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Eocene–Oligocene sea-level fall drove amphipod habitat shift from marine to freshwater in the Far East

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Abstract

The Eocene–Oligocene sea-level fall has been viewed as a primary driver of biological succession. We used Anisogammaridae living in both marine and freshwater habitats to test the hypothesis that Eocene–Oligocene sea-level fall can explain the marine–freshwater habitat shift in the Far East. We obtained three mitochondrial and two nuclear fragments for 138 samples representing 31 species, covering marine and freshwater habitats from latitudes 24 to 50°N. The phylogenetic analyses revealed that freshwater Anisogammaridae is monophyletic. Divergence-time estimation and ancestral range reconstruction indicate that the family originated from a marine habitat in the North Pacific region during the Eocene and separated between marine and freshwater lineages at 38 Ma. The freshwater lineage diversified at 27 Ma, and further diverged into lotic and lentic clades. Our results suggest that the Eocene–Oligocene sea-level fall provided an opportunity for marine-derived Anisogammaridae to shift to new freshwater habitats. The freshwater anisogammarids dispersed from north to south, resulting in the restriction of current marine species restricted to the latitudes 35–50°N and the range of freshwater species in latitudes 24–40°N. Deep divergences within the freshwater lineage were related to the separation of lotic and lentic environments and the opening of the Japan Sea.

KEYWORDS

biogeography, diversification, molecular phylogeny, north-western Pacific, opening of the Japan Sea

1 | INTRODUCTION

The Eocene–Oligocene transition (about 34 Ma) was characterized by a rapid decline in sea level (Hansen, Sato, Russel, & Kharecha, 2013; Miller et al., 2005; Zachos, Pagani, Sloan, Thomas, & Billups, 2001). The sea-level fall led to a major turnover of shallow marine molluscs in the early Oligocene of the US Gulf Coast and Paris Basin (Coxall & Pearson, 2007). Meanwhile, the sea-level fall resulted in the emergence of new freshwater habitats, providing pathways for habitat shifts of many marine-derived organisms (Hou & Li, 2018; Hou, Sket, Fišer, & Li, 2011). Sea catfishes in Australia-New Guinea (Betancur-R, Orti, Stein, Marceniuk, & Pyron, 2012) and gammarid amphipods in Eurasia (Hou, Sket, & Li, 2014) are perhaps the best known cases. However, few attempts have been made to document the impact of sea-level fall in the Far East.

Far East region experienced environmental changes similar to those of other areas during the Eocene–Oligocene transition. The decline in sea level (34–27 Ma) expanded the East Asian continental margin and provided new freshwater niches for aquatic biota to occupy. During the early Miocene (20–15 Ma), the Japan Sea progressively opened to isolate Japan as an island arc system (Isozaki, Aoki, Nakama, & Yanai, 2010), which might have driven the biotic separation between the East Asian mainland and Japan. The sea-level fall and geological events in Far East region are likely associated with the evolutionary history of the family Anisogammaridae.

Amphipods of the family Anisogammaridae are distributed in marine and freshwater habitats along the west and east sides of North Pacific. The species are assigned to 12 genera (Sket & Fišer, 2009), of which marine *Anisogammarus* and freshwater *Ramellogammarus* are endemic to east side of the North Pacific (Bousfield, 2001). In west side of the North Pacific, genera *Barrowgammarus*, *Carineogammarus*, *Locustogammarus*, *Spinulogammarus* and *Spasskogammarus* inhabited coastal marine environments north of latitude 40°N, whereas *Eogammarus* are widespread along coast from latitudes 35 to 50°N (Tomikawa, Morino, Toft, & Mawatari, 2006). The genera *Jesogammarus*, *Fuxigammarus*, *Fuxiana* and *Eurypodogammarus* occur in freshwater environments of north-western Pacific margin, including the Japanese archipelago, the Korean Peninsula and the continental China between latitudes 24 and 40°N (Morino, 1994; Tomikawa, Nakano, & Hanzawa, 2017). The genus *Jesogammarus* contains two subgenera *Jesogammarus* and *Annanogammarus*, however, the subgenus *Annanogammarus* is morphologically distinct (Tomikawa et al., 2017) and treated as a valid genus in this study. The species of *Jesogammarus* mostly lives in lotic waters such as streams or rivers, whereas species of *Annanogammarus* inhabits lentic environments including springs and lakes. The genera *Fuxiana*, *Fuxigammarus* and *Eurypodogammarus* are restricted to lakes in Yunnan, China (Hou, Morino, & Li, 2005).

With distributions spanning both marine and freshwater habitats in the Far East, anisogammarid amphipods can serve as an excellent model system to test the hypothesis of habitat shift from marine to freshwater driven by Eocene–Oligocene sea-level fall. We explore in what sequence diversification proceeded, frequent versus single marine–freshwater shift (Figure 1a): (H1) frequent marine–freshwater shifts, indicating that marine–freshwater transitions have occurred repeatedly during the diversification of the analysed lineages. As freshwater colonizations occurred in parallel in different lineages, closely related marine and freshwater species occur intercalated in this tree. (H2) single marine–freshwater shift, indicating a single freshwater colonization followed by diversification in the new environment. Freshwater species tend to cluster into a monophyletic group.

