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Global biogeographic structuring of tropical shallow-water brittle stars

Running title: Phylodiversity of tropical brittle stars

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ABSTRACT

Aim: Biogeographic barriers emerged in the tropical oceans as continental masses moved with plate tectonics, and as the tropics contracted to lower latitudes from the late Eocene. These barriers have shaped tropical marine biodiversity. We characterise large-scale diversity patterns for tropical brittle stars and investigate the effect of biogeographic barriers on these in space and time.

Location: Shallow-water (<200 m) tropical oceans.

Taxon: Tropical shallow-water brittle stars.

Methods: We integrate phylogenetic and biogeographic modelling to test and quantify the biogeographic structuring across the major ocean basins for five families of brittle stars. These are well sampled in our phylogenies (173 species) and represent an important component of the brittle-star fauna of tropical shallow waters. We define major bioregions based on patterns of compositional and phylogenetic beta diversity.

Results: We find congruence between patterns of shared ancestry of regions and inferred biogeographic histories. Biogeographic reconstructions show that faunal patterns reflect the emergence of biogeographic barriers in the tropical world, with evidence of vicariant events driven by the opening of the Atlantic Ocean, the narrowing of the Tethyan Seaway and the rise of the Isthmus of Panama.

Main conclusions: Biogeographic barriers almost completely isolated regional faunas. However, divergence age estimates predate the onset of the different barriers, suggesting that changes associated with the gradual emergence of the barriers had a strong effect on the evolutionary history of tropical shallow-water brittle stars. Limited, very recent, bi-directional dispersal was detected across the East Pacific Barrier, which is otherwise an important barrier for dispersal of brittle stars.

Keywords: Phylodiversity, tropical realm, Ophiuroidea, biogeographic barriers, plate tectonics, shallow-waters, dispersal

INTRODUCTION

In the tropical oceans, major biogeographic barriers have greatly influenced the diversification of several marine taxa, acting as drivers of speciation (e.g. Floeter et al., 2008; Cowman & Bellwood, 2013). The tropical marine region has been restricted to low latitudes since the late Eocene-early Oligocene, with the initiation of the Antarctic Circumpolar Current (Kamp, Waghorn & Nelson, 1990), and is currently considered to be divided into three major realms (Cowman & Bellwood,

2013): Indo-West Pacific (IWP), Atlantic (A; including Mediterranean Sea) and East Pacific (EP). Barriers to dispersal of marine fauna between these realms have emerged at different points throughout the geological history of the planet and have shaped the current distribution and diversity patterns of tropical shelf (<200 m depth) taxa (Cowman & Bellwood, 2013). The oldest of these, the opening of the Atlantic Ocean (*ca.* 110–65 million years ago [Ma]), separated the East Pacific and West Atlantic from the East Atlantic, Mediterranean Sea and Indo-Pacific (Greiner & Neugebauer, 2013). The East Pacific Barrier (EPB), considered a permeable barrier of *ca.* 5000 km of deep water, has been acting throughout the past 65 Myr, separating the Indo-West Pacific from the East Pacific (Grigg & Hey, 1992). Dispersal between the tropical Atlantic and Indo-West Pacific oceans became progressively restricted by the closure of the Tethys Sea. The final closure, the Terminal Tethyan Event (TTE) when Africa collided with Arabia, occurred 18–12 Ma (Adams, Gentry & Whybrow, 1983). The most recent barrier was the Isthmus of Panama (IoP), which progressively separated the tropical Atlantic from the East Pacific starting 15 Ma with final closure *ca*. 3 Ma (Lessios, 2008).

Brittle stars, a group of widespread benthic invertebrates (class Ophiuroidea), have been the target of recent studies addressing macroevolutionary processes, as an extensive phylogenomic dataset is available (Hugall, O'Hara, Hunjan, Nilsen & Moussalli, 2016; Bribiesca-Contreras, Verbruggen, Hugall & O'Hara, 2017; O'Hara et al., 2018). Most higher taxonomic ranks, down to genus, are widely distributed longitudinally (Stöhr, O'Hara & Thuy, 2012), with regional differences occurring only at species level (O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017). Both shelf (<200 m) and upper-slope (200–2,000 m) depths show a negative latitudinal diversity gradient (O'Hara, Rowden & Bax, 2011; Stöhr et al., 2012). Diversity peaks have been identified in the Indo-West Pacific and western Atlantic Ocean (Woolley et al., 2016). Secondary peaks, such as the North Pacific, South Pacific and the Indian Ocean, rim the diverse Indo-West Pacific (Stöhr et al., 2012).

Improved phylogenies based on extensive genomic datasets are providing a better understanding of biodiversity patterns and its underlying processes. Patterns of diversity accounting for phylogenetic relationships, such as phylogenetic diversity metrics (PD; Faith, 1992), provide insight into the shared ancestry of regional faunas. Probabilistic models of geographic range evolution can identify processes generating spatio-temporal patterns (vicariance and dispersal; e.g. Ree, Moore, Webb & Donoghue, 2005). However, different methods assume that processes shape geographic ranges in various ways, thus affecting the conclusions on biogeographic histories. For instance, some methods do not allow the inheritance of the full ancestral range (DIVA, dispersal-vicariance analysis; Ronquist, 1997), potentially overestimating vicariance (Buerki et al., 2011) in comparison with methods that allow a widespread range to be inherited (DEC, dispersal-extinction-cladogenesis ; Ree et al., 2005; Ree & Smith, 2008). Therefore, biogeographic models should be chosen based on prior knowledge on processes shaping distributional patterns. As suitable data is frequently lacking for many taxa, statistical model comparison has been utilised to determine which model best fits both the

92 phylogenetic and biogeographic data (Matzke, 2013), and model-averaging has also been used to
93 account for model uncertainty (Araujo & New, 2007; Grueber, Nakagawa, Laws & Jamieson, 2011)
94 and the complexity of real world biogeography.

95 The goal of this study is to characterise large-scale diversity patterns for brittle stars, focusing on the
96 effect of biogeographic barriers on the diversity patterns of tropical lineages in space and time. Our
97 approach consists of defining regions of evolutionary significance (RES) based on patterns of
98 turnover of species and of phylogenetic diversity between biogeographic provinces, followed by
99 estimation of ancestral ranges accounting for different scenarios. We use a multi model biogeographic
100 inference approach in a time-calibrated phylogenetic context in order to investigate concordant
101 patterns of diversification associated with biogeographic barriers in the tropical oceans.

102

103 **MATERIALS AND METHODS**

104 **Distributional records**

105 We focus on five families of brittle stars: Ophiocomidae Ljungman, 1867, Ophiolepididae Ljungman,
106 1867, Ophionereididae Ljungman, 1867, Ophiotrichidae Ljungman, 1867, and Ophiodermatidae
107 Ljungman, 1867. These families are an important component of the brittle star fauna of tropical, shelf
108 habitats (<200 m), with most of their species being restricted to this biome (54 to 96 percent; Table 1,
109 Fig. 1a, see also O'Hara et al. (2017)). Species distributional data was extracted from a global
110 distributional dataset (Woolley et al., 2016).

111

112 **Phylogenetic inference and divergence dating**

113 Dated phylogenetic trees for the five families were estimated from a common phylogenomic super-
114 matrix of 781 species comprising 1,462 exons (in 416 genes) and mitochondrial cytochrome oxidase
115 subunit I gene (COI), amounting to a total length of 267k sites, which has been used in several
116 previous studies (Bribiesca-Contreras et al., 2017; O'Hara et al., 2017; O'Hara, Hugall, Woolley,
117 Bribiesca-Contreras & Bax, 2019). Bayesian relaxed-clock analyses of family-taxa subsets of this
118 phylogenomic super-matrix were performed using BEAST v2.4 (Bouckaert et al., 2014). These
119 analyses used sequence model, calibrations, and starting trees determined from those previous studies
120 (see Supplementary Information for details).

