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Historical biogeography of the short-faced scorpionflies (Insecta: Mecoptera: Panorpodidae)

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ABSTRACT

Aim Panorpodidae is a species-poor family of Mecoptera, containing only 13 species in its two genera, *Panorpodes* and *Brachypanorpa*. They are found disjunctly in eastern Asia and North America, and this distribution has been deeply affected by the region's complex geological and climatic history. We calculate a time-calibrated molecular phylogeny and use it to reconstruct the historical biogeography of the Panorpodidae, in order to explore the family's phylogenetic origin and the biogeographical process that resulted in the present disjunct distribution.

Location Eastern Asia and North America.

Methods Sequence data from mitochondrial (*COI* and *COII*) and nuclear DNA (*28S* and *EF-1α*) were assembled from eight ingroup species. A phylogeny was reconstructed using maximum-likelihood analysis and Bayesian inference, and divergence times were estimated using fossil-calibrated Bayesian analysis. Ancestral areas were reconstructed with RASP 3.02, implementing dispersal–vicariance analysis, dispersal–extinction–cladogenesis and Bayesian binary MCMC.

Results The initial diversification of Panorpodidae occurred during the Ypresian (*c.* 53.9 Ma). A wide ancestral distribution in eastern Asia and western North America was inferred from the biogeographical analyses. The original range of *Panorpodes* across eastern Asia and western North America was fragmented by intercontinental vicariance. The genus *Brachypanorpa* was initially restricted to western North America and subsequently dispersed into eastern regions of North America.

Main conclusions Two alternative biogeographical patterns were recovered. Either Panorpodidae was restricted to western North America in the Eocene and subsequently dispersed into eastern Asia or – more reasonably – it was widely distributed in western North America, eastern Asia and Europe during the Eocene. Our biogeographical reconstructions corroborate the significant role of vicariance in shaping the current eastern Asian and North American disjunction in *Panorpodes*. The geographical separation of western and eastern North American *Brachypanorpa* species is likely to have resulted from the uplift of the Rocky Mountains and the emergence of grassland biomes in central North America.

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INTRODUCTION

The short-faced scorpionflies make up a small family – Panorpodidae – of holometabolous insects in the order Mecoptera, consisting of only 13 described species, and exhibiting a disjunct Holarctic distribution (Zhong *et al.*, 2011). The 13 extant species are classified into two genera: *Panorpodes* MacLachlan, 1875 (five species) and *Brachypanorpa* Carpenter, 1931 (eight species). *Brachypanorpa* is a North American endemic, restricted to the wet, coastal regions of the Pacific Northwest and the southern Appalachian Mountains (Byers, 1976, 1990). *Panorpodes* is almost exclusively distributed in eastern Asia, including Japan, Korea and China; *Panorpodes colei* Byers, 2005 from western North America is the only exception (Byers, 2005; Tan & Hua, 2008; Zhong *et al.*, 2011). The various species of Panorpodidae usually live in moist, densely shaded forests with herbaceous ground cover (Byers, 1997; Zhong *et al.*, 2011).

Very few biogeographical studies of Panorpodidae have been published to date. Byers (1988) claimed that Panorpodidae migrated from the Palaearctic to the Nearctic over the Bering land bridge during the early Cenozoic. Pollmann *et al.* (2008) presented the first molecular systematic study of Panorpodidae and assumed that the Bering land bridge was associated with the present East Asian–North American disjunction. Fossil records of *Panorpodes* have been discovered in Baltic amber, implying that Panorpodidae occurred in Europe during the Priabonian (Carpenter, 1954; Weitschat & Wichard, 2010; Soszyńska-Maj & Krzemiński, 2013, 2015). Fossil evidence, thus, provides insights into the historical processes underlying the biogeography of Panorpodidae, but little is known about the origin, divergence and evolutionary history of the panorpodid fauna in the Holarctic region.

A disjunction between Eurasia and North America has been repeatedly demonstrated in plants (Graham, 1972; Manchester, 1999; Tiffney, 2000) and land mammals (Woodburne & Swisher, 1995; Beard & Dawson, 1999; Hooker, 2000; Bowen *et al.*, 2002), and studies have been conducted on numerous disjunctly distributed Holarctic insects, including scorpionflies (Archibald, 2005, 2009; Archibald *et al.*, 2005), lacewings (Archibald & Makarkin, 2006; Makarkin & Archibald, 2013), ants (Archibald *et al.*, 2006, 2011), damselflies (Petrulevičius *et al.*, 2007) and aphids (Ren *et al.*, 2013). The disjunct distribution in Panorpodidae was greatly affected by dispersal or vicariance events between Eurasia and North America and is likely to have been related to the North Atlantic or Bering land bridges (Sanmartín *et al.*, 2001; Tiffney & Manchester, 2001). Molecular phylogenetic methods, including divergence-time estimation and ancestral-area reconstruction, can test whether the present disjunction in Panorpodidae arose through dispersal or vicariance.

In this study, we aim to reconstruct the phylogenetic relationships between four species of *Brachypanorpa* and four species of *Panorpodes* using four molecular markers. Based on the resulting phylogenetic tree and fossil calibration, we will obtain a chronogram of Panorpodidae and use ancestral-area reconstruction techniques to resolve the family's phylogenetic origins and explore the biogeographical process that led to its present disjunction in the Holarctic region.

MATERIALS AND METHODS

Taxon sampling and genetic data

Eight panorpodid species were sampled: five species from North America [*Brachypanorpa carolinensis* (Banks, 1905); *Brachypanorpa jeffersoni* Byers, 1976; *Brachypanorpa oregonensis* (MacLachlan, 1881); *Brachypanorpa sacajawea* Byers, 1990; and *Panorpodes colei* Byers, 2005], two species from Japan (*Panorpodes paradoxus* MacLachlan, 1875; and *Panorpodes pulcher* Issiki, 1927), and one species from China (*Panorpodes kuandianensis* Zhong *et al.*, 2011) (Fig. 1). Four species of Panorpidae, the sister family of Panorpodidae (Willmann, 1987), were chosen as outgroups: *Panorpa acuta* Carpenter, 1931; *Panorpa fulvastra* Chou, 1981; *Panorpa nebulosa* Westwood, 1846; and *Panorpa obtusa* Cheng, 1949.