The aims of this study are: (a) to reconstruct a precise phylogeny of the family Anisogammaridae, including both marine and freshwater species, based on nuclear and mitochondrial genes; and (b) to investigate the divergence times and biogeographic patterns of the group to assess its spatio-temporal evolution associated with Eocene–Oligocene sea-level fall.

2 | MATERIALS AND METHODS

2.1 | Sampling

Samples of marine and freshwater Anisogammaridae were collected from most known distribution ranges along the Far East. A total of 138 individuals of 31 species were examined, including 22 marine individuals of eight species belonging to genera *Spasskogammarus* and *Eogammarus* and 116 freshwater individuals of 23 species belonging to genera *Jesogammarus*, *Annanogammarus*, *Fuxigammarus* and *Eurypodogammarus* (Table S1). We sampled 22 out of the 25 known freshwater species (accounting for 88%), and one undescribed species in the Far East region; only *Annanogammarus koreaensis*, *Jesogammarus ilhoii* and *Fuxiana yangi* were not sampled. Two species from the genus *Gammarus* (*G. nekkensis* and *G. abstrusus*) were selected as outgroup taxa. Voucher specimens were deposited in the Institute of Zoology, Chinese Academy of Sciences. Detailed sample information is presented in the Table S1.

2.2 | Laboratory protocols and phylogenetic analysis

DNA was extracted from the legs of specimens using the Tiangen Genomic DNA kit according to the manufacturer's instructions. Three mitochondrial fragments (cytochrome oxidase subunit I COI-1 and COI-2, and 16S) and two nuclear regions (18S rRNA and 28S rRNA) were amplified with annealing temperatures optimized at 45–50°C. Details of the primers and PCR conditions are provided in Table S2.

All newly generated sequences were proofed and edited with Sequencher 4.5 (Gene Codes Corporation). Alignment was performed on online version of MAFFT 7 with default parameters (http://mafft.cbrc.jp/alignment/server/). The COI-1 and COI-2 sequences were validated by translation into amino acids using the invertebrate mitochondrial genetic code in MEGA 7.0.26 (Kumar, Stecher, & Tamura, 2016). The number of variable sites and parsimony informative sites was calculated using MEGA. The COI-1, COI-2, 16S, 18S and 28S sequences were concatenated using SequenceMatrix 1.7.8 (Vaidya, Lohman, & Meier, 2011). The best-fit partitioning scheme and nucleotide substitution models were selected using PartitionFinder 1.1.1 (Lanfear, Calcott, Ho, & Guindon, 2012) and the Akaike information criterion (AIC; Table S3).

Phylogenetic relationships were inferred using maximum likelihood (ML) and Bayesian inference (BI) for single and concatenated gene datasets. ML analysis was implemented with RAxML 8.2.9 (Stamatakis, 2014) under the substitution model GTRGAMMA. A rapid bootstrap of 1,000 replicates followed by a thorough optimization was performed for each dataset to determine the best-scoring ML tree and nodal support. Bayesian