121 Two independent runs were conducted for each of the five families and convergence assessed by
122 congruence between individual run consensus trees and posterior ESS (>150) of combined runs
123 (BEAST v2.4, TREEANNOTATOR, and TRACER v1.5; see Supplementary files 1–10). Maximum clade

credibility consensus trees (with median node heights) were then derived from the combined posterior samples (Figs S3–S7). Finally, sets of one hundred posterior samples per family were randomly selected to represent phylogenetic variation for biogeographic analyses (Supplementary Files 11–15).

Regions of evolutionary significance

Many different marine bio-regionalisation schemes have been proposed based on animal and algal distributions or environmental surrogates (e.g.Spalding et al., 2007; Costello et al., 2017). In the absence of an agreed scheme, we have derived our own regions of evolutionary significance (RES) based on species and phylogenetic turnover (beta diversity) metrics of our sampled organisms. Distribution records were categorised into local marine provinces from Spalding et al. (2007). The 39 provinces, for which we had relevant distributional records, included tropical and some neighbouring warm-temperate provinces (Table S1 and Fig. S2).

We estimated the Pearson's product-moment correlation coefficient (PPMCC, 'stats' R package; R Core Team, 2017) between species richness by regions, as obtained from the distributional dataset, and the sampled-species richness to assess whether species richness patterns from DNA-sampled taxa (Fig. S2) correlated with the distributional dataset. Deep-sea and non-tropical species, as well as duplicates of tropical shelf species were pruned from each chronogram ('ape' R package; Paradis, Claude & Strimmer, 2004). In most cases, deep-sea or non-tropical taxa represented monophyletic clades which did not contribute to the biogeographical processes being examined here (Table 1; Figs. S3–S7 for details on pruned taxa). Since the distribution of species within the *Ophiothrix fragilis* (Abildgaard in O.F. Müller, 1789) complex along the West African coast is not well understood, we retained only a single sequence to represent this monophyletic complex. Although *Ophiothela mirabilis* Verrill, 1867 has been recorded for both the Eastern Pacific and Atlantic oceans, we assessed it to be an Eastern Pacific endemic as it is considered a recent introduction into the Atlantic Ocean (Mantelatto et al., 2016).

Species, or Compositional, Beta Diversity (CBD) was quantified for all pairs of provinces using Sörensen (Sor) dissimilarity index from a presence/absence matrix obtained from species occurrence data ('betapart' R package; Baselga & Orme, 2012). This index was decomposed into turnover (Sor_{turn}, replacement of species; equivalent to Simpsons dissimilarity index) and nestedness (Sor_{ne}, where assemblages with few species are subsets of richer sites) components (Baselga, 2010; Baselga & Orme, 2012). Phylogenetic Beta Diversity (PBD), which accounts for the phylogenetic relatedness between species, was also quantified for all pairs of provinces using a modified Sörensen index, pSor (Leprieur et al., 2012); and its turnover ($pSor_{turn}$) and nestedness ($pSor_{ne}$) components.

Dissimilarity matrices, for each component of both CBD and PBD, were estimated independently for each family, as they are dispersed throughout the phylogeny of the class Ophiuroidea (Fig. S1) (O'Hara et al., 2017). This also avoided including ancient (>100 Ma) inter-familial relationships that predated the biogeographic processes being investigated. A single dissimilarity matrix was then generated by averaging the dissimilarity matrices of each of the five families. This increased the number of species per province, increasing the power of inference, and subsequent analyses used this averaged dissimilarity matrix.

We used the turnover fraction of both metrics (Sor_{turn} and $pSor_{turn}$) as the basis for grouping provinces into larger RES, performing both hierarchical clustering and nonmetric multidimensional scaling (NMDS). Optimal number of clusters was estimated using the Kelley-Gardner-Sutcliffe penalty function (KGS; see Supplementary Information). Significance of PBD between pairs of RES was assessed by testing if observed values of PBD re explained by taxonomic composition (CBD) alone. This was done by comparing each fraction of the phylogenetic beta diversity metric against a null model based on keeping the species diversity constant but resampling the underlying phylogenetic diversity by randomising the tree tip labels 1,000 times. Standardised effect size (SES) was calculated for each component as in Leprieur et al. (2012), which indicates if regions are less (≤-1.96) or more (≥1.96) phylogenetically similar than expected just from their compositional similarity.

Biogeographic analyses

Historical biogeographic reconstructions were performed under a biogeographic event-based model that considers both vicariance and dispersal as processes, DEC (Ree et al., 2005). The Bayesian implementation of this model (Landis, Matzke, Moore & Huelsenbeck, 2013), in RevBayes (Höhna et al., 2016), has been used for testing different biogeographic scenarios (Lavor, Calvente, Versieux & Sanmartin, 2018). We used species distributions categorised into the three RES, as delimited from beta diversity patterns (A, Atlantic; EP, East Pacific; and IWP, Indo-West Pacific). Simple DEC analyses considered allopatric ('a') and subset sympatric ('s') events, but full sympatry ('f') and jump dispersal ('j') can be included. We did not include jump dispersal due to concerns raised by Ree and Sanmartín (2018). Simple DEC ('s' and 'a') and DEC models with full sympatry ('s', 'a', and 'f') were compared using the ratio of marginal likelihoods with Bayes Factor (Thode, Sanmartin & Lohmann, 2019). Biogeographic inference was performed under both models using the consensus BEAST tree, for each family. Six independent runs of MCMC were performed, sampling every 10 in 10,000 samples, following the RevBayes tutorial (Michael Landis, http://revbayes.github.io/tutorials.html). Marginal likelihood estimators (MLE; log-likelihoods) were estimated both via 50 steps of Stepping Stone (SS) and Path Sampling (PS) during the MCMC and ln-Bayes factor estimated as $lnBF=MLE_{model1}-MLE_{model2}$ (Kass & Raftery, 1995).

Based on lnBF (Table S4), with values <1 (Ophionereididae) supporting the simple model over the more complex DEC model and near zero (Ophiotrichidae, Ophiolepididae, Ophiocomidae, and Ophiodermatidae) indicating no preference for either, biogeographic inferences were performed using simple DEC. To account for both phylogenetic uncertainty and uncertainty in age estimation, analyses were performed using the set of 100 BEAST trees for each family. A single MCMC chain was run sampling 10/10,000 and discarding 25% as burnin.

Ancestral states were summarised across the sample of 100 BEAST trees, for each family, onto the consensus tree. Effective Sample Sizes (ESS) were estimated to check for convergence of each MCMC run, and the run discarded if ESS<200 (none for Ophiocomidae, Ophiotrichidae and Ophionereididae, one for Ophiolepididae, and four for Ophiodermatidae). Only nodes defining clades from the consensus tree were considered in each posterior sample tree, which were identified based on their descendants. Ancestral states for each node, on each tree, were recovered from the end state column corresponding to each node from the ancestral state trace files generated in REVBAYES (Höhna et al., 2016).

As a comparison, biogeographic histories were also inferred under DEC and DIVA, implemented in 'BioGeoBEARS' (Matzke, 2013) R package using a variety of constraints and parameters (see Supplementary), and performing model-averaging based on model weight (wAICc, Table S5).

Faunal splits

In order to investigate the potential effect of the established physical biogeographic barriers considered in this study, divergence times across specific barriers were compared within and between families to look for concordant patterns of lineage splitting across regions. We also recovered transitions at cladogenesis and estimated age for each node, for each BEAST posterior tree sample, as outlined previously. Transitions for each node were recovered from the start state columns, in the ancestral state tree trace files, corresponding to the direct descendants of each node. These transitions represent different speciation modes (e.g. sympatry or allopatry), and were summarised by node (with values from 0 to 1). Faunal splits were only considered from allopatric events where both daughter lineages were inferred to occur in different regions, therefore only including three transitions (A/EP, A/IWP, EP/IWP). The temporal distributional of faunal splits was plotted to show both uncertainty in age estimation and phylogenetic uncertainty in estimation of biogeographic histories. Thus, all transitions recovered from the ancestral state files were plotted ('ggbeeswarm' R package; Clarke & Sherrill-Mix, 2017) to show the fully integrated global biogeographic posterior temporal distribution of faunal splits across the three RES. As suggested by Crisp, Trewick and Cook (2011), vicariance

was rejected for faunal splits if the age range (95% HPD) estimates from the consensus BEAST tree did not overlap with the period associated with the emergence of the relevant biogeographic barrier.

