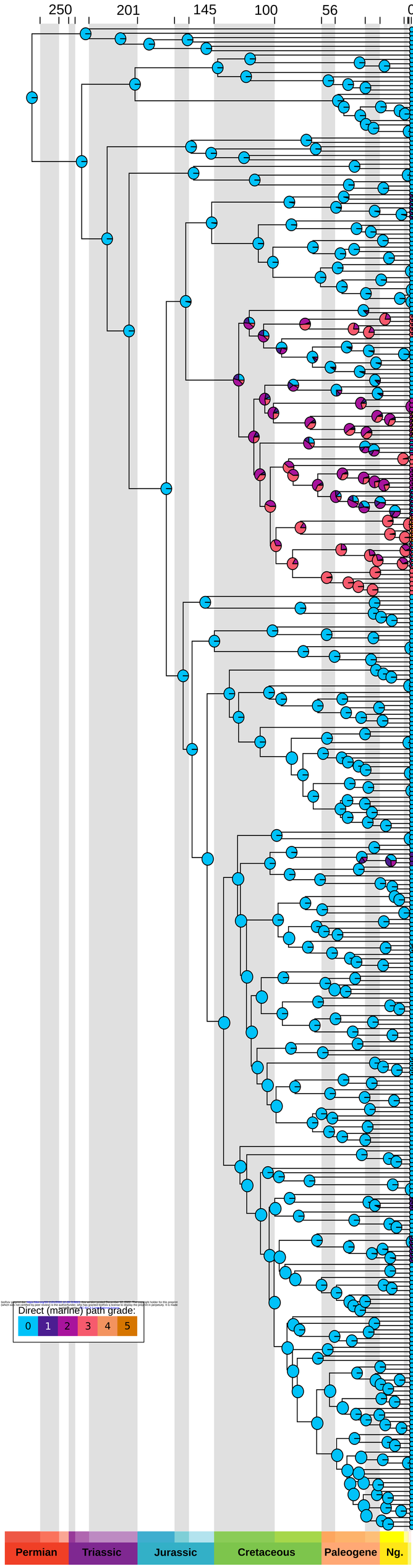

250
201
145
100
56
0
OUT Hippidae Hippa adactyla
OUT Dibbenidae Calparanuis virescens
OUT Porcellanidae Petrolisthes japonicus
OUT Munididae Munida albapicula
OUT Lithodidae Neolithodes hipponensis
OUT Kiwaidae Kiwa hirsuta
Dynomenidae Metadynomene tanensis
Dynomenidae Hirsutodynomene ursula
Dynomenidae Dynomene praedator
Dynomenidae Dynomene hispida
Dromiidae Sphaerodromia sp
Dromiidae Cryptodromia tohkaiana
Dromiidae Conchoecetes artificiosus
Dromiidae Lauridromia dehaanii
Dromiidae Lowindromia unidentata
Homolidae Lamoha kuroiwerisis
Homolidae Lamoha longirostris
Homolidae Paromola japonica