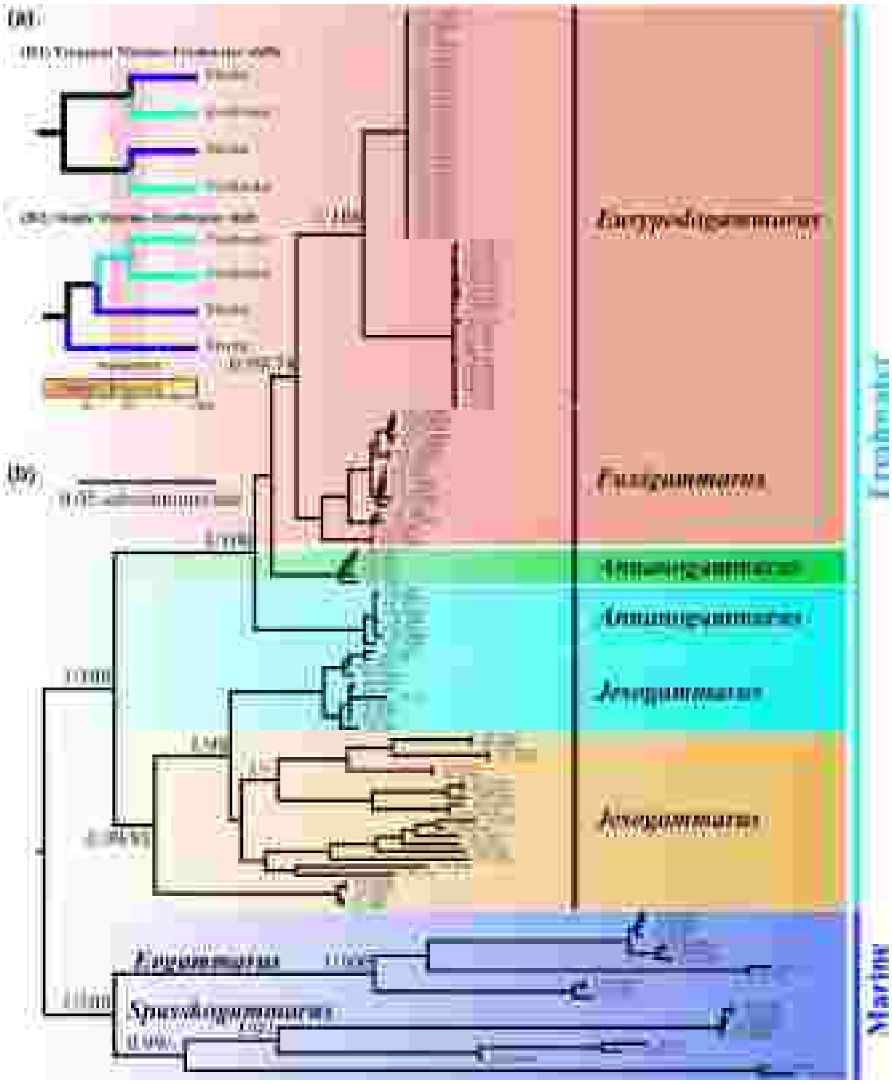

FIGURE 1 Alternative hypotheses for the colonization of freshwater habitats and phylogeny of the family Anisogammaridae. (a) Hypotheses of marine–freshwater shifts. H1 is the frequent marine–freshwater hypothesis, indicating that marine–freshwater shifts have occurred in parallel in different lineages. H2 is a single marine–freshwater hypothesis, indicating a single freshwater colonization followed by diversification in the new environment. (b) Bayesian tree of the family Anisogammaridae derived from the concatenated dataset of three mitochondrial and two nuclear fragments. Support values (Bayesian posterior probabilities ≥0.95/ maximum likelihood bootstrap proportions ≥70) are shown for major nodes. The vertical bars on the right indicate major clades. Branch colours refer to different biogeographic regions: dark blue for the marine clade; orange for north-eastern Japan; light blue for central China; green for south-western Japan; and red for south-western China

analyses were conducted using MrBayes 3.2.6 (Ronquist et al., 2012), with the best-fit substitution model. Two simultaneous runs of four Monte Carlo Markov chains were carried out for 20 million generations and with sampling of 1,000 generations to ensure that the standard deviation of split frequencies was below 0.01. The stationary was assessed by the effective sample size value (>200) for each parameter after burn-in using Tracer 1.6 (Rambaut, Suchard, Xie, & Drummond, 2014). Therefore, we discarded the first 25% of sampled trees as burn-in and the last 15,000 trees were used to construct a majority consensus tree and estimate the Bayesian posterior probabilities. Both ML and BI analyses found no conflict among well-supported nodes for single and concatenated gene datasets; therefore, the five genes were combined for the following analyses.

2.3 | Divergence-time estimation

For molecular dating and ancestral area reconstruction, unequal taxon sampling could induce bias towards better-represented clades. Therefore, single-threshold general mixed Yule coalescent (GMYC) analyses (Pons et al., 2006) were employed to delineate species boundary using the ‘SPLITS’ package (Ezard, Fujisawa, & Barraclough, 2009) in R 3.4.4 (R Core Development Team, 2014). The prior of an ultrametric tree was generated under an uncorrelated lognormal relaxed molecular clock model using BEAST 2.5.1 (Bouckaert et al., 2014), with the clock rate of COI-1 setting to one. The GMYC results revealed 41 entities for the following analyses.

The divergence times were obtained with two different strategies. We first used calibration schemes on a concatenated dataset, with geological events and palaeoclimatic records as calibration points based on Hou, Sket, et al. (2014): the separation of Arctic marine and freshwater *Gammaracanthus*, which was constrained to 6 ± 2 Ma with a normal distribution corresponding to Plio-Pleistocene climatic cycles; the appearance of a Lake Baikal Acanthogammaridae was set at 28 ± 2 Ma; and the divergence of *Sarothrogammarus* and *Rhipidogammarus* was adjusted to 38 ± 2 Ma because of the retreat of the Tethys from the eastern Pamir.

As an alternative to the three independent calibration points, we also used the substitution rate of 0.0115 substitutions per site per million years as a calibration (Brower, 1994). This rate has been widely used in linking contemporary diversification patterns to historical processes in other amphipod phylogenetic studies (Copilaș-Ciocianu & Petrusek, 2017; Grabowski, Mamos, Bazcela-Spychalska, Rewicz, & Wattier, 2017; Hou, Li, & Li, 2014; Yang, Hou, & Li, 2013). We assumed a relaxed clock log normal for COI-1 and COI-2 dataset.

For both calibration strategies, Bayesian analyses were carried out in BEAST using the CIPRES Science Gateway (Miller, Pfeiffer, & Schwartz, 2010). The Yule tree prior was used for best-fit partitions. Two independent runs of 300 million generations were conducted, sampling every 5,000 generations and discarding the first 25% as burn-in. Then, two tree-subsets were combined using LogCombiner 2.5.1 (Bouckaert et al., 2014). A maximum clade credibility tree with median node ages was calculated in TreeAnnotator 2.5.1 (Bouckaert et al., 2014).