RESULTS

Patterns of tropical beta diversity

Species richness for tropical brittle star peaked in provinces in the Central Indo-Pacific (Fig. 1a), with up to 90 species. The peripheral Indo-Pacific provinces, as well as Eastern Atlantic and Eastern Pacific provinces showed lower taxonomic diversity. The pattern of sampled-species richness by province (Table S1 and Fig. S2) was highly correlated with that for all species in the distributional dataset (Fig. 1a, PPMCC = 0.984, p-val < 2.2e-16).

Three optimal clusters from the hierarchical clustering of CBD index Sor_{turn} (Fig. 1b and Fig. S8) were recovered, that could be designated as RES: 1) East Pacific (EP, yellow), 2) Atlantic (A, blue) and 3) Indo-West Pacific (IWP, red). The warm temperate African provinces of Agulhas and Benguela (Fig. 1d) were compositionally more similar to the Indo-West Pacific and Atlantic, respectively. Within-RES provinces, species turnover was low (Table S2). Alternatively, five optimal clusters were suggested from hierarchical clustering based on the PBD index $pSor_{turn}$ (Fig. 1c), including two new clusters in addition to the three previously identified: 1) Benguela and 2) a cluster of three peripheral Indo-West Pacific provinces (Hawaii, Easter Island and Southern Polynesia). However, both these clusters were characterised by low species richness and some old endemic species (Table S1). The 3D nonmetric multidimensional scaling (NMDS) ordination of provinces based on $pSor_{turn}$ values recovered Benguela as a transitional or an overlap region between the Atlantic+East Pacific and Indo-West Pacific provinces, while the three peripheral Indo-West Pacific provinces were grouped with other IWP provinces (Figs. 1a, d, S2, and S8). In addition, the few species distributed across both Atlantic and Indo-West Pacific mainly overlapped in Benguela and Agulhas (Fig. 1c). Therefore, these two additional clusters were considered unsuitable as separate regions in our selected macro-evolutionary analyses and we based subsequent biogeographic analyses on the dominant three major RES.

Within-RES provinces, phylogenetic beta diversity was mostly explained by nestedness (Table S2). No other subregional patterns of phylogenetic turnover were recovered within the Indo-West Pacific (e.g. separation of eastern African provinces). Within the Atlantic, provinces between East and West coasts appeared to be more phylogenetically dissimilar (median $pSor_{turn}$: 0.3, Table S3, Figs. 1d and S8) than between provinces within coasts (median $pSor_{turn}$ west: 0.07; east excluding Benguela: 0.0; east including Benguela: 0.15).Between RES, the highest phylogenetic separation occurred between

the Indo-West Pacific and both the Atlantic and East Pacific RES (SES ≥ 1.96; Table 2, Fig. S8). On the contrary, the East Pacific and Atlantic were recovered as being phylogenetically similar despite their dissimilarity in compositional (species-level) assemblages (SES ≤ -1.96; Table 2).

Biogeographic histories and regional faunal splits

Biogeographic histories

The frequency of EP/IWP faunal splits peaked during the Pliocene/Pleistocene (A, Fig. 2), long after the establishment of the East Pacific Barrier (65 Ma). In the case of A/IWP faunal splits, four frequency peaks were observed (B–E). Three of these predated the TTE (B–D), with one coinciding with the time associated to the opening of the Atlantic Ocean (B) and two during the narrowing of the Tethyan Seaway (C–D). Most transitions were recovered within the narrowing of the Tethyan Seaway (C–D) Additionally, A/IWP faunal splits also peaked after the TTE, during the Late Miocene (E). Splits between East Pacific and Atlantic faunas peaked during the late Miocene (F), after the land bridge started to form (from mid Miocene) but before the complete emergence of the Isthmus of Panama in the Pliocene (~2.8 Ma), with some coinciding with the final emergence (G).

Concordant patterns of regional transitions

Faunal splits (allopatric events) were recovered for 29 nodes (Fig. 3). As a result of higher uncertainty in the ancestral range estimation for older nodes, mostly associated with A/IWP splits (Fig. 2), older faunal splits tended to have lower frequencies than recent nodes. In comparison, most A/EP faunal splits were recovered with higher frequencies.

Concordant patterns of faunal splits were observed across the five families (Fig. 3, S9a), which were also temporally concordant with the emergence of biogeographic barriers. These results were also concordant with biogeographic inferences performed in BioGeoBEARS (Fig. S9), where the preferred biogeographic model for each of the five families included dispersal constraint between RES after the emergence of the relevant biogeographic barriers (Table S5). Faunal splits between the Atlantic and Indo-West Pacific were estimated very early in the history of the families Ophiodermatidae (Fig. S9a) and Ophiotrichidae, in the former, during the time associated with the opening of the Atlantic Ocean. Across all families, half of the nodes (6/12) with A/IWP splits were concordant with the narrowing of the Tethyan Seaway, but pre-dated the TTE. A/IWP splits after the closure of the Tethyan Seaway were only recovered for a single node in the family Ophiocomidae (see also peak E in Fig. 3), associated with the genus *Ophiocomella* A.H. Clark, 1939. The fissiparous *Ophiocomella* species complex was longitudinally widespread in all three RES, but direction of dispersal is unclear as node

states for this species complex were not decisive in our analyses (Figs. 3, S10). In all families, Atlantic+East Pacific lineages were estimated to have diverged from Indo-West Pacific lineages. Only a few species within these clades are also distributed in the Indo-West Pacific, and only one restricted to the IWP (*Ophiothrix echinotecta* Müller & Troschel, 1840), distributed in the east African coast. In Ophiodermatidae, Ophiotrichidae, and Ophionereididae, the Atlantic+East Pacific species formed monophyletic clades, whereas in Ophiocomidae and Ophiolepididae, at least two divergence events were recovered.

Splits between the Atlantic and Indo-West Pacific were followed in time by multiple splits between the Atlantic and East-Pacific lineages, all except one occurring in a narrow time range corresponding to the emergence of the Isthmus of Panama (15–2.8 Ma). East-Pacific lineages, mostly represented by a single species, were recovered nested within Atlantic clades in all families. These faunal splits were estimated to occur 13 times, with at least two events recovered in each family (Table 3, Fig. 3).

Faunal splits between the East and Indo-West Pacific Oceans were only recovered with high frequencies for the families Ophiocomidae and Ophiotrichidae (Table 3, Fig. 3). However, these were inferred to occur very recently (Pliocene/Pleistocene). Since the EPB has been in place since the Paleocene, we interpret these as dispersal events across the barrier. An eastward dispersal was recovered for *Ophiocoma erinaceus* Müller & Troschel, 1842 (Ophiocomidae; Fig. S10). Although the dispersals of *Ophiothela mirabilis* Verrill, 1867 (Ophiotrichidae; Fig. S14) and *Ophiocomella sexradia* (Duncan, 1887) (Ophiocomidae; Fig. S10) were inferred to occur eastward and westward, respectively, there was no certainty in the direction of these recent dispersals. EP/IWP faunal splits were also recovered with low frequency for Ophionereididae during the Paleocene–Eocene (Figs. S9a, S13).

Discussion

Biogeographic studies have transitioned from describing patterns to inferring processes that shape spatio-temporal patterns (Sanmartín, 2007). Here, we reassessed diversity patterns in tropical shelf brittle stars, and reconstructed their biogeographic history to investigate the effect of the emergence of biogeographic barriers in their evolution. To improve biogeographic inferences, model selection was performed based on Bayes factor and phylogenetic uncertainty and uncertainty in divergence ages were taken into account. Additionally, the regions used for our global-scale analysis were defined based on patterns of beta diversity, as areas should be relevant to the hypotheses being tested (Ree & Sanmartín, 2009).

