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Intercontinental dispersal of giant thermophilic ants across the Arctic during early Eocene hyperthermals

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Early Eocene land bridges allowed numerous plant and animal species to cross between Europe and North America via the Arctic. While many species suited to prevailing cool Arctic climates would have been able to cross throughout much of this period, others would have found dispersal opportunities only during limited intervals when their requirements for higher temperatures were met. Here, we present *Titanomyrma lubei* gen. et sp. nov. from Wyoming, USA, a new giant (greater than 5 cm long) formiciine ant from the early Eocene (approx. 49.5 Ma) Green River Formation. We show that the extinct ant subfamily Formiciinae is only known from localities with an estimated mean annual temperature of about 20°C or greater, consistent with the tropical ranges of almost all of the largest living ant species. This is, to our knowledge, the first known formiciine of gigantic size in the Western Hemisphere and the first reported cross-Arctic dispersal by a thermophilic insect group. This implies intercontinental migration during one or more brief high-temperature episodes (hyperthermals) sometime between the latest Palaeocene establishment of intercontinental land connections and the presence of giant formiciines in Europe and North America by the early middle Eocene.

Keywords: Formicidae; Formiciinae; *Titanomyrma*; Holarctic dispersal; hyperthermals

1. INTRODUCTION

Holarctic interchanges of plants and animals during the Eocene have long been known [1–13]; however, details of their nature and timing remain little understood. Eocene North America and Europe were only a short distance apart (figure 1), which, combined with eustatic sea-level drop, resulted in land connections between them. Dispersal was possible across a forested, unglaciated Arctic via Greenland by a northern 'De Geer' route through Fennoscandia and a southern 'Thulean' route through Iceland, the Faroe Islands and Great Britain [2–7,10,12]. An epicontinental seaway (figure 1) probably restricted dispersal between Europe and Asia at least some of this time.

The mammal fossil record shows discrete waves of intercontinental migrations during this interval, most notably at the Palaeocene/Eocene boundary 'mammalian dispersal event', when major groups simultaneously appeared across the Holarctic [4,10]. Early Eocene Europe and North America shared the highest number of mammal genera in the Cenozoic [2]; they also had pronounced floral similarities, indicating numerous intercontinental range extensions of plant taxa [3,5,7]. While it has long been recognized that the distributions of modern insect taxa implies Eocene cross-North Atlantic migrations [1], direct fossil evidence has only been reported recently [8,9,11,13].

Increasingly, fine-scale variations in early Eocene Arctic climate are becoming known, with mostly cool, but seasonally equable temperatures prevailing, but with episodic hyperthermal intervals of increased temperatures, some brief and intense [14–18]. Insect taxa previously shown to have co-occurred in Europe and North America in the early Eocene all had ranges including localities where mean annual temperature (MAT) is estimated as cool (far-western North America) or is not known (Fur Formation, Denmark). The new, giant formiciine ant from the Eocene of Wyoming described here, however, was a thermophilic insect, providing evidence of the role played by early Eocene hyperthermal events in facilitating selective trans-Arctic intercontinental dispersals [3–7,12]. Variations in climate would have then acted as a filter gate across high latitudes, mediating differential access between continents for species populations according to their individual physiological requirements.

2. MATERIAL AND METHODS

We follow the morphological terminology used by Lutz [19,20] and Wappler [21], except in referring to abdominal, not gaster, segment identifying numbers (abdominal segments A3–7 = gaster segments I–V). Palaeoclimatic analysis of

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