2.4 | Ancestral area and habitat reconstructions

The distributions were assigned to five biogeographic ecoregions: A, south-western China; B, central China; C, south-western Japan; D, north-eastern Japan; and E, Hokkaido, East Russia and the North China coast area. We distinguished regions C and D based on the Fossa Magna of central Japan (Li, Fu, & Lei, 2011).

The ancestral distribution of Anisogammaridae was inferred using the DEC and DEC + J models in the R package BioGeoBEARS (Matzke, 2014), allowing dispersal between all regions at any time. The AIC criterion was used to compare models and determine the best-fitting model. In comparison, we also applied statistical dispersal–vicariance analysis (S-DIVE) implemented in RASP 3.1 (Yu, Harris, Blair, & He, 2015).

To reconstruct the ancestral habitat, a ML approach with two-parameter Markov k-state model was used to map habitat onto the Anisogammaridae chronogram (Figure 2a) using Mesquite 3.51 (Maddision & Maddision, 2018). Freshwater and marine states were coded as binary characters.

3 | RESULTS

3.1 | Data characteristics

A total of 420 sequences were newly generated from three mitochondrial and two nuclear fragments for 106 specimens in this study, and 103 additional sequences for *Jesogammarus hebeiensis*, Anisogammaridae specimens from Japan and outgroup species were downloaded from GenBank. The final alignments contained 107 terminals with 640 bp for COI-1, 90 terminals with 659 bp for COI-2, 126 terminals with 1,016 bp for 16S, 69 terminals with 1,909 bp for 18S and 131 terminals with 1,281 bp for 28S. The protein-coding fragments could be successfully translated into amino acids without stop codons. The concatenated dataset contained 140 terminals with 5,505 bp, including 138 Anisogammaridae ingroups and two outgroup taxa. All new sequences were deposited in GenBank. Detailed information on samples and sequences is presented in Tables S1 and S3.

3.2 | Phylogeny reconstruction

Maximum likelihood and BI analyses produced congruent phylogenetic trees for single genes and the concatenated dataset, and most clades are well supported (bootstrap ≥ 70, Bayesian posterior probability ≥ 0.95). We used the BI tree obtained from the concatenated dataset for our phylogenetic assessment (Figure 1b). The phylogenetic relationships indicate that the family Anisogammaridae is split into marine and freshwater lineages. The marine lineage includes the species belonging to the genera *Eogammarus* and *Spasskogammarus*, which occur in the North Pacific rim region between latitudes 35 and 50°N. The freshwater lineage is further separated into lotic and lentic clades, reflecting their habitat separation. The lotic clade is composed of species of the genus *Jesogammarus*, which mainly live in mountain streams and rivers. The lentic clade contains species of the genus *Annanogammarus* and the genera *Fuxigammarus* and *Eurypodogammarus*, which occupy spring and lake environments. The freshwater species are distributed in continental East Asia at latitudes 24–40°N.

Our results suggest that taxonomic revisions are needed. The genus *Annanogammarus* is paraphyletic, because the genera *Fuxigammarus* and *Eurypodogammarus* are nested in it.

3.3 | Divergence times

The BEAST analyses based on 41 GMYC entities yielded a similar topology to the BI tree, except for the marine lineage being paraphyletic (Figure 2a). The timetree derived from three calibration points revealed that the common ancestor of the family Anisogammaridae is estimated to have existed during the Eocene, around 48 Ma (95% HPD: 63.5–34.7 Ma). The split between the marine lineage of *Eogammarus* and the freshwater lineage is predicted to have occurred at around 38 Ma (95% HPD: 49.6–28.0 Ma); subsequent, the freshwater lineage started to diversify at 27 Ma (95% HPD: 35.0–19.7 Ma), during the