Regional faunas and shared ancestry

Both phylodiversity and model-based biogeographical approaches revealed a clear picture of the role of Earth history in shaping tropical brittle star diversity. Patterns of species and phylogenetic turnover (Fig. 1) across biogeographic provinces (Spalding et al., 2007) recovered three main regions, the Atlantic, East Pacific and Indo-West Pacific, which we used as RES. We also recovered strong patterns of phylogenetic regionalisation, with large clades being endemic to different RES. The Atlantic and East Pacific have a long history of shared ancestry and independent evolution from the Indo-West Pacific (Tables 2 and S2), suggesting a more recent isolation.

In reef fishes, conspicuous patterns of phylogenetic diversity were found within the Indo-West Pacific and the Atlantic Oceans (Cowman, Parravicini, Kulbicki & Floeter, 2017). For these taxa, the African coast and the Red Sea diversity differed from the rest of the Indo-West Pacific (Cowman et al., 2017). In other groups, diversity patterns differed between the West Indian Ocean and the West Pacific (e.g. Lessios, Kessing & Pearse, 2001), while we recovered no clear patterns within the Indo-West Pacific RES across the five families of brittle stars.

Differences in tropical reef fish diversity patterns were also found between the east and west Atlantic coasts (Cowman et al., 2017), where the mid-Atlantic represents a filter for dispersal with only few species dispersing through this wide stretch of water, mostly eastwards (Floeter et al., 2008). In brittle stars, we found Atlantic provinces to be more phylogenetically dissimilar between than within coasts, concordant with the patterns described for tropical reef fishes (Cowman et al., 2017). Most Atlantic brittle stars included in this study are restricted to either the east or west coast, with many more species occurring in the West. The lower diversity of the East Atlantic could be attributed to less extensive survey effort in the East, to restricted dispersal across the basin (Floeter et al., 2008) or to the lack of extensive coral reefs on the west African coast. The lack of coral reefs have been evident since a massive extinction event, possibly due to cold currents, during the late Miocene (Boekschoten & Best, 1988). The same extinction event could have also had a similar effect on the tropical brittle star fauna off this coast. Lastly, phylogenetic diversity turnover between Benguela and the rest of the east Atlantic provinces was estimated to be high. This province, that contains several old temperate endemics as well as a few tropical species (Figs. 1d, and S8), is characterised by an upwelling of colder water (Lutjeharms, 2007) that could limit dispersal of tropical species.

Our data contains most of the common tropical brittle star species. Common species frequently dominate major large-scale patterns (Pos et al., 2014), and we do not expect these patterns of evolutionary history between RES to substantially alter with increased sampling.

Global historical biogeography of tropical brittle stars

Our findings based on ancestral range estimations were congruent with other studies showing that the emergence of barriers heavily structured the biogeography of extant tropical marine taxa (Cowman & Bellwood, 2013). We found patterns of regional splits within the five families, which were consistent under both maximum Likelihood and Bayesian approaches (Figs. S9–S14). These splits were also temporally concordant with the known emergence times of biogeographic barriers in an unconstrained model (Figs. 2–3). Moreover, a biogeographic model with dispersal constraints in accordance with the emergence of biogeographic barriers showed strong statistical support (Table S5).

Atlantic Opening

We infer that the five families of tropical shallow-water brittle stars included in this study have a Tethyan origin, as ancestral ranges recovered an IWP or IWP+A distribution for the deeper nodes (Figs. S10–S14). These reconstructions were consistent with fossil records across the north and west of the Tethys Sea (Harzhauser et al., 2007; Štorc & Žítt, 2008; Thuy & Kroh, 2011). Tethyan lineages subsequently regionalised into Atlantic and Indo-West Pacific faunas, as shown by both phylogenetic diversity metrics and biogeographic reconstructions (Figs. 1 and 3). A similar Tethyan origin has also been inferred for several other extant tropical marine taxa (staghorn corals, Wallace & Rosen, 2006), from which sister Indo-West Pacific and Atlantic faunas diverged as a result of the closure of the Tethys Seaway (TTE: Terminal Tethyan Event, 18-12 Ma; Hou & Li, 2018).

In general, A/IWP faunal splits were estimated to have occurred much more frequently during the Eocene, and less frequently during the late Cretaceous (Ophiodermatidae) and Pliocene (Figs. 2 and S9a). The older splits in Ophiodermatidae suggested that the opening of the Atlantic Ocean during the late Cretaceous (110-65 Mya; Perez-Diaz & Eagles, 2017; Hou & Li, 2018) might have affected the evolution of brittle stars, by acting as an important filter for dispersal, as has been found in fishes (Floeter et al., 2008).

East Pacific Barrier

The East Pacific Barrier, one of the greatest marine biogeographic barriers for shallow-water species (Briggs, 1961) can be breached by some taxa (Lessios & Robertson, 2006). We recovered three recent (Pliocene and Pleistocene) dispersals between the East Pacific and the Indo-West Pacific (Figs. 1–3, and S10–S14). Although it has been shown that the transport times across the EPB exceeds the larval life span of most marine taxa, El Niño events could speed up dispersal enough for larvae with longer life spans (i.e. planktotrophic larvae) to cross this barrier (Wood et al., 2016). *Ophiocoma erinaceus* is an Indo-West Pacific sexually reproducing species with planktotrophic larvae that has been recorded

from the Clipperton Islands, the most western province of the East Pacific. Interestingly, the other two species with transpacific dispersals (*Ophiocomella sexradia* and *Ophiothela mirabilis*) are fissiparous (reproducing asexually, but also have sexual reproduction), for which their ability to reproduce asexually would aid rapid proliferation (Boissin, Egea, Féral & Chenuil, 2015), and successful colonisation (Mantelatto et al., 2016).

Tethyan Seaway

Faunal splits between the Atlantic and Indo-Pacific were estimated with high frequency during the Eocene (Fig. 2). These divergence events were concordant with the narrowing of the Tethyan Seaway (50–18 Ma), suggesting it was a driver of divergence events shaping current distributions of tropical brittle stars (Ophiocomidae, Ophiolepididae, Ophionereididae, and Ophiotrichidae). Although the splits pre-dated the TTE, our results are congruent with previous findings in other marine taxa (reviewed in Hou & Li, 2018), for which pre-TTE vicariance has been explained by the emergence of genetic barriers driven by ecological changes resulting from plate tectonics (Liu, Li, Ugolini, Momtazi & Hou, 2018). Apparent vicariant events pre-dating the TTE have also been attributed to calibration errors (Malaquias & Reid, 2009) or selective extinction concealing patterns (Cowman & Bellwood, 2013). An example of the latter might be the deep (Eocene) split within *Ophionereis* Lütken, 1859 between the East Atlantic *O. perplexa* (Ziesenhenne, 1940) and an Atlantic clade (Figs. 2, S9, and S13). However, the concordant patterns independently estimated here across five families, under an unconstrained model (Figs. 2 and 3) and several averaged models (Fig. S9 and Table S5), suggest a common process driving the evolution of tropical brittle stars.

Transitions between the Indo-West Pacific and Atlantic that post-date the TTE can be attributed to dispersal around South Africa. Dispersals occurring in this region have been documented from fossil (Vermeji & Rosenberg, 1993) and molecular evidence (Bowen, Muss, Rocha & Grant, 2006), in which lineages from the Indian Ocean colonised the west Atlantic, with further dispersals into islands from the Mid-Atlantic Ridge. However, regional transitions inferred from our study did not conform to this pattern. Species of *Ophiocomella* might have dispersed through South Africa, but the dispersal route across the three RES was uncertain in our data. Four other dispersals might be inferred around South Africa, but these represent species (Ophiotrichidae: *Ophiothrix (Ophiothrix) aristulata Lyman, 1879*; Ophiodermatidae: *Ophioderma wahlbergii* Müller & Troschel, 1842*, Cryptopelta aster* (Lyman, 1879)*, Ophiarachnella capensis* (Bell, 1888)) with narrow distribution across the Atlantic and Indo-West Pacific RES (Table S1). Only the deeper species *O. aristulata* (50-650 m; O'Hara, 1998) has a significant distribution outside southern Africa, being also reported from Australia and New Zealand (O'Hara, England, Gunasekera & Naughton, 2014), and represents a significant incursion of an Atlantic clade across the Indian Ocean. However, its pattern of distribution may be

more indicative of southern upper bathyal species rather than shallow-water tropical fauna. The other three species were restricted mostly to South Africa, at the boundaries of both RES. Disjunct distributional ranges around South Africa have been reported for several taxa, but the site of disjunction varies (Waters, 2008), consistent with the variable limits of distributional ranges on these three species of brittle stars. These apparent range expansions could represent warm-adapted taxa that successfully adapted to more temperate conditions as the tropics contracted, becoming restricted to South Africa. They could also represent recent (e.g. *O. capensis*) or ancient (e.g. *O. wahlbergii*) offshoots of a regionalised fauna, but without data on other closely related species it is not possible to determine the timing and causes of these distributions.