Most of the DNA sequence data were obtained from Pollmann *et al.* (2008). Two mitochondrial gene fragments, cytochrome *c* oxidase subunits I and II (*COI* and *COII*), and two nuclear gene fragments, 28S ribosomal RNA (*28S*) and elongation factor-1 alpha (*EF-1α*), were used. We generated DNA sequences from *Panorpodes kuandianensis*, *Panorpa fulvastra* and *Panorpa obtusa* using primers from Whiting (2002) and Pollmann *et al.* (2008) and deposited the resulting sequence data in GenBank (see Appendix S1). In total, DNA sequences of 12 species were used in this study. (See Appendix S1 in Supporting Information for details of the species investigated.)

DNA sequences were checked, assembled and edited with SeqMan (Swindell & Plasterer, 1997). Multiple sequence alignment was performed with muscle (Edgar, 2004) using the default parameters. The best partition schemes and models were estimated for the whole data matrix with PartitionFinder 1.1.1 (Lanfear *et al.*, 2012) and were first codon position of *COI* and *COII*, TrN+I; second codon position of *COI* and *COII*, TrN+I; third codon position of *COI* and *COII*, HKY+Γ+I; first and second codon positions of *EF-1α*, JC; third codon position of *EF-1α*, K81uf; *28S*, GTR+Γ.

Phylogenetic analyses and dating

Phylogenetic analyses using partitioned maximum likelihood (ML) were run in RAxML-VI-HPC (Stamatakis, 2006) using the graphical interface raxmlGUI 1.3 (Silvestro & Michalak, 2012). Ten runs were started from random seeds, and bootstrap values were evaluated across 1000 replicates under the GTR+Γ model.

Partitioned Bayesian inference (BI) was performed in beast 1.8.0 (Drummond *et al.*, 2012) and used to infer phylogenetic relationships and estimate divergence times. Fossil
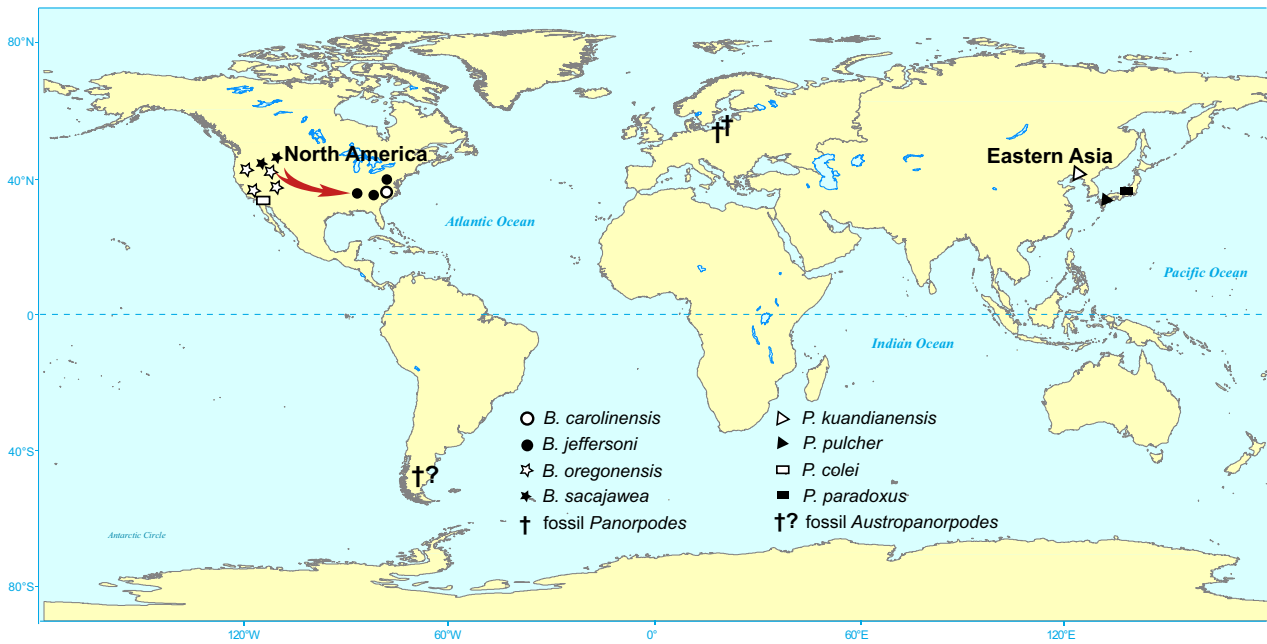
Figure 1 Geographical distribution of the examined *Brachypanorpa* and *Panorpodes* species and fossil panorpodids. '†?' indicates the uncertain fossil record of *Austropanorpodes*. The red arrow represents the dispersal event of *Brachypanorpa* species.

data were used to time calibrate the phylogenetic tree. The node age of *Panorpodes* was constrained to a normal distribution of 35.9 Ma ± 1.2 Myr, based on panorpodid fossils from Baltic amber of Priabonian age (Perkovsky *et al.*, 2007; Soszyńska-Maj & Krzemiński, 2013, 2015). The age of the family is less clear. Ding *et al.* (2014) reported a putative earliest fossil record of Panorpidae from the Middle Jurassic of China, but we consider this record to be doubtful, because of the scant evidence that the fossils belong to the Panorpidae and because the character states cited in support of the family determination may be convergent. These fossils may represent a stem group that pre-dates the divergence of Panorpidae and Panorpodidae or an independent branch that diverged from an orthophlebiid grade of scorpionflies. The earliest fossils that can be confidently assigned to the family Panorpidae are, therefore, Ypresian specimens from the Okanagan Highland deposits in far-western North America (Archibald *et al.*, 2013). The time to the most recent common ancestor (TMRCA) of *Panorpa* was thus defined as Ypresian (52.90 Ma ± 0.83 Myr) based on specimens from McAbee, Canada (Archibald *et al.*, 2010).

We analysed the data under an uncorrelated log-normal relaxed clock and assuming a Yule speciation process. Four runs were conducted with randomly generated starting trees and a chain length of 800 million generations, sampling every 1000 generations. The stationarity and convergence of chains were checked with TRACER 1.5 (Rambaut & Drummond, 2009), ensuring that effective sample sizes were greater than 200 for all parameters. The first 50% of generations were discarded as burn-in, and the remaining trees were used to generate a maximum-clade-credibility tree with

TREEANNOTATOR 1.8.0 (Drummond *et al.*, 2012); the results were visualized in FIGTREE 1.3.1 (available at http://tree.bio.ed.ac.uk/software/figtree/).