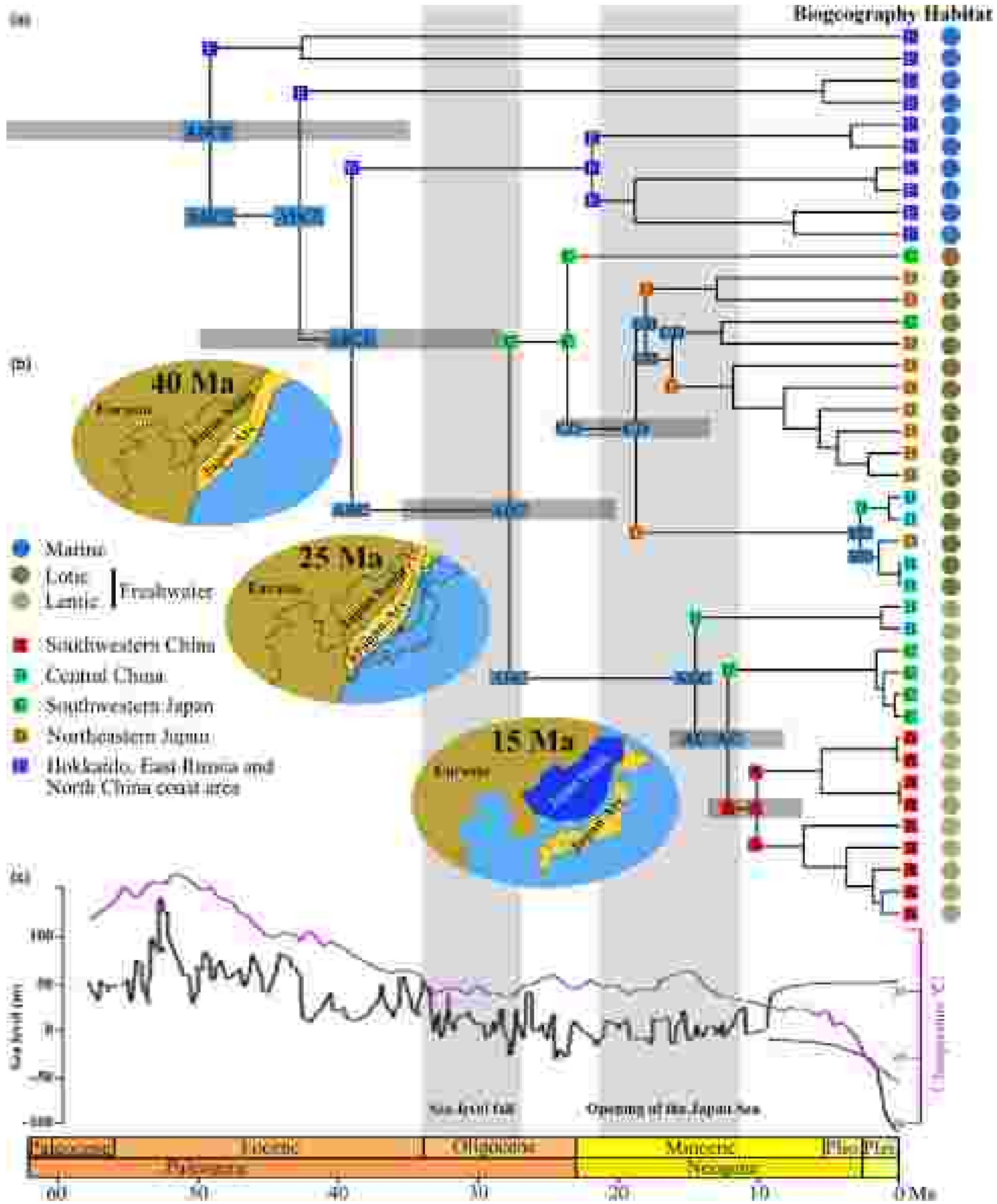

FIGURE 2 Biogeographical scenario for the diversification of the Anisogammaridae. (a) Phylogenetic timetree inferred from a geological calibration scheme with BEAST analysis based on 41 general mixed Yule coalescent entities. The bars on nodes indicate the 95% highest posterior density (HPD) interval of the divergence times of major clades. The ancestral range reconstructions from the DEC model in BioGeoBEARS are indicated at the internal nodes. The grey vertical shadings indicate the Eocene–Oligocene sea-level fall (34–27 Ma), and the opening of the Japan Sea (21–11 Ma). (b) Palaeogeographic reconstruction of the Japan Sea after Isozaki et al. (2010): the Japan basin was connected to the East Asian continent at 40 Ma; the Japan Sea started to open at 25 Ma; and the Japan Sea was fully open at 15 Ma. (c) Sea-level fluctuations (black line) modified from Miller et al. (2005), and surface temperature changes (purple line) modified from Hansen et al. (2013)

middle Oligocene. The successive freshwater diversification separated the lotic and lentic clades at 23 Ma (95% HPD: 29.9–16.5 Ma) and 14 Ma (95% HPD: 19.1–9.8 Ma), respectively. The lotic clade gradually diversified into species of the genus *Jesogammarus*, followed by vicariance between species from Japan and China at 18 Ma (95% HPD: 23.9–13.2 Ma). The lentic clade successively speciated forming three clusters: species of *Annanogammarus* from China; species of *Annanogammarus* from Japan; and local species of the genera *Fuxigammarus* and *Eurypodogammarus* that emerged around 10 Ma (95% HPD: 13.5–6.8 Ma), during the Miocene.

The alternative chronogram constructed with a substitution rate of 0.0115 yielded age estimates compatible with the time estimation inferred from geological calibrations, with all of the median nodal ages within the confidence intervals (Figures S1 and S2).

3.4 | Biogeographic and habitat reconstruction

The DEC + J model (InL = −30.76) significantly increased the likelihood of the DEC model (InL = −36.08). However, the biogeographic inference of the DEC + J model has a tendency towards a single area, with more jump dispersals. The results of S-DIVA and DEC models produced similar scenarios for major clades, indicating widespread across two or more areas for ancestral ranges (Table S4). Therefore, the results generated from the DEC model were used to discuss the biogeographic history (Figure 2a).

The family Anisogammaridae originated in the North Pacific coastal region at 48 Ma and occupied continental East Asia at 27 Ma. The lotic and lentic freshwater clades differentiated between the Chinese mainland and Japan, with the opening of the Japan Sea. The lentic clade further expanded from central China to south-western China at 10 Ma. Overall, the family Anisogammaridae experienced a habitat shift from marine to freshwater, and had a broader range from latitude 24 to 50°N as a result of a north-to-south dispersal.