Isthmus of Panama

The full emergence of the Isthmus of Panama occurred during the late Pliocene (*c*. 2.8 Ma), and caused the divergence of lineages in several marine taxonomic groups (reviewed by Lessios, 2008). Faunal splits between these two regions also pre-dated the full emergence of the barrier (Figs. 2 and 3), being more frequent during the mid to late Miocene. Geochemical, geochronological and biological evidence have suggested a complex history of gradual uplift, with deep water seaways being extinguished during the late Miocene (around 9.2 Ma ago; O'Dea et al., 2016), and reduced water flow from west to east (Newkirk & Martin, 2009) that might have affected connectivity or reduced suitable habitat. No separation events were inferred to occur after the complete closure of the Panamanian Seaway. The only exception to this was the introduced eastern Pacific species *Ophiothela mirabilis* (Mantelatto et al., 2016).

Concluding remarks

Phylogenetic diversity and biogeographic historical reconstructions provided evidence of the key role that tropical biogeographic barriers have played in the diversification of tropical brittle stars. The extant tropical shallow-water brittle stars were inferred to have a Tethyan origin, from which Atlantic and Indo-West Pacific faunas diverged. However, these divergence age estimates predate the TTE, suggesting that changes driven by the narrowing of the Tethyan Seaway shaped spatio-temporal assemblages more than its final closure. The EPB barrier played an extremely important role in the evolution of this group, as it has largely prevented colonisation of the East Pacific from the Indo-West Pacific. Instead, the extant East Pacific fauna diverged from the Atlantic, due to the gradual emergence of the Isthmus of Panama.

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Code and data availability

See supplementary.

Conflict of interest

All authors declare no conflict of interest.

622

623 **Biosketch**

624 The list of authors includes echinoderm researchers with experience in taxonomy, phylogenetics and
625 biogeography.

626

627 **Author contributions**

628 G.B.C., H.V. A.H. and T.O.H. conceived the study. T.O.H. and A.H. contributed data. G.B.C.
629 performed analyses and drafted the manuscript. All authors contributed to the final manuscript.

630

631 **Supplementary information**

632 Table S1. Absence/presence of species of brittle stars by biogeographic provinces.

633 Table S2. Pairwise comparisons of phylogenetic beta diversity of brittle stars between biogeographic
634 provinces based on the phylogenetic Sörensen (pSor) dissimilarity index, and decomposition into
635 turnover ($pSor_{turn}$) and nestedness ($pSor_{ne}$).

636 Figure S1. Time-calibrated phylogeny of the class Ophiuroidea.

637 Figure S1. Sampled-species richness of brittle stars by biogeographic province.Figure S2. Time-
638 calibrated tree of the family Ophiocomidae.Figure S3. Time-calibrated tree of the family
639 Ophiodermatidae.

640 Figure S4. Time-calibrated tree of the family Ophiolepididae.

641 Figure S5. Time-calibrated tree of the family Ophionereididae.

642 Figure S6. Time-calibrated tree of the family Ophiotrichidae.

643 Figure S7. Turnover component from brittle star beta diversity index of biogeographic provinces.

644 Table S3. Within-RES statistics for brittle star phylogenetic turnover estimates between provinces.

645 Table S4. Ln-Bayes factors for biogeographic model selection for each brittle star family.

646 Table S5. Different models considered for the biogeographic history of tropical shallow brittle stars.

647 Figure S8. Integrated posterior temporal distribution of brittle star faunal splits.

648 Figure S9. Biogeographic history of the family Ophiocomidae.

649 Figure S10. Biogeographic history of the family Ophiodermatidae.

650 Figure S11. Biogeographic history of the family Ophiolepididae.

651 Figure S12. Biogeographic history of the family Ophionereididae.

652 Figure S13. Biogeographic history of the family Ophiotrichidae.

653 Supplementary File 1. BEAST xml file for the family Ophiocomidae.

654 Supplementary File 2. BEAST xml file for the family Ophiodermatidae.

655 Supplementary File 3. BEAST xml file for the family Ophiolepididae.

656 Supplementary File 4. BEAST xml file for the family Ophionereididae.

657 Supplementary File 5. BEAST xml file for the family Ophiotrichidae.

658 Supplementary File 6. Combined log files from two BEAST runs for the family Ophiocomidae.

659 Supplementary File 7. Combined log files from two BEAST runs for the family Ophiodermatidae.

660 Supplementary File 8. Combined log files from two BEAST runs for the family Ophiolepididae.

661 Supplementary File 9. Combined log files from two BEAST runs for the family Ophionereididae.

662 Supplementary File 10. Combined log files from two BEAST runs for the family Ophiotrichidae.

663 Supplementary File 11. Sample of 100 BEAST posterior sample trees from two combined runs for the
664 family Ophiocomidae.

665 Supplementary File 12. Sample of 100 BEAST posterior sample trees from two combined runs for the
666 family Ophiodermatidae.

667 Supplementary File 13. Sample of 100 BEAST posterior sample trees from two combined runs for the
668 family Ophiolepididae.

669 Supplementary File 14. Sample of 100 BEAST posterior sample trees from two combined runs for the
670 family Ophionereididae.

671 Supplementary File 15. Sample of 100 BEAST posterior sample trees from two combined runs for the
672 family Ophiotrichidae.

673 Supplementary File 16. R scripts.

674 Supplementary File 17. RevBayes scripts.

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677

678 **Table 1. Number of described species of brittle stars according to O'Hara et al (2017) per family, tropical**
679 **shallow-water species and species contained in the phylogenies.**

FAMILY	NUMBER OF DESCRIBED SPECIES	NUMBER OF KNOWN TROPICAL SPECIES	TROPICAL SPECIES WITH SEQUENCES	NUMBER OF MONOPHYLETIC CLADES AND SPECIES PRUNED
Ophiocomidae	45	43 (96%)	41 (95%)	0+ 1 spp
Ophiodermatidae	57	41 (72%)	28 (68%)	1(2 spp) + 6 spp
Ophionereididae	56	49 (88%)	27 (55%)	3 (2, 2, and 6 spp) + 5 spp*
Ophiolepididae	38	20 (53%)	17 (85%)	2 (4 and 4 spp)
Ophiotrichidae	170	135 (79%)	60 (36%)	1(4 spp) + 1 spp*

680 * Two additional tips were removed as they represent cryptic species of known species that are already
681 included.
682 Details of the number of described species, species inhabiting tropical shallow-water habitats, species with
683 genetic data available and number of monophyletic clades and species pruned from family-level phylogenies are
684 shown. Additionally, percentage of tropical species, as well as percentage of tropical taxa sampled per family is
685 shown in brackets. Pruned species represent deep-sea taxa, non-tropical or duplicates of tropical shelf taxa
686 (details in Figs. S3–S7).