Ancestral-area reconstruction

The samples were categorized into four areas (A, western North America; B, eastern North America; C, Japan; D, China), based on geographical distributions obtained from Zhong *et al.* (2011) and the associated database (available at http://researcharchive.calacademy.org/research/entomology/Entomology_Resources/mecoptera/).

On the basis of the phylogenetic and distributional data, the ancestral areas and biogeographical history of the Panorpodidae were inferred with a combination of analytical approaches, all implemented in RASP 3.02 (Yu *et al.*, 2015).

First, we ran the parsimony-based statistical dispersal–vicariance analysis (S-DIVA) (Yu *et al.*, 2010) – a modified form of dispersal–vicariance analysis (Ronquist, 1997) – accounting for the uncertainty in the phylogenetic and biogeographical reconstructions (Nylander *et al.*, 2008; Harris & Xiang, 2009). The maximum number of ancestral areas was restricted to four for each node, and 600,000 post burn-in trees from the BEAST analysis were used.

Second, we executed a maximum-likelihood analysis under the dispersal–extinction–cladogenesis (DEC) model (Ree *et al.*, 2005; Ree & Smith, 2008). Almeida *et al.* (2012) noted that no significant difference was observed between stratified DEC models and an unconstrained model. Movements between the areas were, therefore, unconstrained: all values in the dispersal constraint matrix were set to 1. The total

number of the ancestral ranges of DEC model was constrained to four.

Third, a Bayesian binary MCMC (BBM) method was used for biogeographical inference, using the model F81+Γ, which is considered the most general and complex model in RASP (Sanmartín *et al.*, 2008). The MCMC chains were run for 10 million generations, and sampled every 1000 generations; the first 25% samples were discarded as burn-in. The biogeographical results were summarized on the maximum-clade-credibility tree from the BEAST analysis.

RESULTS

Phylogeny of the Panorpodidae

The data matrix contained a total of 3195 aligned base pairs, 600 of which were parsimony informative. The ML and BI methods generated identical and strongly supported topologies (Fig. 2): the monophyly of the family Panorpodidae was supported, and the family was divided into two distinct clades with high support values (maximum-likelihood bootstrap support, BS, 100%; Bayesian posterior probability, PP, 1.0). One clade consisted of *B. carolinensis*, *B. jeffersoni*, *B. oregonensis* and *B. sacajawea*, suggesting that the genus *Brachypanorpa* is a robust monophyletic group (BS 100%; PP 1.0). The other clade contained species of the genus *Panorpodes*, the monophyly of which is also strongly supported (BS 90%; PP 1.0). The recently described Chinese species *P. kuandianensis* forms the sister group to the Japanese species *P. pulcher* + *P. paradoxus*, and these three species together constitute the sister group to the North American *P. colei*.

Molecular dating

The divergence-time chronogram (Fig. 2) places the origin of Panorpodidae at a mean age of 118.3 Ma (95% highest posterior density interval, HPD, 76.2–165.7 Ma). The estimated divergence time between *Brachypanorpa* and *Panorpodes* was 53.9 Ma (95% HPD, 38.7–71.8 Ma). The species of *Panorpodes* diverged *c.* 36.3 Ma (95% HPD, 33.9–38.7 Ma), and the TMRCA of the *Brachypanorpa* clade was estimated at 29.9 Ma (95% HPD, 18.0–43.2 Ma). (See Table 1 for mean divergence times and 95% HPD intervals for each node.)

Biogeography

The optimal ancestral-area reconstruction under the DEC model (Fig. 3b) was highly congruent (Table 1) with the reconstruction through S-DIVA (Fig. 3a), but strikingly different from the inferred range evolution under BBM (Fig. 3c).

Three possible ancestral ranges for the Panorpodidae were inferred with the same marginal probability using S-DIVA. They were (1) western North America; (2) western North America + Japan and (3) western North America + Japan +

China. The inference from DEC favoured western North America + Japan + China as the most likely ancestral area of the Panorpodidae, whereas western North America was preferred under BBM.

Western North America + Japan + China was inferred as the ancestral range for *Panorpodes* by DEC, although it is only one of three equally likely ancestral scenarios under S-DIVA. In the BBM reconstruction, however, western North America was considered the most likely ancestral area, with *Panorpodes* having subsequently dispersed westwards into eastern Asia. All three biogeographical reconstructions indicated that *Brachypanorpa* was initially restricted to western North America, and later expanded eastwards.

DISCUSSION

The order Mecoptera first appeared in the Early Permian and was remarkably diverse and common until the Cretaceous, although its species diversity and abundance has declined progressively in more recent deposits (Novokshonov, 1997; Grimaldi & Engel, 2005). Mecoptera are now a small relict group consisting of only nine extant families (Penny, 1975; Willmann, 1987). Based on the present molecular dating analysis (Fig. 2), Panorpodidae had a relatively recent origin, with most of its diversification and speciation occurring between the Priabonian and the Tortonian.

Two different biogeographical patterns for Panorpodidae were recovered using ancestral-area reconstruction techniques. In the first, based on the BBM analysis, Panorpodidae was distributed in western North America in the Eocene and subsequently dispersed into eastern Asia. This result contradicts the character evolution of the rostrum from short in *Panorpodes* to virtually absent in *Brachypanorpa* (Byers, 1988). In the second, based on the results of S-DIVA and DEC reconstructions and the fossil record, ancestral *Panorpodes* had a wide distribution in western North America, eastern Asia and Europe during the Eocene. Previous studies on the evolutionary trend of the rostrum concluded that Panorpodidae migrated from the Palaearctic to the Nearctic region (Byers, 1988, 1997; Downes & Kavanaugh, 1988), but the discovery of *Panorpodes colei* in North America and our present analysis imply that the ancestral range of Panorpodidae may have covered both the Palaearctic and the Nearctic.