4 | DISCUSSION

4.1 | Habitat shift from marine to freshwater at the Eocene–Oligocene transition

Our study is the first to use a molecular dataset to illustrate the evolutionary history of the family Anisogammaridae in the Far East. Phylogenetic inferences, molecular dating and biogeographic reconstruction of Anisogammaridae support the single marine–freshwater shift hypothesis (H2; Figure 1a). The origin of the family Anisogammaridae can be traced back to the Eocene (48 Ma), from ancestors living in marine habitats along the North Pacific rim across latitudes 35–50°N and covering approximately the coasts of Japan, Far East Russia and North China (Figures 2a and 3).

Around 38 Ma, Anisogammaridae apparently underwent an important split between marine and freshwater lineages and began to diversify in freshwater habitats at 27 Ma (Figure

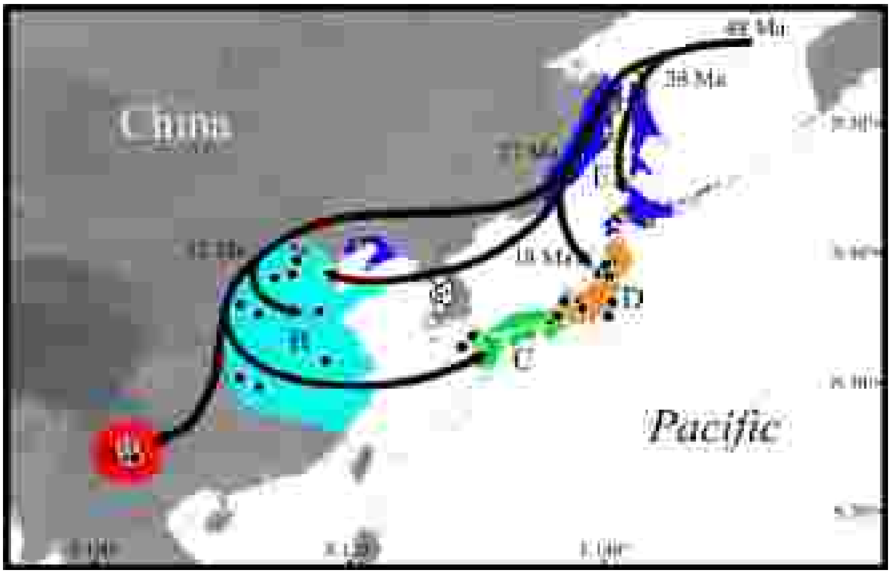

FIGURE 3 Map of the Far East region showing sampling sites and dispersal routes. Green triangles represent marine samples, and circles represent freshwater samples (black circles for our collections, white for recorded sites in South Korea). The biogeographic areas include A for south-western China, B for central China, C for south-western Japan, D for north-eastern Japan, E for Hokkaido, East Russia and North China coast area. The Anisogammaridae originated in marine habitat from North Pacific region, followed by split between marine and freshwater at 38 Ma. Freshwater Anisogammaridae diversified at 27 Ma and dispersed southward with the opening of Japan Sea within the interval 21–11 Ma

2a). This marine–freshwater segregation corresponds well with the Eocene–Oligocene sea-level fall. At the Eocene–Oligocene transition, the sea level dropped by 55 m (Miller et al., 2005), and new freshwater ecosystems formed on the newly exposed landmass (Figure 2c). A marine ancestor of Anisogammaridae colonized freshwater habitats of the Far East. Then, freshwater Anisogammaridae radiated southward across latitudes 24–40°N, extending far more southerly than marine forms (Figure 3).

The species of the family Anisogammaridae are widely distributed in both sides of the North Pacific. The inclusion of taxa from North America will give us a global picture of the habitat shift.

4.2 | Lotic–lentic separation and vicariance between Japan and the East Asian mainland during the early Miocene

After the successful colonization of freshwater habitats, Anisogammaridae diversified into two clades occupying lotic and lentic niches around 23 and 14 Ma, respectively (Figures 2b and 3). The lotic clade includes species of the genus *Jesogammarus*, which inhabit mountain streams and rivers and are widely distributed across Japan and central China (Tomikawa et al., 2017). The lentic clade comprises the genera *Annanogammarus*, *Fuxigammarus* and *Eurypodogammarus*, which are found in ponds, springs and lakes across south-western Japan, South Korea and central China (Lee & Seo, 1990). Lotic and lentic environments differ in water velocity, productivity, thermal regime and depth. These variables can interact with body size and life history to shape the spatial ecology of freshwater animals.

The lotic clade of the genus *Jesogammarus* diverged into the current Japan and central China subclades at 18 Ma. The lentic clade of *Annanogammarus* split between central China and south-western Japan at 14 Ma. These vicariant events can be explained by the progressive opening of the Japan Sea at 21–11 Ma (Figure 2b). The Sea of Japan opened with a "double door" movement, the islands in north-eastern Japan rotated counterclockwise by 47° and the islands in south-western Japan rotated 56° clockwise (Isozaki et al., 2010; Otofuji, Matsuda, & Nohda, 1985). Similar diversification patterns have been documented in other groups, such as *Hynobius* salamanders (Li et al., 2011) and spiders (Ballarin & Li, 2018).