Latreillidae Edumunja phalangium
Latreillidae Latreillia elegans
Latreillidae Latreillia valida
Homolidae Homola orientalis
Homolidae Paromolopsis boasi
Homolidae Homologenus rostratus
Homolidae Homologenus malayensis
Raninidae Raninoides benedicti
Raninidae Ranina ranina
Raninidae Raniila muricata
Raninidae Cosmonotus grayii
Lyreididae Lyreidus tridentatus
Lyreididae Lyreidus tridentatus
Cyclodorippidae Tymolus japonicus
Cyclodorippidae Tymolus brucei
Cyclodorippidae Corycodus sp
Cyclodorippidae Corycodus disunctipes
Cymonomidae Cymonomus sp
Cymonomidae Cymonomus quadratus
Cymonomidae Cymonomus digeneres
Hymenosomatidae Neorhynchoplax bovis
Hymenosomatidae Hymenosoma orbiculare
Hymenosomatidae Amarinus paralacustris
Hymenosomatidae Elamena producta
Hymenosomatidae Halicarcinus innominatus
Hymenosomatidae Halicarcinus cookii
Deckeniidae Seychellum alluaudi
Potamonautidae Platythelphusa armata
Potamonautidae Rotundopotamonautes subukia
Potamonautidae Potamonautes perlatus
Potamidae Potamon persicum
Potamidae Potamon fluviatile
Potamidae Johora tiomanensis
Potamidae Isolapotamon griswoldi
Potamidae Nanhaipotamon hongkongense
Potamidae Cryptopotamon anacoluthon
Gecarcinucidae Gubernatoriana gubernatoris
Gecarcinucidae Barytelphusa sp
Gecarcinucidae Barytelphusa cunicularis