The fossil record of Panorpodidae is extremely poor, with only one fossil species of *Austropanorpodes* and four fossil species of *Panorpodes* so far discovered (Carpenter, 1954; Petrulevičius, 2009; Soszyńska-Maj & Krzemiński, 2013, 2015). The four reliable fossil species of *Panorpodes* were found in Baltic amber, and the more uncertain *Austropanorpodes gennaken* Petrulevičius, 2009 comes from the Ypresian (52 Ma) of Argentina, indicating that panorpodid species were distributed in Europe and possibly also in South America in the Eocene (Carpenter, 1954; Perkovsky *et al.*, 2007; Petrulevičius, 2009; Weitschat & Wichard, 2010). The fossil evidence implies that the family is likely to have had a much wider global distribution in the Eocene than now, although
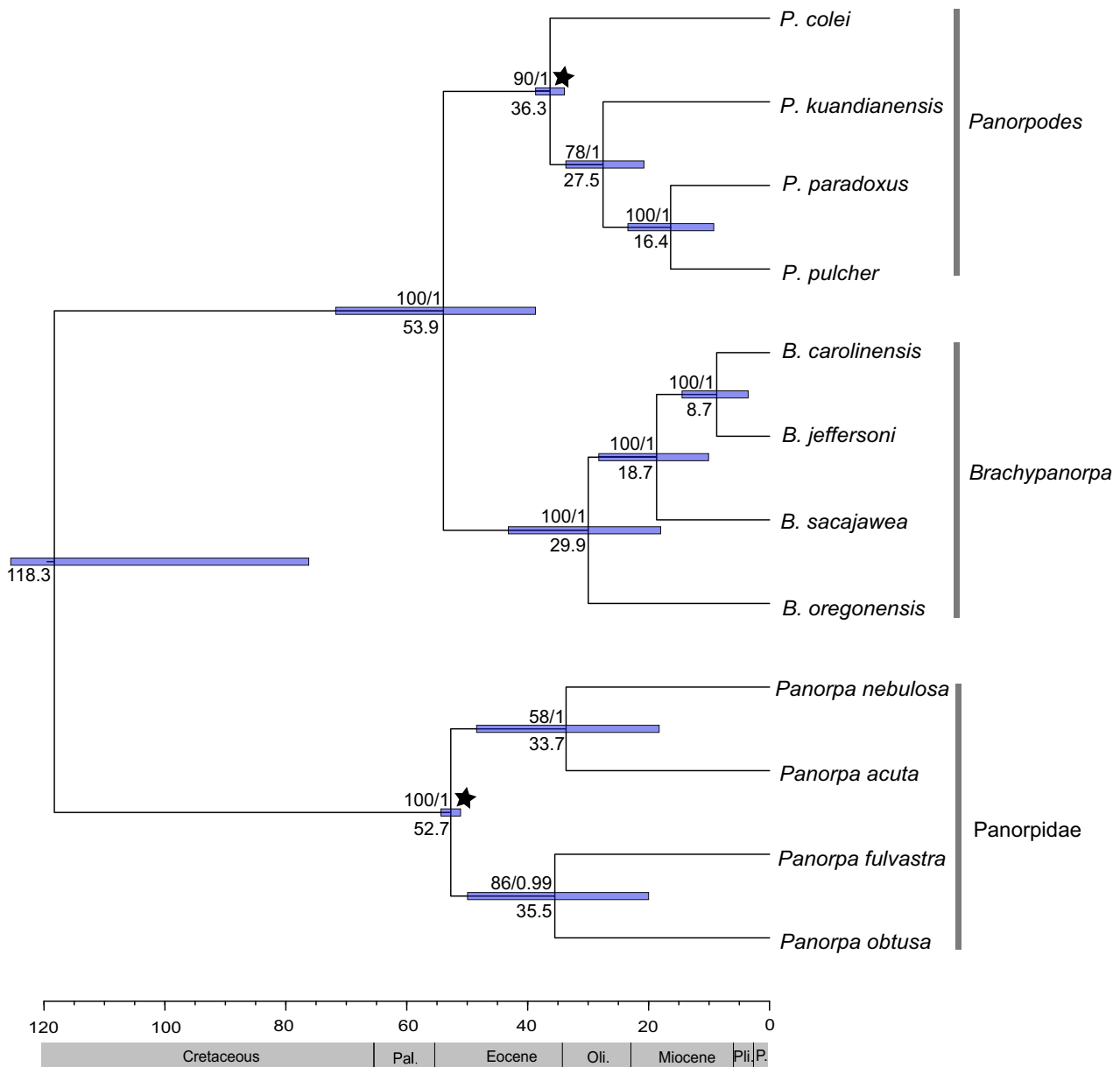
Figure 2 Bayesian maximum-clade-credibility tree based on the concatenated dataset (*COI*, *COII*, *28S* and *EF-1α*) in BEAST 1.8.0 with a relaxed clock and Yule speciation process. Node numbers above blue bars show maximum-likelihood bootstrap support (BS) and Bayesian posterior probabilities (PP); node numbers below blue bars indicate the mean estimated divergence times of Panorpodidae in millions of years ago. Fossil calibration points are indicated with black stars. Horizontal blue bars at nodes represent 95% highest posterior density date ranges. Pal., Palaeocene; Oli., Oligocene; Pli., Pliocene; P., Pleistocene.

the relationships between the extant panorpodids and the fossil species have not been well established.

The distribution of Panorpodidae has been deeply affected by the region's complex geological and climatic history. During the Eocene, Europe was separated from Asia by the epicontinental Turgai Strait, which is often considered to have formed a dispersal barrier to animals, although there was still a direct route westwards from Europe across a forested Arctic into eastern Asia (Tiffney, 1985b; Sanmartín *et al.*, 2001; Archibald *et al.*, 2011; Eberle & Greenwood, 2011). The climate in the Ypresian was warm with high levels of precipitation, and the Arctic was

generally temperate except for brief hyperthermal intervals (Basinger, 1991; Basinger *et al.*, 1994; Sluijs *et al.*, 2006, 2009; Jahren, 2007; Greenwood *et al.*, 2010; Eberle & Greenwood, 2011). The Baltic forests were composed of warm-temperate subtropical oaks and pines (Penney, 2010), and the diversity of aquatic insect fossils in the Baltic amber suggests that there was flowing water (Wichard *et al.*, 2009). The ancient Baltic forests, with warm temperatures and moist air, were covered with abundant trees (including oaks and hickories) and herbaceous understorey plants, providing suitable habitats for panorpodid species (Byers, 1997; Zhong *et al.*, 2011).

Table 1 Estimated divergence times and the ancestral-area reconstructions of *Panorpodes* and *Brachypanorpa* implemented in RASP under statistical dispersal–vicariance analysis (S-DIVA), dispersal–extinction–cladogenesis (DEC) and Bayesian binary MCMC (BBM).