4.3 | Recent diversification in south-western China

The common ancestor of the lentic genera *Fuxigammarus* and *Eurypodogammarus* originated in south-western China at 10 Ma and was restricted to Yangzonghai Lake, Dianchi Lake and Fuxian Lake. The genus *Fuxigammarus* is restricted to Fuxian Lake, which was collected under gravel and aquatic plants at a depth of 0.5 m (Sket & Fišer, 2009). The genus *Eurypodogammarus* occurs from the littoral zone to 80–150 m depth in Fuxian Lake, and the lakesides of Dianchi Lake and Yangzonghai Lake. This diversification may have been driven by the formation of these ancient lakes in south-western China. Fuxian Lake is believed to have formed during the Pliocene, at roughly 3 Ma, and gradually became deeper. The modern distribution of Anisogammaridae in south-western China is thought to be the result of intralacustrine radiation at different depths (Sket & Fišer, 2009).

5 | CONCLUSIONS

The current study revealed a direct correlation between Eocene–Oligocene sea-level fall and the evolution of the family Anisogammaridae in the Far East region. The sea-level fall drove a habitat shift from marine to freshwater, followed by diversification from north to south in continental East Asia. Further parallel studies comparing other organisms possessing similar habitat preferences and geographical distributions to Anisogammaridae could shed light on the impact of Eocene–Oligocene sea-level fall on the diversification of the Far East aquatic fauna.

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REFERENCES

Ballarin, F., & Li, S. (2018). Diversification in tropics and subtropics following the mid-Miocene climate change: A case study of the spider genus *Nesticella*. *Global Change Biology*, *24*, e577–e591. https://doi.org/10.1111/gcb.13958

Betancur-R, R., Orti, G., Stein, A. M., Marceniuk, A. P., & Pyron, R. A. (2012). Apparent signal of competition limiting diversification after ecological transitions from marine to freshwater habitats. *Ecology Letters*, *15*, 822–830. https://doi.org/10.1111/j.1461-0248.2012.01802.x

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C. H., Xie, D., … Drummond, A. J. (2014). BEAST 2: A software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, *10*, e1003537. https://doi.org/10.1371/journal.pcbi.1003537

Bousfield, E. L. (2001). The amphipod genus *Anisogammarus* (Gammaroidea: Anisogammaridae) on the Pacific coast of North America. *Amphipacifica*, *3*, 29–47.

Brower, A. V. Z. (1994). Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. *Proceedings of the National Academy of Sciences of the United States of America*, *91*, 6491–6495. https://doi.org/10.1073/pnas.91.14.6491

Copilas-Ciocianu, D., & Petrusek, A. (2017). Phylogeography of a freshwater crustacean species complex reflects a long-gone archipelago. *Journal of Biogeography*, *44*, 421–432. https://doi.org/10.1111/jbi.12853

Coxall, H. K., & Pearson, P. N. (2007). The Eocene-Oligocene Transition. In M. Williams, A. M. Haywood, F. J. Gregory, & D. N. Schmidt (Eds.), *Deep-time perspectives on climate change: Marrying the signal from computer models and biological proxies* (pp. 351–387). London, UK: The Micropalaeontological Society Special Publications 2.

Ezard, T., Fujisawa, T., & Barraclough, T. G. (2009). *Splits: SPecies' limits by threshold statistics. R package version.0-11/r29*. Retrieved from http://R-Forge.R-project.org/projects/splits/

Grabowski, M., Mamos, T., Bazcela-Spychalska, K., Rewicz, T., & Wattier, R. A. (2017). Neogene paleogeography provides context for understanding the origin and spatial distribution of cryptic diversity in a widespread Balkan freshwater amphipod. *PeerJ*, *5*, e3016. https://doi.org/10.7717/peerj.3016

Hansen, J., Sato, M., Russell, G., & Kharecha, P. (2013). Climate sensitivity, sea level and atmospheric carbon dioxide. *Philosophical Transactions of the Royal Society A*, *371*, 20120294. https://doi.org/10.1098/rsta.2012.0294

Hou, Z., Li, J., & Li, S. (2014). Diversification of low dispersal crustaceans through mountain uplift: A case study of *Gammarus* (Amphipoda: Gammaridae) with descriptions of four novel species. *Zoological Journal of the Linnean Society*, *170*, 591–633. https://doi.org/10.1111/zoj.12119

Hou, Z., & Li, S. (2018). Tethyan changes shaped aquatic diversification. *Biological Reviews*, *93*, 874–896. https://doi.org/10.1111/brv.12376

Hou, Z., Morino, H., & Li, S. (2005). A new genus and species of freshwater Anisogammaridae (Crustacea, Amphipoda) from Yunnan, China. *Acta Zootaxonomica Sinica*, *30*, 737–747.