Gecarcinucidae Spiralothelphusa senex
Gecarcinucidae Ceylonthelphusa sp
Gecarcinucidae Sohannadhelphusa sp
Gecarcinucidae Somannahelphusa cf zanklon
Gecarcinucidae Syntripsa flavichela
Gecarcinucidae Parathelphusa sp
Gecarcinucidae Parathelphusa pantherina
Glyptograspidae Platychirograpsus spectabilis
Glyptograspidae Glyptograpsus jamaicensis
Ocypodidae Ocypode sinensis
Ocypodidae Ocypode ceratophthalmus
Ocypodidae Ausfruca lactea
Ocypodidae Paraleptuca crassipes
Ocypodidae Gelasimus borealis
Xenophthalmidae Xenophthalmus pinnotheroides
Pinnotheridae Pinnixa cylindrica
Pinnotheridae Bathyrukia pearsei
Pinnotheridae Scleroplax tubicola
Pinnotheridae Scleroplax schmitti
Pinnotheridae Pinnaxodes chilensis
Pinnotheridae Holothuriophilus pacificus
Pinnotheridae Nepinnothres cf affinis
Pinnotheridae Arcotheres sp
Xenograspidae Xenograpsus testudinatus
Xenograspidae Xenograpsus ngatama
Cryptichirridae Hapalocarcinus marsupialis
Cryptochiridae Fungicola fagei
Cryptochiridae Dactyomasia sp
Pelocnidae Percnon planissimum
Percnidae Percnon affine ourdata
Percnidae Percnon affine
Grapsidae Metopograpsus frontalis
Grapsidae Metopograpsus quadridentatus
Grapsidae Metopograpsus thessor
Grapsidae Pachygrapsus marmoratus
Grapsidae Pachygrapsus plicatus
Grapsidae Geograpsus albolineatus
Plagusiidae Dalvisia dilabra