Node	Mean estimated divergence time (95% HPD) (Ma)	S-DIVA		DEC		BBM	
		Areas*	Probability, %	Areas*	Probability, %	Areas*	Probability, %
13	16.4 (9.2–23.4)	C	100.00	C	100.00	C	99.09
14	27.5 (20.8–33.7)	CD	100.00	CD	100.00	D	34.85
						C	27.17
						A	25.05
15	36.3 (33.9–38.7)	ACD	33.33	ACD	100.00	A	94.66
		AC	33.33				
		AD	33.33				
16	8.7 (3.5–14.5)	B	100.00	B	100.00	B	93.67
17	18.7 (10.1–28.2)	AB	100.00	AB	100.00	A	93.60
18	29.9 (18.0–43.2)	A	100.00	A	54.23	A	98.71
				AB	45.77		
19	53.9 (38.7–71.8)	ACD	33.33	ACD	57.94	A	96.99
		AC	33.33	ABCD	18.81		
		A	33.33	AD	14.47		

*Only ancestral areas with a marginal probabilities above 10% are presented. A, western North America; B, eastern North America; C, Japan; D, China.

The demise of the Turgai Strait coincided with global cooling in the Eocene–Oligocene transition period, leading to extensive biogeographical exchange between Europe and Asia (Tiffney & Manchester, 2001). McKenna (1983) demonstrated major faunal turnovers in Europe at the Eocene–Oligocene boundary, during which most of the endemic European fauna became extinct, probably including panorpodids.

Based on our research, *Panorpodes* is likely to have originated during the Ypresian (*c.* 53.9 Ma), at which time the Holarctic region was still held together by the Bering and North Atlantic land bridges (McKenna, 1983). It is, therefore, reasonable to assume that *Panorpodes* existed in eastern Asia and North America as well as Europe in the Eocene. During the warm-temperate and humid early Eocene, boreotropical forests dominated the whole Northern Hemisphere and spread between North America and Eurasia across the two land bridges (Wolfe, 1978; Tiffney, 1985b). The terrestrial connection between Europe and North America ended during the Ypresian (50 Ma) (Tiffney, 1985b), preceding the divergence of *Panorpodes* at 36.3 Ma and so preventing any dispersal of *Panorpodes* across the North Atlantic land bridge. During the Lutetian and Bartonian ages, Beringia was covered with deciduous hardwood forests and evergreen communities, and the Arctic forests consisted mainly of deciduous conifers, allowing extensive intercontinental interchange across Beringia (Sanmartín *et al.*, 2001; LePage, 2003; Jahren, 2007; Greenwood *et al.*, 2010). After the Eocene–Oligocene boundary, however, the climate continued to become cooler and drier until the Pleistocene glaciations (Wolfe, 1978; Tiffney, 1985a). Thereafter, the Beringian region was less suitable as a dispersal route, and the exchange of *Panorpodes* between Eurasia and North America through Beringia was disrupted. Eventually, the Asian *Panorpodes* species became geographically isolated from the North American species.

The eastern Asian *Panorpodes* species are restricted to China, Japan and Korea (Tan & Hua, 2008; Zhong *et al.*, 2011). We estimate that the Japanese *Panorpodes paradoxus* and *P. pulcher* split from the Chinese *P. kuandianensis c.* 27.5 Ma (Fig. 2), preceding the Messinian (6.0 Ma) isolation of the Japanese islands from the rest of East Asia, which suggests that vicariance rather than dispersal led to the isolation of Japanese *Panorpodes*. The close geographical affinities between China, Japan and Korea probably resulted in frequent exchanges of eastern Asian *Panorpodes* species, as occurred in the genus *Panorpa* (Hu *et al.*, 2015).

The genus *Brachypanorpa* is endemic to North America and geographically separated into western and eastern species. Our biogeographical analyses imply that the range of *Brachypanorpa* was initially restricted to western North America and that the genus subsequently spread eastwards. The genus diversified in the Rupelian (*c.* 29.9 Ma), when the early Rocky Mountains were levelled by erosion, the entire North American Cordillera became a peneplain (Sanmartín *et al.*, 2001), and the boreotropical vegetation of the Rocky Mountains region was replaced by a mixture of conifers and broad-leaved deciduous forests (Wing, 1987). This encouraged the extensive eastward migration of *Brachypanorpa* species out of western North America. During the Chattian (Oligocene) and Miocene, orogenic activity in the western Nearctic resulted in the uplift of the Rocky Mountains, which eventually led to the emergence of the extensive grasslands in central North America (Axelrod, 1985; Graham, 1993). These grassland biomes presented a barrier to dispersal and presumably led to the isolation of western and eastern *Brachypanorpa* species. *Brachypanorpa carolinensis* and *B. jeffersoni* are currently restricted to the southern
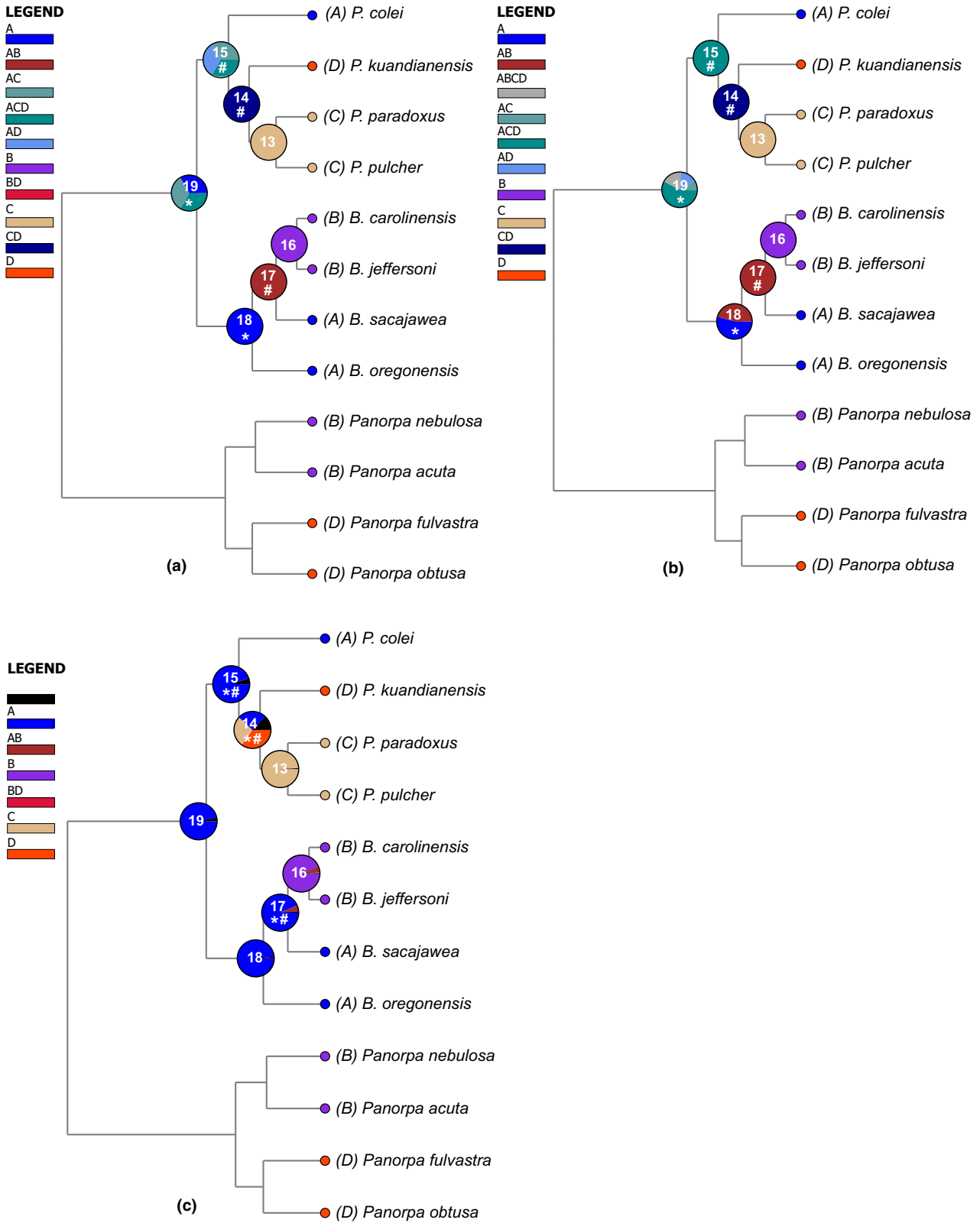
Figure 3 Ancestral-area reconstructions of Panorpodidae using RASP 3.02: (a) parsimony-based statistical dispersal–vicariance analysis (S-DIVA); (b) dispersal–extinction–cladogenesis (DEC) model; (c) Bayesian binary MCMC (BBM) method. A, western North America; B, eastern North America; C, Japan; and D, China; black indicates other ancestral ranges. Pie charts at internal nodes depict the probabilities for respective areas. #, vicariance event; *, dispersal event, "*B.*" stands for *Brachypanorpa*, "*P.*" stands for *Panorpodes*.