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688

689 **Table 2. Metrics of phylogenetic beta diversity of brittle star assemblages, and corresponding turnover**
690 **and nestedness fractions for delimited regions of evolutionary significance (RES).**

	REGIONS OF EVOLUTIONARY SIGNIFICANCE	pSor	$pSor_{turn}$	$pSor_{ne}$
Observed	Atlantic/East Pacific	0.529	0.359	0.169
	East Pacific/Indo-West Pacific	0.854	0.629	0.225

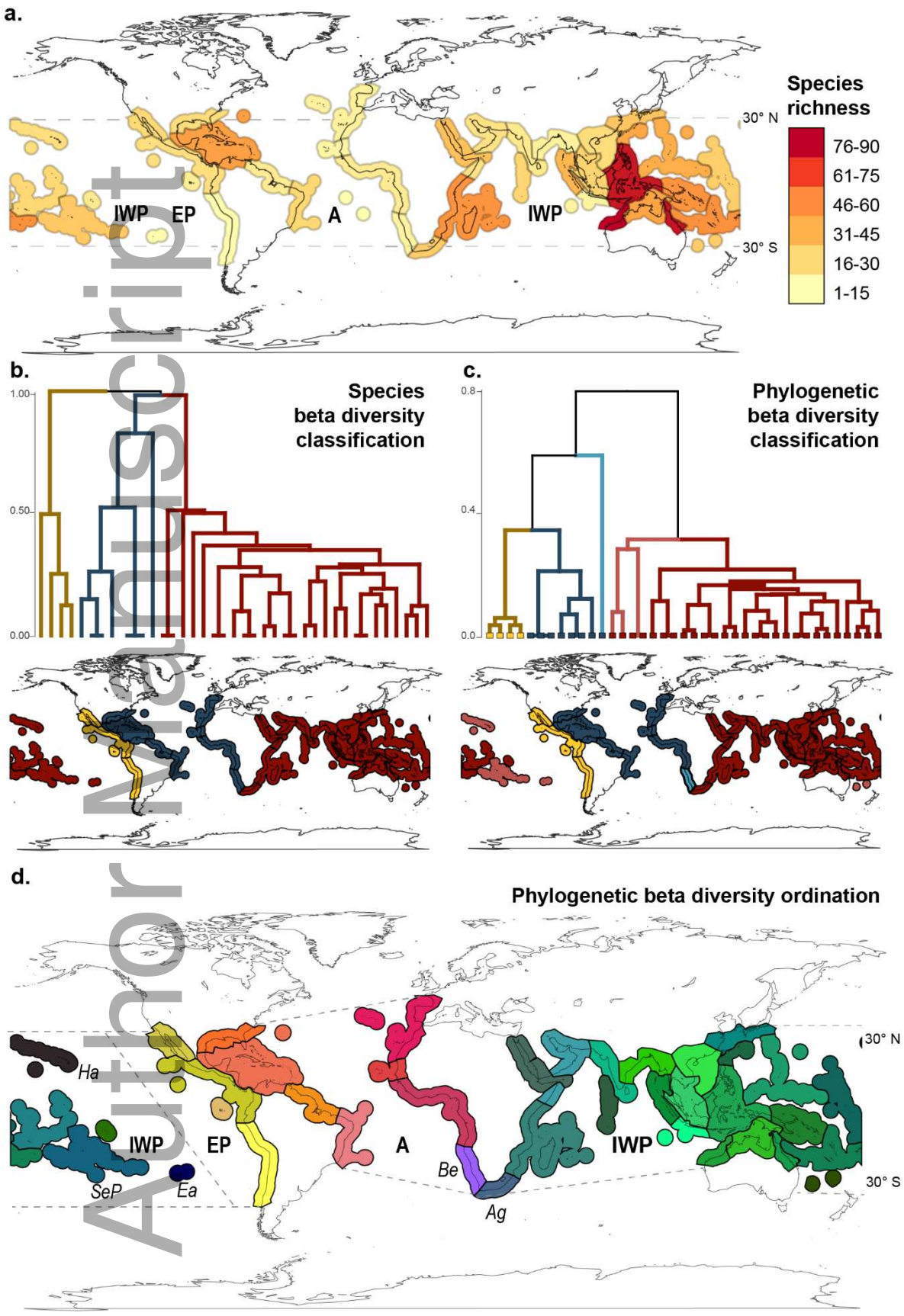
	Atlantic/Indo-West Pacific	0.779	0.675	0.104
Standardised Effect Size (SES)*	Atlantic/East Pacific	-1.751	-2.655	3.072
	East Pacific/Indo-West Pacific	5.795	5.166	-2.283
	Atlantic/Indo-West Pacific	6.403	7.264	-4.449

*SES values ≥ 1.96 and ≤ -1.96 indicated a PBD higher and lower, respectively, than expected from taxonomic assemblages. pSor, phylogenetic Sörensen index; $pSor_{turn}$, phylogenetic turnover; $pSor_{ne}$, phylogenetic nestedness.

Table 3. Summary of numbers of nodes associated with brittle star faunal splits between Atlantic, Indo-West Pacific and East Pacific oceans.

FAMILY	A/EP		A/IWP			EP/IWP
	ALL	**IoP**	**ALL**	**AO**	**NTS**	**ALL**
Ophiocomidae	2	2	5	0	4	2
Ophiodermatidae	5	5	2	2	0	0
Ophiolepididae	2	2	2	0	1	0
Ophionereididae	3	1	1	0	1	1
Ophiotrichidae	2	2	2	0	1	1
TOTAL	**14**	**12**	**12**	**2**	**7**	**4**

Columns include the number of nodes for which brittle star faunal splits were recovered with at least 10% frequency and temporally consistent with biogeographic events. Atlantic Opening (AO), narrowing of the Tethyan Seaway (NTS), rise of the Isthmus of Panama (IoP), Atlantic (A), East Pacific (EP), and Indo-West Pacific (IWP).



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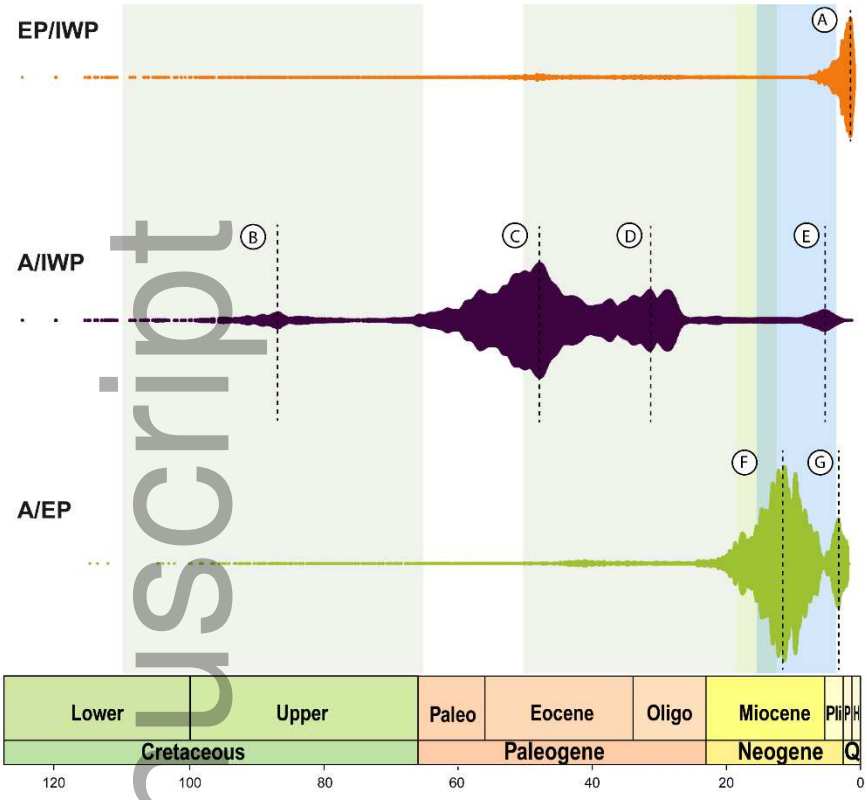

