which they are adapted [12,23,64]. Eocene Arctic fossil floras indicate that temperate (i.e. upper microthermal to lower mesothermal) conditions predominated across intercontinental connections, with early to middle Eocene floras from Greenland and Axel Heiberg Island (50–40 Myr ago) giving MAT estimates of 12–16°C, probably too cool to support dispersal of Formiciinae throughout much of the time when this must have occurred [12–16]. Brief, cyclic warming events of approximately 2–4°C possibly driven by ventilation of oceanic carbonates were unlikely to have been of sufficient intensity to facilitate formiciine dispersal [65]. However, during larger global hyperthermal events linked to injection of greenhouse gasses into the atmosphere from sedimentary reservoirs, Arctic MAT increased by 5–10°C to perhaps approximately 23°C, with the coldest month mean temperature greater than 8°C at approximately 85° N palaeolatitude [18], which would have been suitable for formiciine dispersal across high latitudes. These include the brief (approx. 170 kyr) Palaeocene–Eocene Thermal Maximum at the Palaeocene–Eocene boundary (about 55.5 Ma); the Eocene Thermal Maximum 2 (about 53.5 Ma); and the longer Early Eocene Climatic Optimum, about 2 Myr of the latest early Eocene [14,17,18]. That is, the early Eocene physical bridge between Europe and North America that was normally climatically impassable for Formiciinae must have had episodic openings of a physiological gate allowing the dispersal of these giant ants and other thermophilic organisms across the Arctic.

We thank L. Lube, collector and donor of the specimen; J. Baldwin for software consultation; G. Alpert, B. Bolton, E. Jarzembowski, H. Lutz, V. Makarkin, M. Moffett, D. Notton, M. Pfeiffer, Z. Qian, S. Robson, A. Ross, B. Taylor, R. Taylor, T. Wappler and S. Watanasit for discussion and information. We thank C. Labandeira and an anonymous reviewer for helpful comments. This research was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC) through a postdoctoral fellowship to S.B.A., and Discovery Grants to R.W.M. and D.R.G.

REFERENCES

1 Matthews Jr, J. V. 1979 Tertiary and Quaternary environments: historical background for an analysis of the Canadian insect fauna. In *Canada and its insect fauna*, Memoirs of the Entomological Society of Canada, no. 108, (ed. H. V. Danks), pp. 31–86. Ottawa, Canada: Entomological Society of Canada.

2 Woodburne, M. O. & Swisher III, C. C. 1995 Land mammal high-resolution geochronology, intercontinental overland dispersals, sea level, climate, and vicariance. In *Geochronology, time scales, and global stratigraphic correlations*, vol. 54 (eds W. A. Berggren, D. V. Kent, M.-P. Aubry & J. Hardenbol), pp. 335–364. Tulsa, OK: Society for Sedimentary Geology.

3 Manchester, S. R. 1999 Biogeographical relationships of North American Tertiary floras. *Ann. Miss. Bot. Gard.* **86**, 472–522. (doi:10.2307/2666183)

4 Hooker, J. J. 2000 Paleogene mammals: crisis and ecological change. In *Biotic responses to global change: the last 145 million years* (eds S. J. Culver & P. F. Rawson), pp. 333–349. Cambridge, UK: Cambridge University Press.

5 Tiffney, B. H. 2000 Geographic and climatic influences on the Cretaceous and Tertiary history of Euramerican floristic similarity. *Acta. Univ. Carol. Geol.* **44**, 5–16.

6 Sanmartín, I., Enghoff, H. & Ronquist, F. 2001 Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biol. J. Linn. Soc. Lond.* **73**, 343–390. (doi:10.1006/bijl.2001.0542)

7 Tiffney, B. H. & Manchester, S. R. 2001 The use of geological and paleontological evidence in evaluating plant phylogenetic hypotheses in the Northern Hemisphere Tertiary. *Int. J. Plant Sci.* **162**(Suppl. 6), S3–S17. (doi:10.1086/323880)

8 Archibald, S. B. & Makarkin, V. N. 2006 Tertiary giant lacewings (Neuroptera: Polystoechotidae) revision and description of new taxa from western North America and Denmark. *J. Syst. Palaeontol.* **4**, 119–155. (doi:10.1017/S1477201906001817)

9 Archibald, S. B., Cover, S. D. & Moreau, C. S. 2006 Bulldog ants of the Eocene Okanagan Highlands, and the history of the subfamily (Hymenoptera: Formicidae: Myrmeciinae). *Ann. Entomol. Soc. Am.* **99**, 487–523. (doi:10.1603/0013-8746(2006)99[487:BAOTEO]2.0.CO;2)

10 Smith, T., Rose, K. D. & Gingerich, P. D. 2006 Rapid Asia–Europe–North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene–Eocene Thermal Maximum. *Proc. Natl Acad. Sci. USA* **103**, 11 223–11 227. (doi:10.1073/pnas.0511296103)

11 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.

12 Tiffney, B. H. 2008 Phylogeography, fossils, and Northern Hemisphere biogeography: the role of physiological uniformitarianism. *Ann. Miss. Bot. Gard.* **95**, 135–143. (doi:10.3417/2006199)

13 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.

14 Westerhold, T., Röhl, U., Laskar, J., Raffi, I., Bowles, J., Lourens, L. J. & Zachos, J. C. 2007 On the duration of magnetochrons C24r and C25n and the timing of early Eocene global warming events: implications from the Ocean Drilling Program Leg 208 Walvis Ridge depth transect. *Paleoceanography* **22**, 1–19. (doi:10.1029/2006PA001322)

15 Eldrett, J. S., Greenwood, D. R., Harding, I. C. & Huber, M. 2009 Increased seasonality through the Eocene to Oligocene transition in northern high latitudes. *Nature* **459**, 969–974. (doi:10.1038/nature08069)

16 Greenwood, D. R., Basinger, J. F. & Smith, R. Y. 2010 How wet was the Arctic Eocene rainforest? Estimates of precipitation from Paleogene Arctic macrofloras. *Geology* **38**, 15–18. (doi:10.1130/G30218.1)

17 Zachos, J. C., Dickens, G. R. & Zeebe, R. E. 2008 An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451**, 279–283. (doi:10.1038/nature06588)

18 Sluijs, A. *et al.* 2009 Warm and wet conditions in the Arctic region during Eocene thermal maximum 2. *Nat. Geosci.* **2**, 777–780. (doi:10.1038/NGEO668)

19 Lutz, H. 1990 Systematische und palökologische Untersuchungen an Insekten aus dem Mittel-Eozän der Grube Messel bei Darmstadt. *Cour. Forschungstinst. Senckenb.* **124**, 1–165.

20 Lutz, H. 1986 Eine neue Unterfamilie der Formicidae (Insecta: Hymenoptera) aus dem mittel-eozänen Ölschiefer der 'Grube Messel' bei Darmstadt (Deutschland, S-Hessen). *Senckenb. lethaea* **67**, 177–218.

21 Wappler, T. 2003 Die Insekten aus dem Mittel-Eozän des Eckfelder Maars, Vulkaneifel. *Mainzer naturwiss. Arch. Beiheft.* **27**, 1–234.