Plagusiidae Euchirograpsus americanus
Plagusiidae Plagusia squamosa
Plagusiidae Metaplagusia kingsleyi
Mictyridae Mictyris longicarpus
Mictyridae Mictyris brevidactylus
Helderciidae Helpecus corbiformis
Macrophthalmidae Macrophthalmus setosus
Macrophthalmidae Macrophthalmus telescopicus
Macrophthalmidae Macrophthalmus erato
Macrophthalmidae Macrophthalmus definitus
Macrophthalmidae Chaenostoma boscii
Varunidae Metaplax longipes
Varunidae Gaetice depressus
Varunidae Hemigrapsus penicillatus
Varunidae Eriocheir japonica
Varunidae Hemigrapsus crenulatus
Varunidae Cyclograpsus cinereus
Gecarcinidae Gelarcinus lateralis
Gecarcinidae Gecarcoidea natalis
Gecarcinidae Gecarcoidea lalandii
Gecarcinidae Luerkyana hirtipes
Gecarcinidae Cardisoma guanhumi
Gecarcinidae Cardisoma crassum
Sesarmidae Armases cinereum
Sesarmidae Parasesarma pictum
Sesarmidae Parasesarma affine
Sesarmidae Nanosesarma minutum
Sesarmidae Perisesarma bidens
Sesarmidae Parasesarma eumolpe
Dotillidae Dotilla wichmanni
Dotillidae Dotilla myctiroides
Dotillidae Scopimera propinqua
Dotillidae Scopimera globosa
Dotillidae Scopimera ceratophora
Dotillidae Scopimera intermedia
Retropluminidae Retropluma denticulata
Ellipiidae Ellipiidae Ellipiidae Ellipiocerdae Ellipiocerdae Ellipiocerd


250
201
145
100
56
0