Hou, Z., Sket, B., Fišer, C., & Li, S. (2011). Eocene habitat shift from saline to freshwater promoted Tethyan amphipod diversification. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 14533–14538. https://doi.org/10.1073/pnas.1104636108

Hou, Z., Sket, B., & Li, S. (2014). Phylogenetic analyses of Gammaridae crustacean reveal different diversification patterns among sister lineages in the Tethyan region. *Cladistics*, *30*, 352–365. https://doi.org/10.1111/cla.12055

Isozaki, Y., Aoki, K., Nakama, T., & Yanai, S. (2010). New insight into a subduction-related orogen: A reappraisal of the geotectonic framework and evolution of the Japanese Islands. *Gondwana Research*, *18*, 82–105. https://doi.org/10.1016/j.gr.2010.02.015

Kumar, S., Stecher, G., & Tamura, K. (2016). MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, *33*, 1870–1874. https://doi.org/10.1093/molbev/msw054

Lanfear, R., Calcott, B., Ho, S. Y. W., & Guindon, S. (2012). PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, *29*, 1695–1701. https://doi.org/10.1093/molbev/mss020

Lee, K. S., & Seo, I. S. (1990). One new species of freshwater *Jesogammarus* (Crustacea, Amphipoda, Anisogammaridae) from South Korea. *The Korean Journal of Systematic Zoology*, *6*, 251–260.

Li, J., Fu, C., & Lei, G. (2011). Biogeographical consequences of Cenozoic tectonic events within East Asian margins: A case study of *Hynobius* biogeography. *PLoS ONE*, *6*, e21506. https://doi.org/10.1371/journal.pone.0021506

Maddison, W. P., & Maddison, D. R. (2018). *Mesquite: A modular system for evolutionary analysis. Version, 3.51*. Retrieved from http://www.mesquiteproject.org

Matzke, N. J. (2014). Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology*, *63*, 951–970. https://doi.org/10.1093/sysbio/syu056

Miller, K. G., Kominz, M. A., Browning, J. V., Wright, J. D., Mountain, G. S., Katz, M. E., … Pekar, S. F. (2005). The Phanerozoic record of global sea-level change. *Science*, *310*, 1293–1298. https://doi.org/10.1126/science.1116412

Miller, M. A., Pfeiffer, W., & Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, LA, 411–418. https://doi.org/10.1109/GCE.2010.5676129

Morino, H. (1994). The phylogeny of *Jesogammarus* species (Amphipoda: Anisogammaridae) and life history features of two species endemic to Lake Biwa, Japan. *Archiv fur Hydrobiologie Beiheft Ergebnisse der Limnolgie*, *44*, 257–266.

Otofuji, Y. I., Matsuda, T., & Nohda, S. (1985). Opening mode of the Japan Sea inferred from the palaeomagnetism of the Japan Arc. *Nature*, *317*, 603–604. https://doi.org/10.1038/317603a0

Pons, J., Barraclough, T. G., Gomez-Zurita, J., Cardoso, A., Duran, D. P., Hazell, S., … Vogler, A. P. (2006). Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology*, *55*, 595–609. https://doi.org/10.1080/10635150600852011

Rambaut, A., Suchard, M. A., Xie, D., & Drummond, A. J. (2014). *Tracer 1.6*. Retrieved from http://beast.bio.ed.ac.uk/tracer

R Core Development Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org

Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D. L., Darling, A., Höhna, S., … Huelsenbeck, J. P. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, *61*, 539–542. https://doi.org/10.1093/sysbio/sys029

Sket, B., & Fišer, C. (2009). A new case of intralacustrine radiation in Amphipoda. A new genus and three new species of Anisogammaridae (Crustacea, Amphipoda) from the ancient lake Fuxian Hu in Yunnan, China. *Journal of Zoological Systematics and Evolutionary Research*, *47*, 115–123. https://doi.org/10.1111/j.1439-0469.2008.00477.x

Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, *30*, 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Tomikawa, K., Morino, H., Toft, J., & Mawatari, S. F. (2006). A revision of *Eogammarus* Birstein, (Crustacea, Amphipoda, Anisogammaridae), with a description of a new species. *Journal of Natural History*, *40*, 1083–1148. https://doi.org/10.1080/00222930600828859

Tomikawa, K., Nakano, T., & Hanzawa, N. (2017). Two new species of *Jesogammarus* from Japan (Crustacea, Amphipoda, Anisogammaridae), with comments on the validity of the subgenera *Jesogammarus* and *Annanogammarus*. *Zoosystematics and Evolution*, *93*, 189–210. https://doi.org/10.3897/zse.93.12125

Vaidya, G., Lohman, D. J., & Meier, R. (2011). SequenceMatrix: Concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics*, *27*, 171–180. https://doi.org/10.1111/j.1096-0031.2010.00329.x

Yang, L., Hou, Z., & Li, S. (2013). Marine incursion into East Asia: A forgotten driving force of biodiversity. *Proceedings of the Royal Society of London B: Biological Sciences*, *280*, 20122892. https://doi.org/10.1098/rspb.2012.2892

Yu, Y., Harris, A. J., Blair, C., & He, X. J. (2015). RASP (Reconstruct Ancestral State in Phylogenies): A tool for historical biogeography. *Molecular Phylogenetics and Evolution*, *87*, 46–49. https://doi.org/10.1016/j.ympev.2015.03.008

Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, *292*, 686–693. https://doi.org/10.1126/science.1059412

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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