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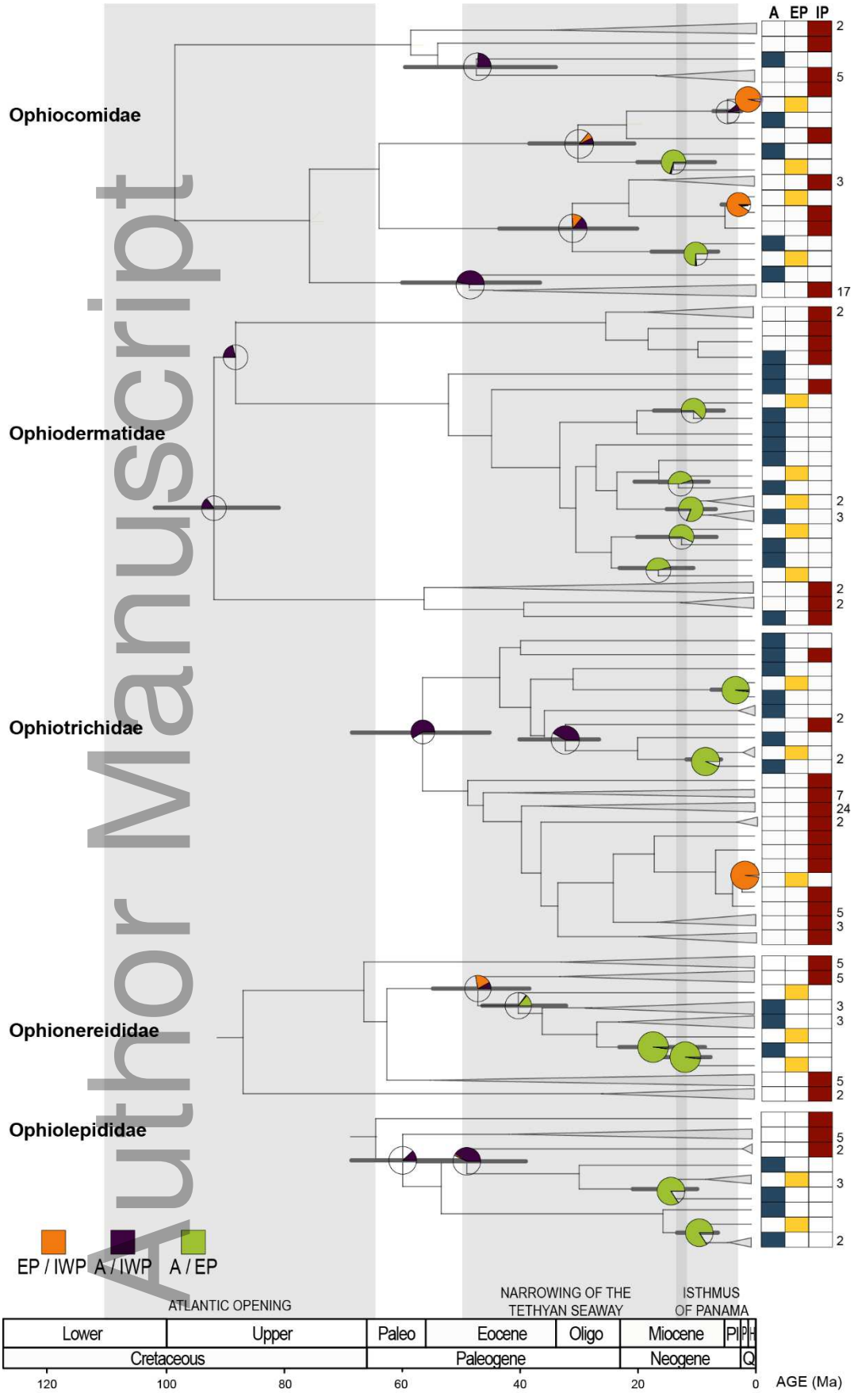

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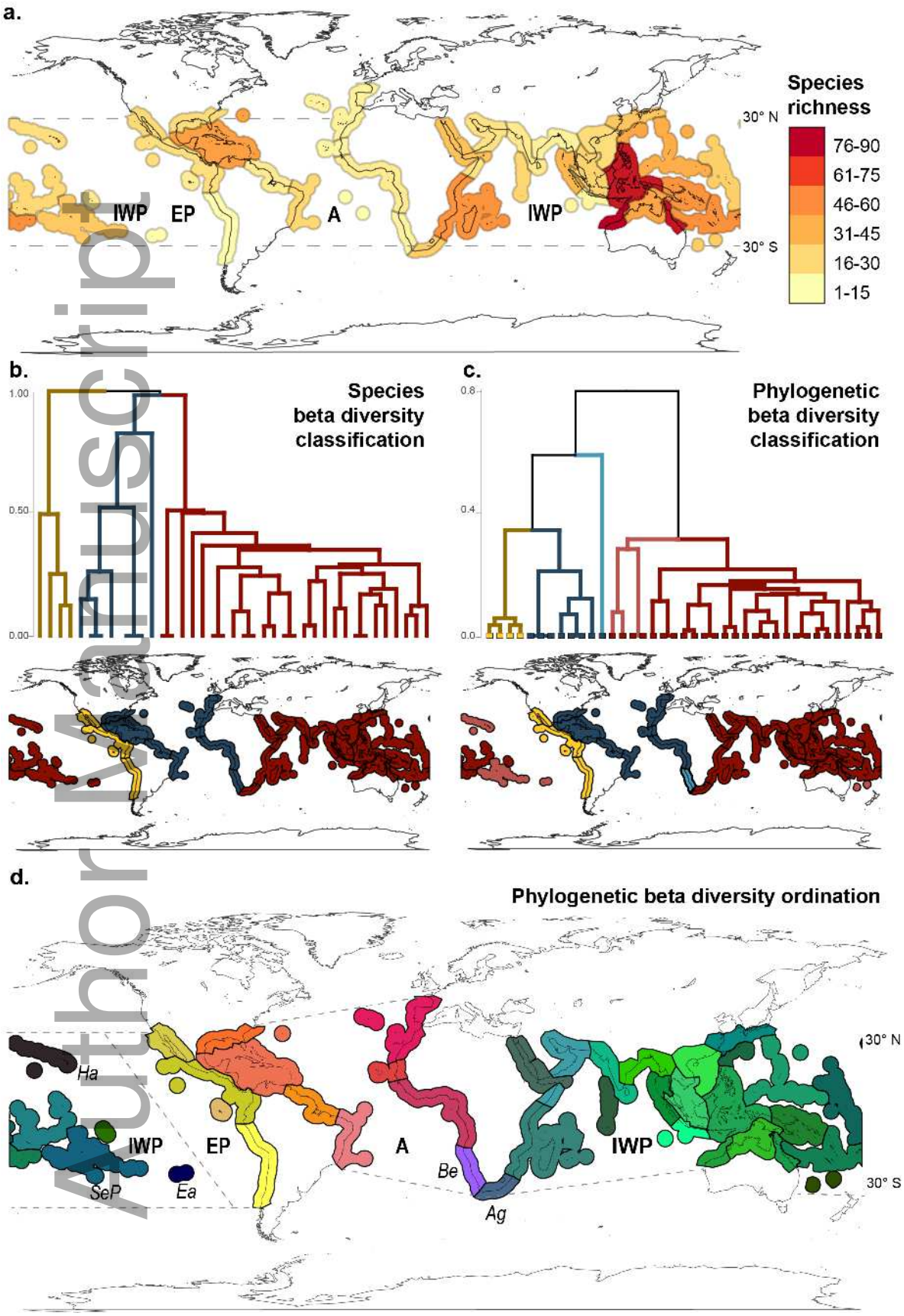
705

706 **Figure legends**

707 **Figure 1. Distribution of beta diversity of five families of tropical shelf brittle stars** | (a) Species
708 richness by tropical/temperate MEOW provinces (Spalding et al., 2007). Provinces clustered, using
709 UPGMA, as potential regions of evolutionary significance (RES) using metrics of species turnover
710 (Sor_{turn}, b) and phylogenetic turnover ($pSor_{turn}$, c) are shown in yellow (EP), blue (A) and red (IWP).
711 Two smaller clusters, recovered by phylogenetic turnover, have branches shown in pink and light
712 blue, while leaves in dendrogram show our three chosen RES. (d) RGB representation of the three
713 axes of a NMDS ordination of phylogenetic turnover between provinces, with similar colours
714 indicating regions that are phylogenetically similar. IWP, Indo-West Pacific; EP, East Pacific; A,
715 Atlantic; Ha, Hawaii; SeP, Southeast Polynesia; Ea, Easter Island; Be, Benguela; Ag, Agulhas (for
716 other province names, see Spalding et al., 2007).