Direct (marine) path grade:
0
1
2
3
4
5
Permian
Triassic
Jurassic
Cretaceous
Paleogene
Ng.

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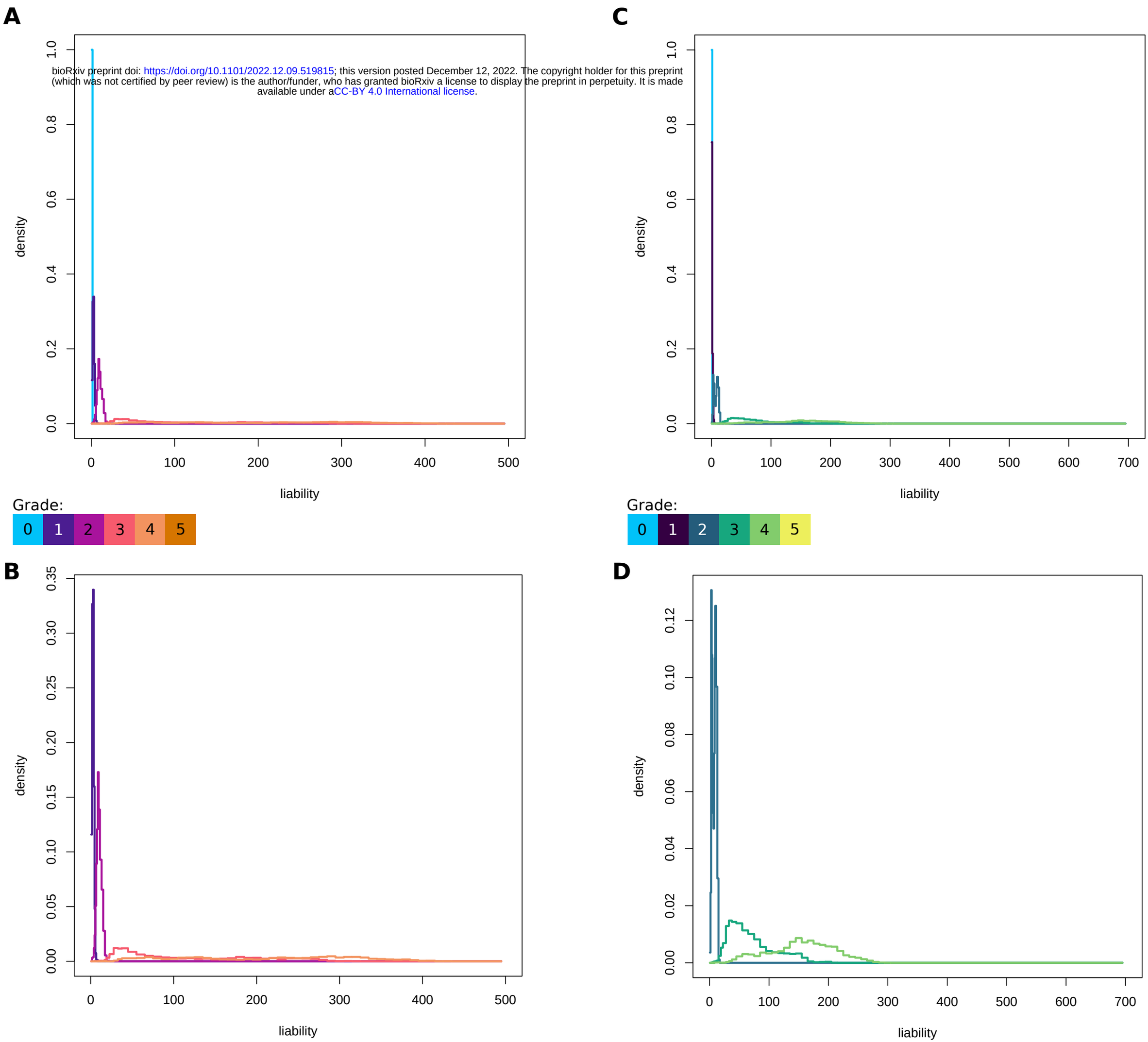

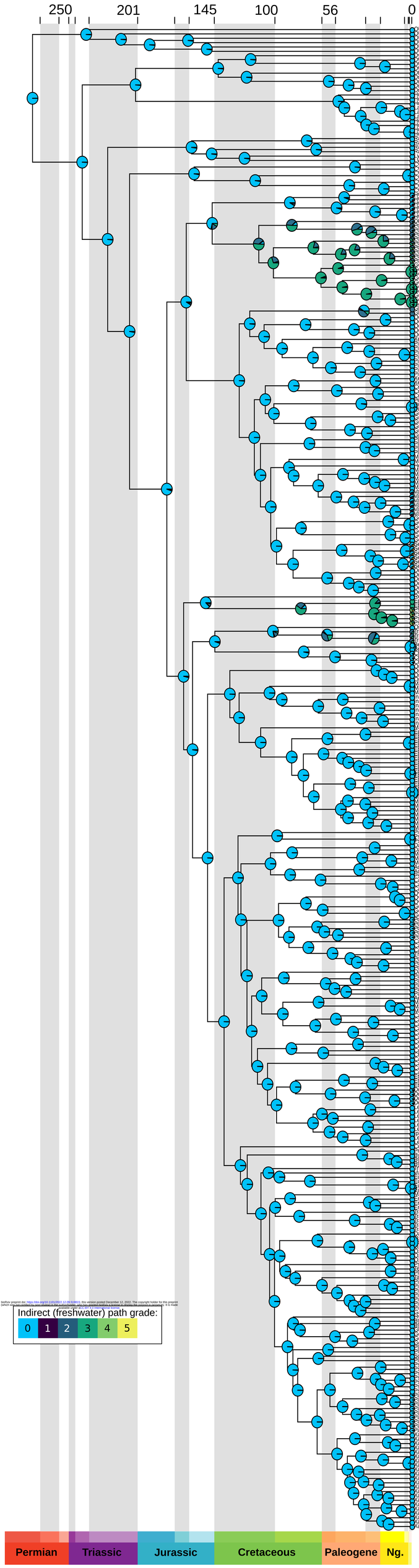

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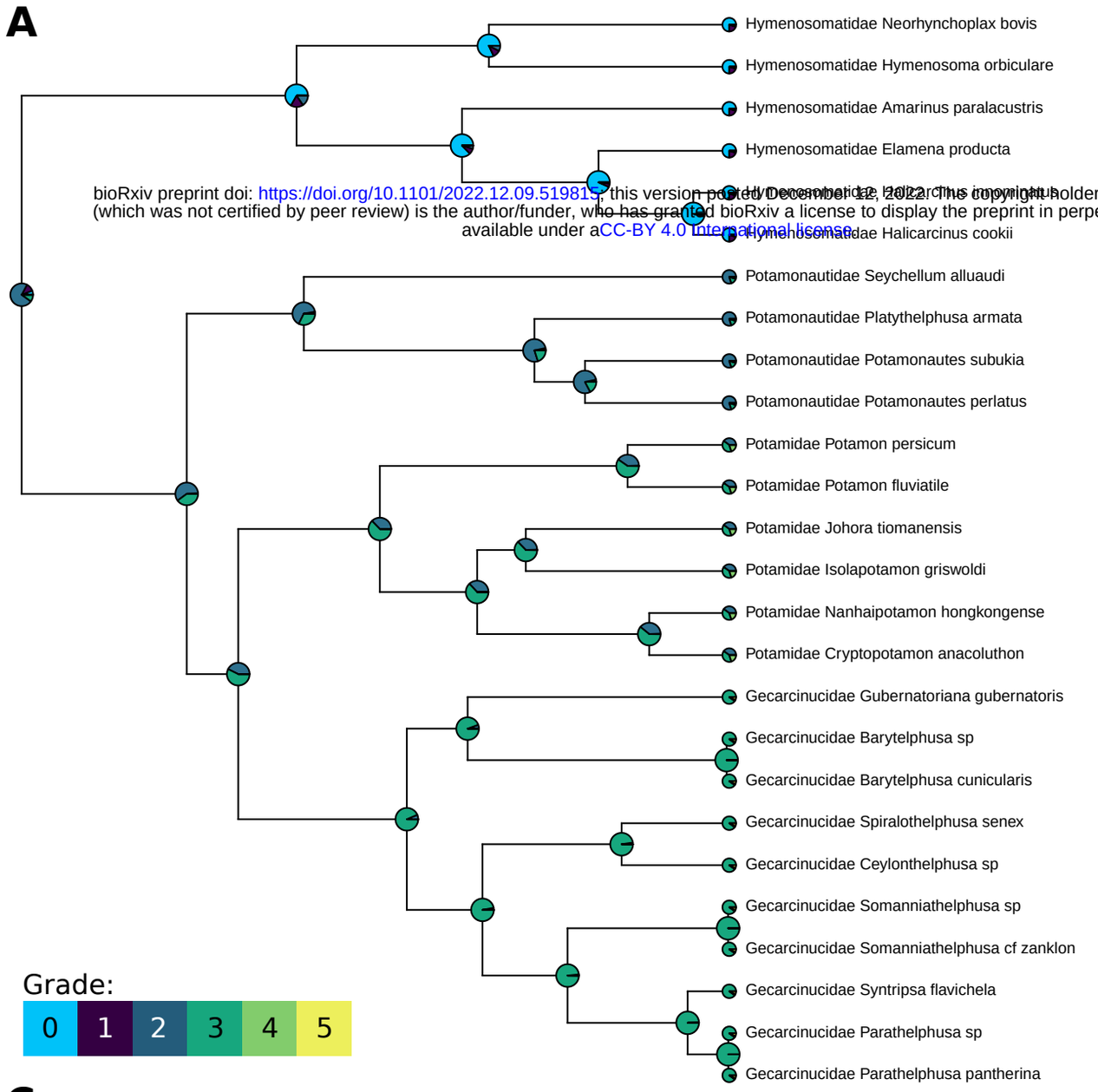

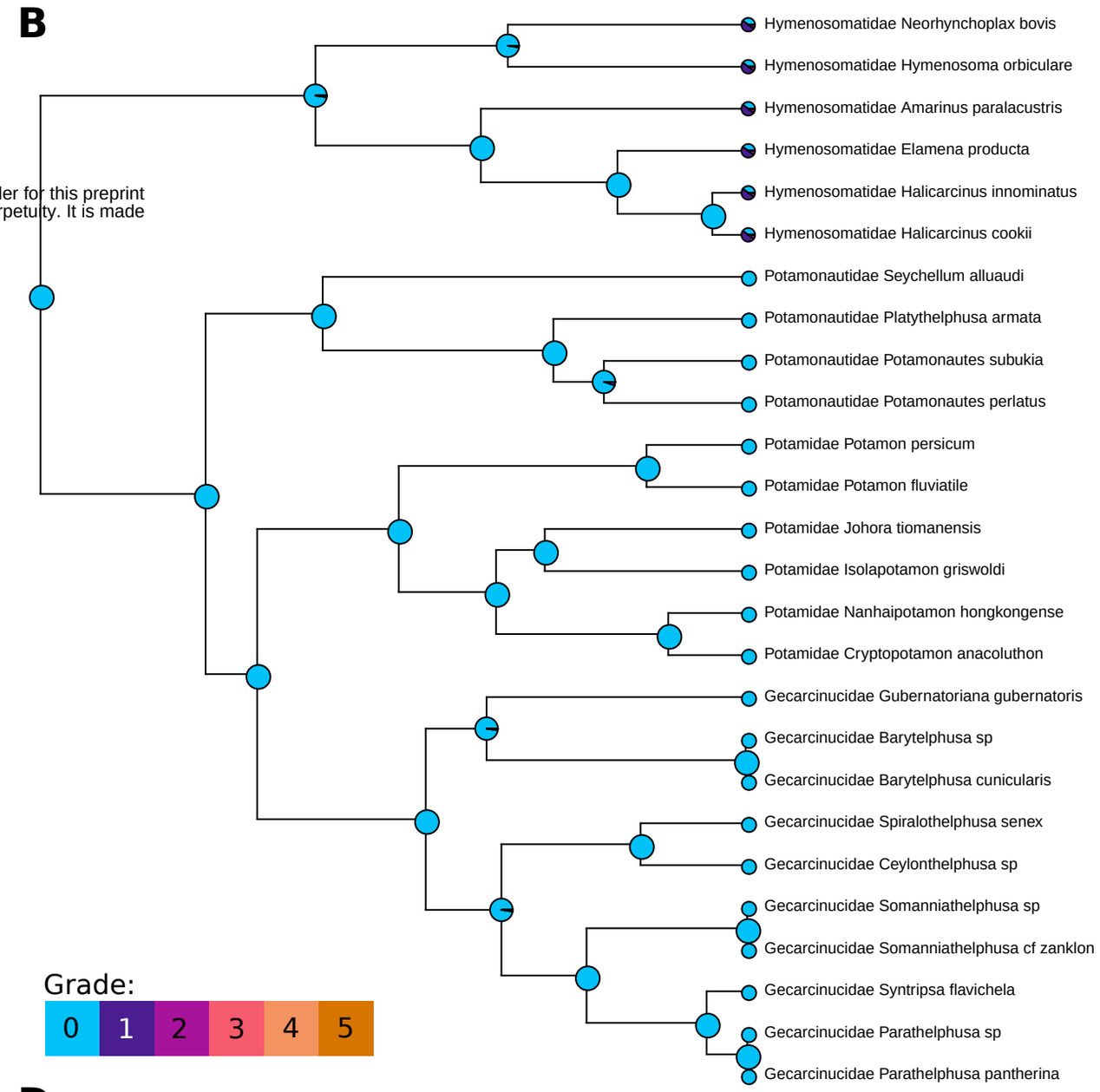

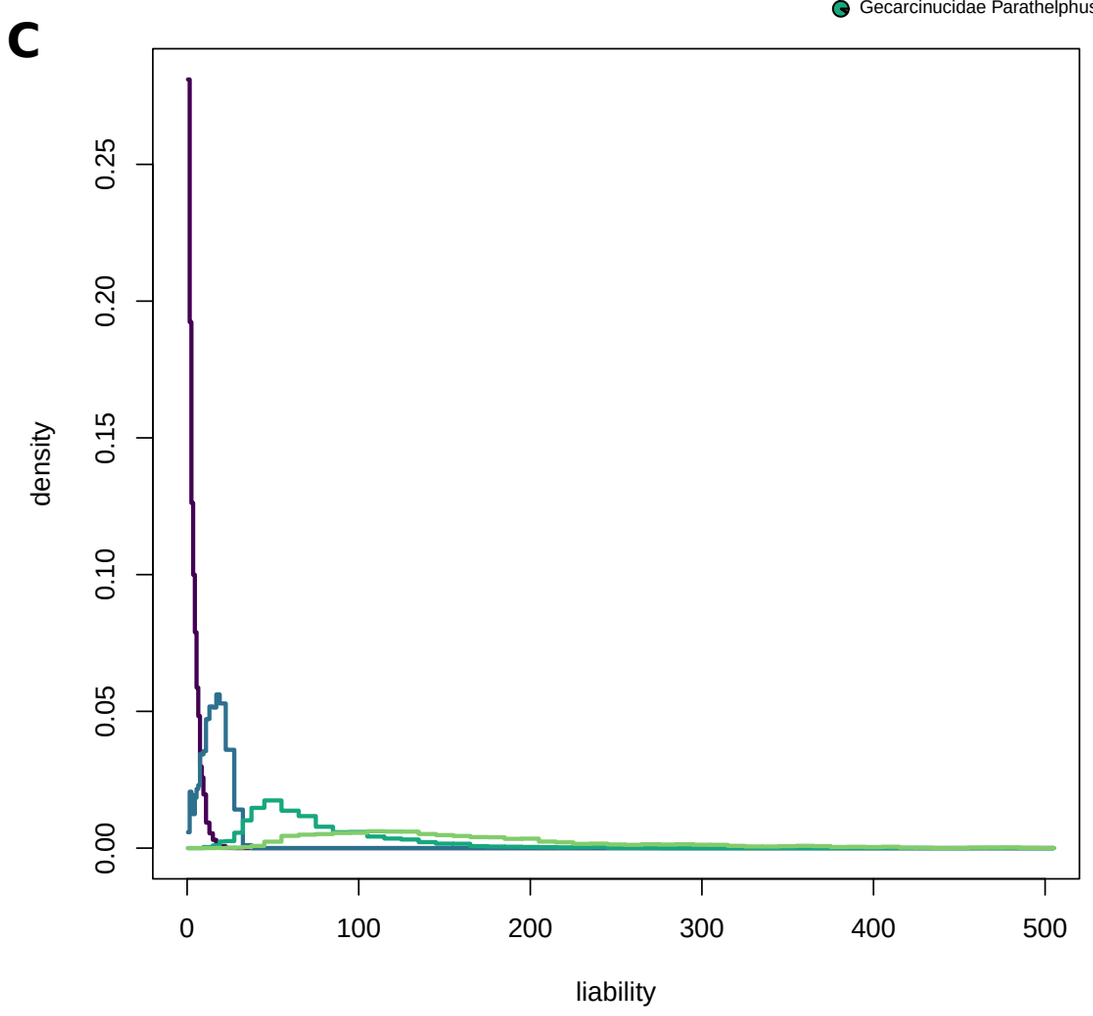

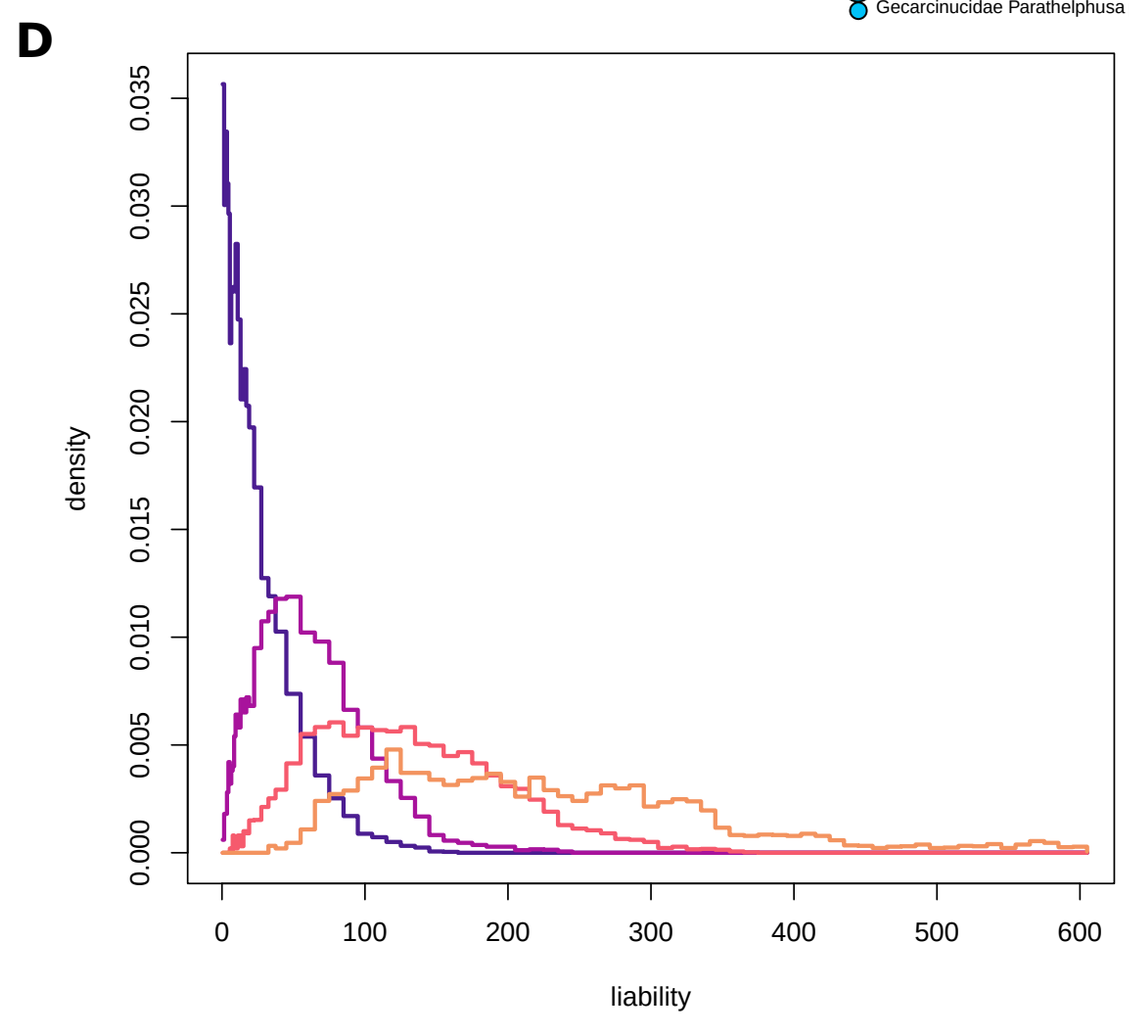
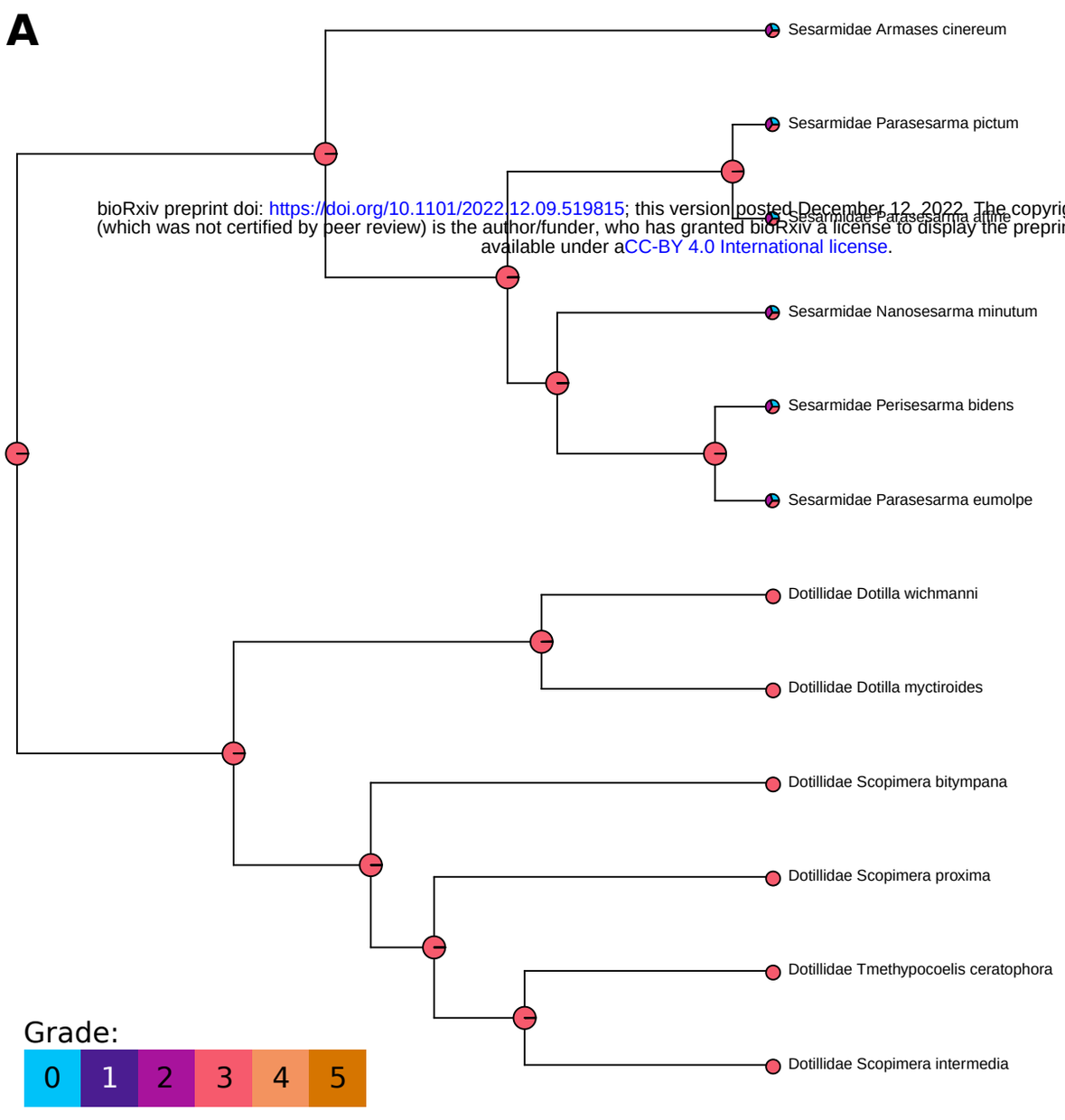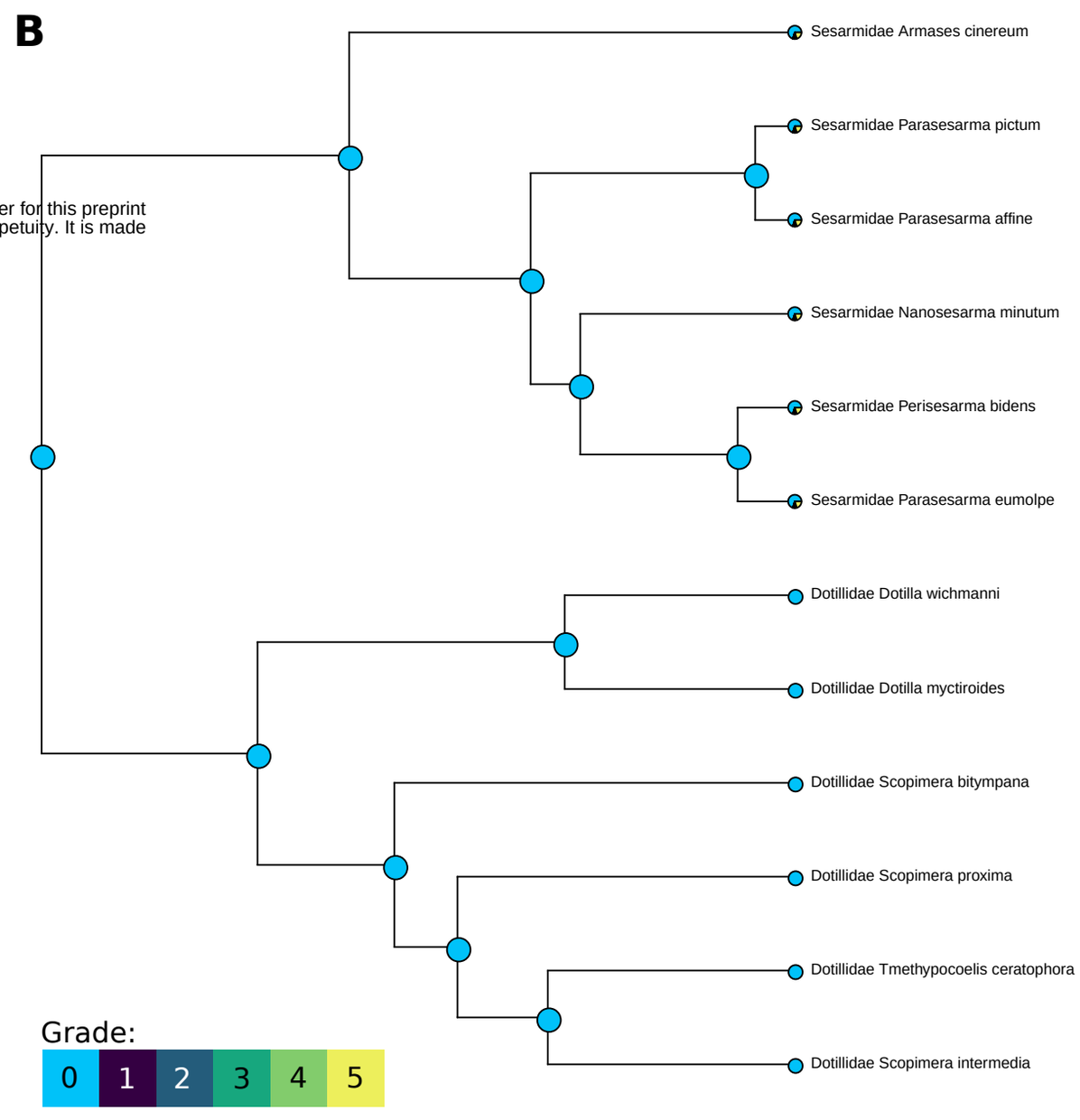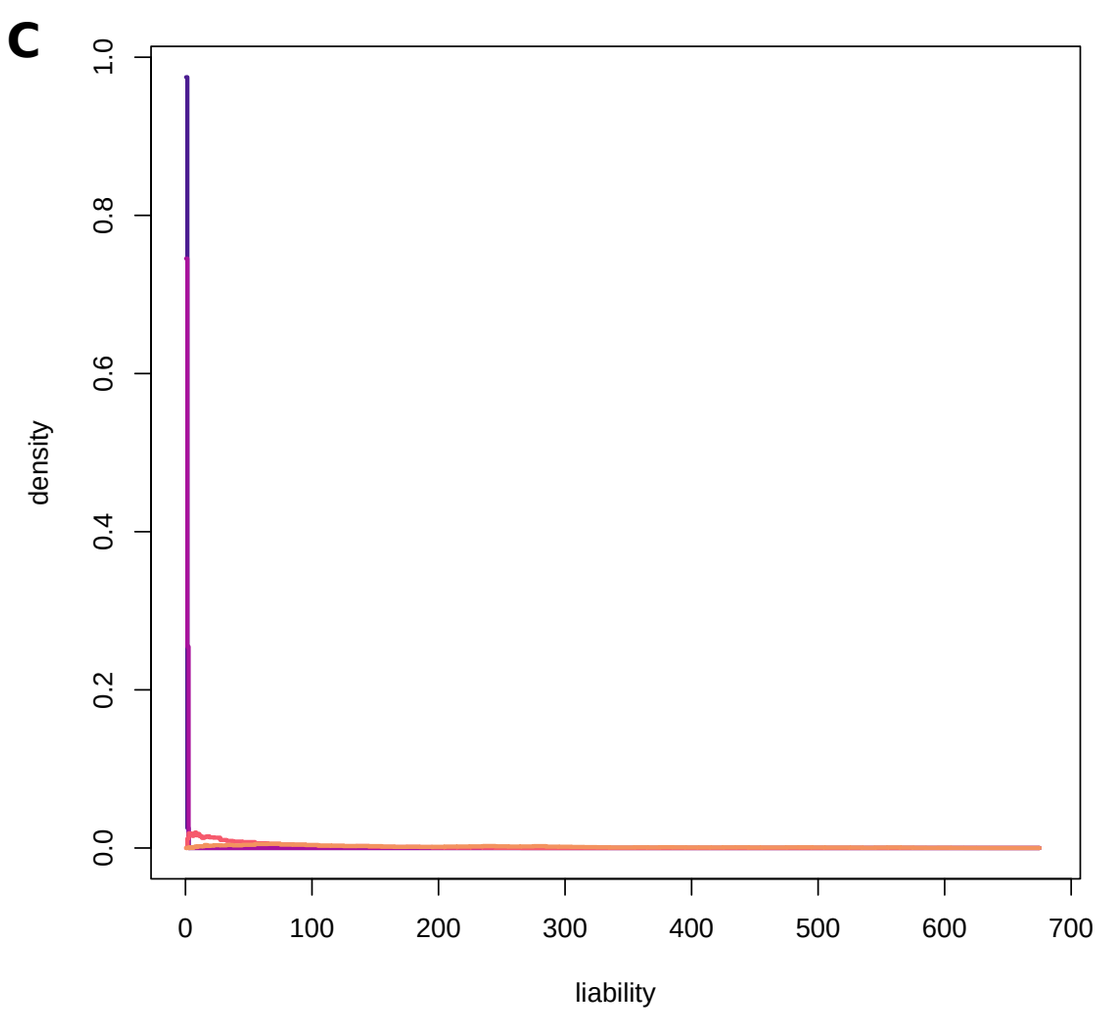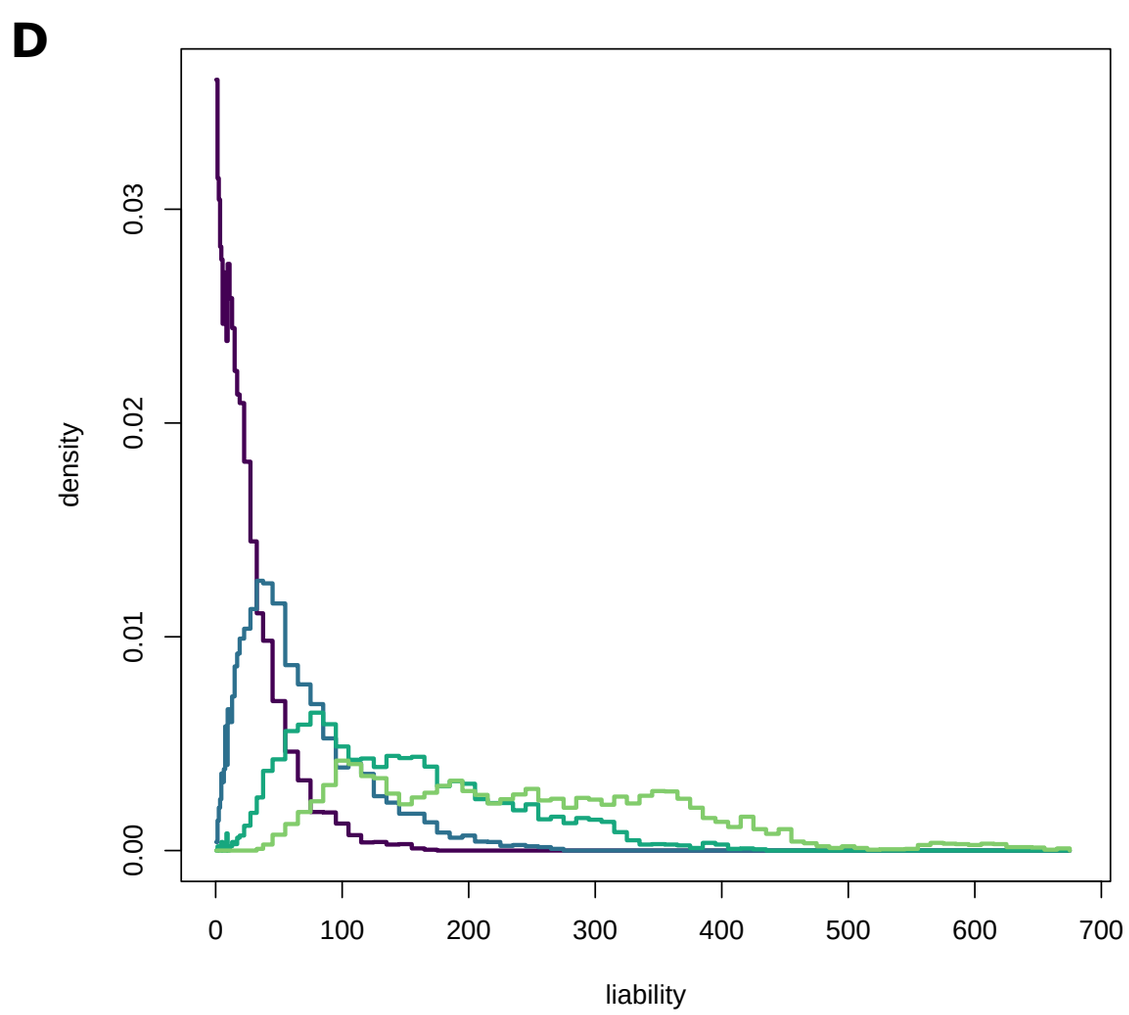
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