Appalachian Mountains (Byers, 1976), which are thought to have acted as a refugium during the Pleistocene glaciations (Grimaldi & Engel, 2005; Pollmann et al., 2008).

CONCLUSIONS

The fossil-calibrated molecular dating with BEAST and ancestral-area reconstructions with RASP provide a detailed description of the processes behind the historical biogeography of the Panorpodidae. The family is very likely to have originated in the Early Cretaceous. Biogeographical analyses and fossil records reveal that the ancestral range of *Panorpodes* is likely to have covered North America, eastern Asia and Europe and that vicariance played a significant role in shaping the current biogeographical disjunction. *Brachypanorpa* initially dispersed into western North America and subsequently spread into eastern regions of North America. The uplift of the Rocky Mountains and the emergence of grassland biomes in central North America may provide a historical explanation for the geographical separation between western and eastern *Brachypanorpa* species.

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REFERENCES

Almeida, E.A.B., Pie, M.R., Brady, S.G. & Danforth, B.N. (2012) Biogeography and diversification of colletid bees (Hymenoptera: Colletidae): emerging patterns from the southern end of the world. *Journal of Biogeography*, **39**, 526–544.

Archibald, S.B. (2005) New Dinopanorpidae (Insecta: Mecoptera) from the Eocene Okanagan Highlands (British Columbia, Canada and Washington State, USA). *Canadian Journal of Earth Sciences*, **42**, 119–136.

Archibald, S.B. (2009) New Cimbrophlebiidae (Insecta: Mecoptera) from the early Eocene at McAbee, British Columbia, Canada and Republic, Washington, USA. *Zootaxa*, **2249**, 51–62.

Archibald, S.B. & Makarkin, V.N. (2006) Tertiary giant lacewings (Neuroptera: Polystoechotidae): revision and description of new taxa from western North America and Denmark. *Journal of Systematic Palaeontology*, **4**, 119–155.

Archibald, S.B., Rasnitsyn, A.P. & Akhmetiev, M.A. (2005) Ecology and distribution of Cenozoic Eomeropidae (Mecoptera), and a new species of *Eomerope* Cockerell from the Early Eocene McAbee locality, British Columbia, Canada. *Annals of the Entomological Society of America*, **98**, 503–514.

Archibald, S.B., Cover, S.P. & Moreau, C.S. (2006) Bulldog ants of the Eocene Okanagan Highlands and history of the subfamily (Hymenoptera: Formicidae: Myrmeciinae). *Annals of the Entomological Society of America*, **99**, 487–523.

Archibald, S.B., Bossert, W.H., Greenwood, D.R. & Farrell, B.D. (2010) Seasonality, the latitudinal gradient of diversity, and Eocene insects. *Paleobiology*, **36**, 374–398.

Archibald, S.B., Johnson, K.R., Mathewes, R.W. & Greenwood, D.R. (2011) Intercontinental dispersal of giant thermophilic ants across the Arctic during early Eocene hyperthermals. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 3679–3686.

Archibald, S.B., Mathewes, R.W. & Greenwood, D.R. (2013) The Eocene apex of panorpoid scorpionfly family diversity. *Journal of Paleontology*, **87**, 677–695.

Axelrod, D.I. (1985) Rise of the grassland biome, central North America. *The Botanical Review*, **51**, 163–201.

Basinger, J. (1991) The fossil forests of the Buchanan Lake Formation (early Tertiary), Axel Heiberg Island, Canadian Arctic archipelago: preliminary floristics and paleoclimate. *Tertiary fossil forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago* (ed. by R.L. Christie and N.J. Macmillan), pp. 39–66. Geological Survey of Canada, Ottawa.