717 **Figure 2. Integrated posterior temporal distribution of brittle star faunal splits. |** Posterior
718 density of faunal splits recovered for all nodes, under a simple DEC model, on 100 posterior sample
719 trees for each of the five families of brittle stars. Width (y axis) of the violin plots is proportional to
720 the number of data points. Peaks on the frequency of faunal splits between EP/IWP (A), A/IWP (B–E)
721 and A/EP (F) are indicated. A, Atlantic; IWP, Indo-West Pacific; EP, East Pacific. Time associated
722 with the emergence of specific barriers is indicated with coloured bands, from left to right: Atlantic
723 Opening, narrowing of the Tethyan Seaway, Terminal Tethyan Event, and rise of the Isthmus of
724 Panama.

725 **Figure 3. Inferred biogeographic histories of five families of tropical shelf brittle stars. |** Faunal
726 splits (A/IWP, EP/IWP, A/EP), as estimated from a simple DEC model and averaged across 1-100
727 posterior sample trees, mapped onto family-level BEAST consensus trees. Only nodes for which
728 faunal splits were recovered with at least 10% frequency are annotated with age 95%CI bars and
729 transition frequency pie-charts. Node pie-charts are coloured according to each of the three faunal
730 splits, with no colour indicating other events at cladogenesis (e.g. sympatry). Species distributions are
731 shown for each of the three regions: Atlantic (A), East Pacific (EP) and Indo-West Pacific (IWP).
732 Clades endemic to a region are collapsed, not to scale, but the number of species in each is indicated
733 on the right.



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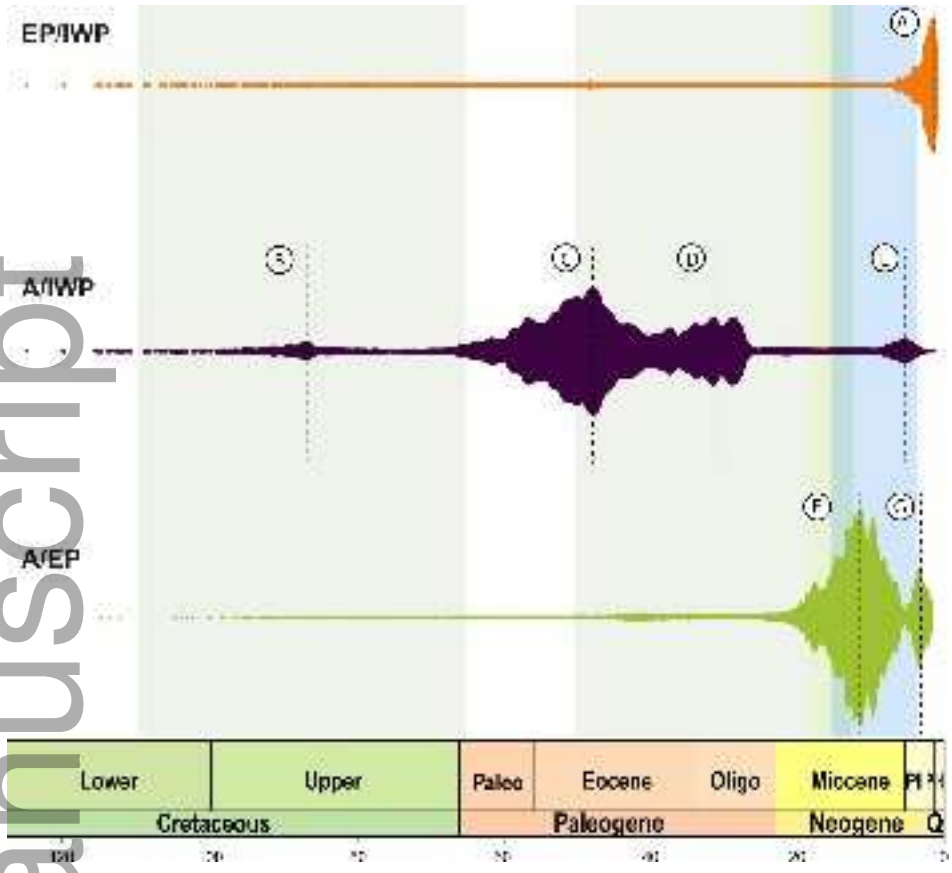

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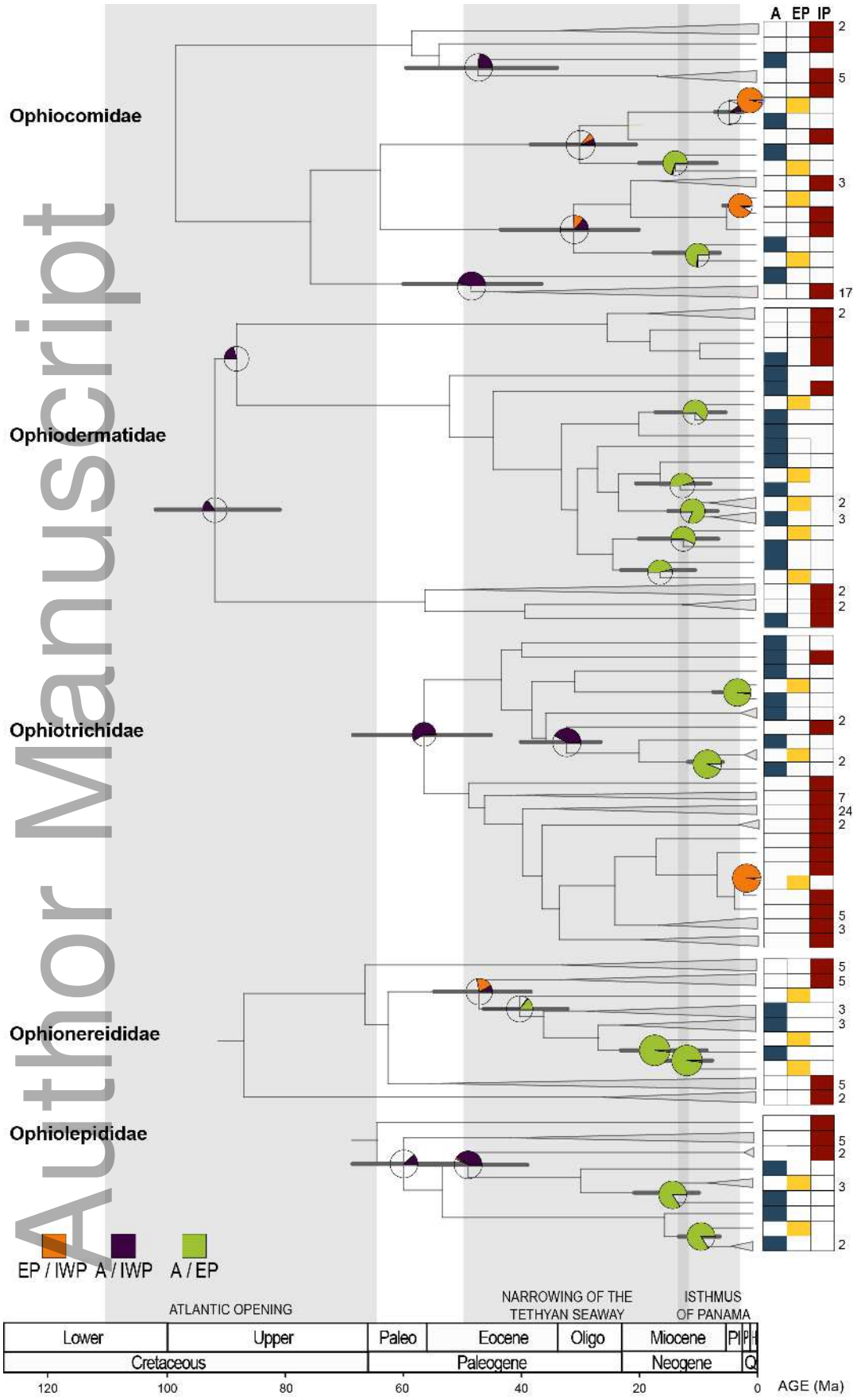

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