Basinger, J.F., Greenwood, D. & Sweda, T. (1994) Early Tertiary vegetation of Arctic Canada and its relevance to paleoclimatic interpretation. *Cenozoic plants and climates of the Arctic* (ed. by M.C. Boulter and H.C. Fisher), pp. 175–198. Springer, Berlin.

Beard, K.C. & Dawson, M.R. (1999) Intercontinental dispersal of Holarctic land mammals near the Paleocene/Eocene boundary: paleogeographic, paleoclimatic and biostratigraphic implications. *Bulletin de la Société Géologique de France*, **170**, 697–706.

Bowen, G.J., Clyde, W.C., Koch, P.L., Ting, S., Alroy, J., Tsubamoto, T., Wang, Y. & Wang, Y. (2002) Mammalian dispersal at the Paleocene/Eocene boundary. *Science*, **295**, 2062–2065.

Byers, G.W. (1976) A new Appalachian *Brachypanorpa* (Mecoptera: Panorpodidae). *Journal of the Kansas Entomological Society*, **49**, 433–440.

Byers, G.W. (1988) Geographic affinities of the North American Mecoptera. *Memoirs of the Etomological Society of Canada*, **120**(Suppl. S144), 25–30.

Byers, G.W. (1990) *Brachypanorpa sacajawea* n. sp. (Mecoptera: Panorpodidae) from the Rocky Mountains. *Journal of the Kansas Entomological Society*, **63**, 211–217.

Byers, G.W. (1997) Biology of *Brachypanorpa* (Mecoptera: Panorpodidae). *Journal of the Kansas Entomological Society*, **70**, 313–322.

Byers, G.W. (2005) *Panorpodes* discovered in North America (Mecoptera: Panorpodidae). *Journal of the Kansas Entomological Society*, **78**, 71–74.

Carpenter, F.M. (1954) The Baltic amber Mecoptera. *Psyche*, **61**, 31–40.

Ding, H., Shih, C., Bashkuev, A., Zhao, Y. & Ren, D. (2014) The earliest fossil record of Panorpidae (Mecoptera) from the Middle Jurassic of China. *ZooKeys*, **431**, 79–92.

Downes, J.A. & Kavanaugh, D.H. (1988) Origins of the North American insect fauna. *Memoirs of the Entomological Society of Canada*, **120**(Suppl. S144), 1–11.

Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, **29**, 1969–1973.

Eberle, J.J. & Greenwood, D.R. (2011) Life at the top of the greenhouse Eocene world – a review of the Eocene flora and vertebrate fauna from Canada's High Arctic. *Geological Society of America Bulletin*, **124**, 3–23.

Edgar, R.C. (2004) MUSCLE: a multiple sequence alignment method with reduced time and space complexity. *BMC Bioinformatics*, **32**, 1792–1797.

Graham, A. (1972) Outline of the origin and historical recognition of floristic affinities between Asia and eastern North America. *Floristics and paleofloristics of Asia and eastern North America* (ed. by A. Graham), pp. 1–18. Elsevier, Amsterdam.

Graham, A. (1993) History of the vegetation: Cretaceous (Maastrichtian)–Tertiary. *Flora of North America*, **1**, 57–70.

Greenwood, D.R., Basinger, J.F. & Smith, R.Y. (2010) How wet was the Arctic Eocene rain forest? Estimates of precipitation from Paleogene Arctic macrofloras. *Geology*, **38**, 15–18.

Grimaldi, D. & Engel, M.S. (2005) *Evolution of the insects*. Cambridge University Press, Cambridge.

Harris, A.J. & Xiang, Q.-Y. (2009) Estimating ancestral distributions of lineages with uncertain sister groups: a statistical approach to Dispersal-Vicariance Analysis and a case using Aesculus L. (Sapindaceae) including fossils. *Journal of Systematics and Evolution*, **47**, 349–368.

Hooker, J.J. (2000) Paleogene mammals: crises and ecological change. *Biotic responses to global change: the last 145 million years* (ed. by S.J. Culver and P.F. Rawson), pp. 333–349. Cambridge University Press, Cambridge.

Hu, G.-L., Yan, G., Xu, H. & Hua, B.-Z. (2015) Molecular phylogeny of Panorpidae (Insecta: Mecoptera) based on mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution*, **85**, 22–31.

Jahren, A.H. (2007) The Arctic Forest of the middle Eocene. *Annual Review of Earth and Planetary Sciences*, **35**, 509–540.

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.

LePage, B.A. (2003) The evolution, biogeography and palaeoecology of the *Pinaceae* based on fossil and extant representatives. *Acta Horticulturae*, **615**, 29–52.

Makarkin, V.N. & Archibald, S.B. (2013) A diverse new assemblage of green lacewings (Insecta, Neuroptera, Chrysopidae) from the early Eocene Okanagan Highlands, western North America. *Journal of Paleontology*, **87**, 123–146.

Manchester, S.R. (1999) Biogeographical relationships of North American Tertiary floras. *Annals of the Missouri Botanical Garden*, **86**, 472–522.

McKenna, M.C. (1983) Holarctic landmass rearrangement, cosmic events, and Cenozoic terrestrial organisms. *Annals of the Missouri Botanical Garden*, **70**, 459–489.

Novokshonov, V.G. (1997) *Early evolution of scorpionflies (Insecta: Panorpida)*. Nauka Press, Moscow.

Nylander, J.A.A., Olsson, U., Alström, P. & Sanmartín, I. (2008) Accounting for phylogenetic uncertainty in biogeography: a Bayesian approach to dispersal-vicariance analysis of the thrushes (Aves: *Turdus*). *Systematic Biology*, **57**, 257–268.

Penney, D. (2010) *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, UK.

Penny, N.D. (1975) Evolution of the extant Mecoptera. *Journal of the Kansas Entomological Society*, **48**, 331–350.

Perkovsky, E.E., Rasnitsyn, A.P., Vlaskin, A.P. & Taraschuk, M.V. (2007) A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples. *African Invertebrates*, **48**, 229–245.

Petrulevičius, J.F. (2009) A panorpoid (Insecta: Mecoptera) from the Lower Eocene of Patagonia, Argentina. *Journal of Paleontology*, **83**, 994–997.

Petrulevičius, J.F., Nel, A., Rust, J., Bechly, G. & Kohls, D. (2007) New Paleogene Epallagidae (Insecta: Odonata) recorded in North America and Europe. Biogeographic implications. *Alavesia*, **1**, 15–25.

Pollmann, C., Misof, B. & Sauer, K.P. (2008) Molecular phylogeny of panorpodid scorpionflies: an enigmatic, species-poor family of Mecoptera (Insecta). *Organisms Diversity and Evolution*, **8**, 77–83.

Rambaut, A. & Drummond, A.J. (2009) *Tracer version 1.5.0*. University of Edinburgh, Edinburgh, UK. Available at: http://beast.bio.ed.ac.uk/Tracer/.

Ree, R.H. & Smith, S.A. (2008) Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, **57**, 4–14.

Ree, R.H., Moore, B.R., Webb, C.O. & Donoghue, M.J. (2005) A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution*, **59**, 2299–2311.

Ren, Z., Zhong, Y., Kurosu, U., Aoki, S., Ma, E., von Dohlen, C.D. & Wen, J. (2013) Historical biogeography of Eastern Asian-Eastern North American disjunct Melaphidina aphids (Hemiptera: Aphididae: Eriosomatinae) on Rhus hosts (Anacardiaceae). *Molecular Phylogenetics and Evolution*, **69**, 1146–1158.

Ronquist, F. (1997) Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, **46**, 195–203.

Sanmartín, I., Enghoff, H. & Ronquist, F. (2001) Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biological Journal of the Linnean Society*, **73**, 345–390.

Sanmartín, I., Van Der Mark, P. & Ronquist, F. (2008) Inferring dispersal: a Bayesian approach to phylogeny-based island biogeography, with special reference to the Canary Islands. *Journal of Biogeography*, **35**, 428–449.

Silvestro, D. & Michalak, I. (2012) raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity and Evolution*, **12**, 335–337.

Sluijs, A., Schouten, S., Pagani, M., Woltering, M., Brinkhuis, H., Sinninghe Damsté, J.S., Dickens, G.R., Huber, M., Reichart, G.-J., Stein, R., Matthiessen, J., Lourens, L.J., Pedentchouk, N., Backman, J. & Moran, K.; the Expedition 302 scientists (2006) Subtropical Arctic Ocean temperatures during the Palaeocene/Eocene thermal maximum. *Nature*, **441**, 610–613.

Sluijs, A., Schouten, S., Donders, T.H., Schoon, P.L., Röhl, U., Reichart, G.-J., Sangiorgi, F., Kim, J.-H., Sinninghe Damsté, J.S. & Brinkhuis, H. (2009) Warm and wet conditions in the Arctic region during Eocene Thermal Maximum 2. *Nature Geoscience*, **2**, 777–780.

Soszyńska-Maj, A. & Krzemiński, W. (2013) Family Panorpodidae (Insecta, Mecoptera) from Baltic amber (upper Eocene): new species, redescription and palaeogeographic remarks of relict scorpionflies. *Zootaxa*, **3636**, 489–499.

Soszyńska-Maj, A. & Krzemiński, W. (2015) New representative of the family Panorpodidae (Insecta, Mecoptera) from Eocene Baltic amber with a key to fossil species of genus *Panorpodes*. *Palaeontologia Electronica*, **18.2.33A**, 1–7

Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, **22**, 2688–2690.

Swindell, S.R. & Plasterer, T.N. (1997) SEQMAN. Contig assembly. *Methods in Molecular Biology*, **70**, 75–89.

Tan, J.-L. & Hua, B.-Z. (2008) The second species of the Chinese Panorpodidae (Mecoptera). *Panorpodes brachypodus sp. nov. Zootaxa*, **1751**, 59–64.

Tiffney, B.H. (1985a) Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. *Journal of the Arnold Arboretum*, **66**, 73–94.

Tiffney, B.H. (1985b) The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the Northern Hemisphere. *Journal of the Arnold Arboretum*, **66**, 243–273.

Tiffney, B.H. (2000) Geographic and climatic influences on the Cretaceous and Tertiary history of Euramerican floristic similarity. *Acta Universitatis Carolinae Geologica*, **44**, 5–16.

Tiffney, B.H. & Manchester, S.R. (2001) The use of geological and paleontological evidence in evaluating plant phylogeographic hypotheses in the Northern Hemisphere Tertiary. *International Journal of Plant Sciences*, **162**, S3–S17.

Weitschat, W. & Wichard, W. (2010) Baltic amber. *Biodiversity of fossils in amber from the major world deposits* (ed. by D. Penney), pp. 80–115. Siri Scientific Press, Manchester.

Whiting, M.F. (2002) Mecoptera is paraphyletic: multiple genes and phylogeny of Mecoptera and Siphonaptera. *Zoologica Scripta*, **31**, 93–104.

Wichard, W., Gröhn, C. & Seredszus, F. (2009) *Aquatic insects in Baltic amber/Wasserinsekten im baltischen Bernstein*. Kessel, Remagen.

Willmann, R. (1987) The phylogenetic system of the Mecoptera. *Systematic Entomology*, **12**, 519–524.

Wing, S.L. (1987) Eocene and Oligocene floras and vegetation of the Rocky Mountains. *Annals of the Missouri Botanical Garden*, **74**, 748–784.

Wolfe, J.A. (1978) A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere: data from fossil plants make it possible to reconstruct Tertiary climatic changes, which may be correlated with changes in the inclination of the Earth's rotational axis. *American Scientist*, **66**, 694–703.

Woodburne, M.O. & Swisher, C.C., III (1995) Land mammal high-resolution geochronology, intercontinental overland dispersals, sea level, climate, and vicariance. *Geochronology, time scales, and global stratigraphic correlations* (ed. by W.A. Berggren, D.V. Kent, M.-P. Aubry and J. Hardenbol), pp. 335–364. Society for Sedimentary Geology, Tulsa, OK.

Yu, Y., Harris, A.J. & He, X. (2010) S-DIVA (Statistical Dispersal-Vicariance Analysis): a tool for inferring biogeographic histories. *Molecular Phylogenetics and Evolution*, **56**, 848–850.

Yu, Y., Harris, A.J., Blair, C. & He, X. (2015) RASP (Reconstruct Ancestral State in Phylogenies): a tool for historical biogeography. *Molecular Phylogenetics and Evolution*, **87**, 46–49.

Zhong, W., Zhang, J.-X. & Hua, B.-Z. (2011) *Panorpodes kuandianensis*, a new species of short-faced scorpionflies (Mecoptera, Panorpodidae) from Liaoning, China. *Zootaxa*, **2921**, 47–55.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Details of the species investigated and GenBank accession numbers.

BIOSKETCHES

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