



Figure 1. Reconstructed early Eocene northern continental positions and shorelines in polar view with Formiciinae fossil localities (G, Germany; B, Britain; W, Wyoming; T, Tennessee), and dispersal routes across the Arctic indicated by red arrows.

MAT of the fossil ant localities (table 1) used either published proxies for MAT [18,22–24], or new analyses based on previously published data on the proportion of dicot leaf morphotypes with non-toothed margins using the leaf margin analysis equation of Miller *et al.* [25], and the leaf area analysis equation for estimating mean annual precipitation (MAP) from Wilf *et al.* [26]. Occurrence data for modern large ants were gathered from published records and personal communications (electronic supplementary material). The latitude and longitudes of these records were entered into the WORLDCLIM software [27], which provided estimates of MAT, coldest yearly quarter mean temperature and MAP to a square kilometre level of spatial resolution.

3. SYSTEMATIC PALAEOONTOLOGY

Formicidae Latreille 1802;

Formiciinae Lutz [20];

Titanomyrma lubei gen. et sp. nov.

(a) Etymology

Genus name derived from the Greek *Titan*, often used to indicate large size, and *myrmex* (Greek: ant), gender feminine. The specific epithet is formed from the surname of the collector of the holotype, Louis Lube.

(b) Holotype

Denver Museum of Nature and Science no. 9041 (labelled DMNH 9041); part only, body in dorsal aspect, anterior portions of right forewing, very little of left.

(c) Locality and age

DMNS locality 784, Farson Fish Beds, Laney Member of the Green River Formation; Sweetwater County, Wyoming; latest early Eocene, approximately 49.5 Ma [28].

(d) Type and included species of *Titanomyrma*

Titanomyrma giganteum comb. nov. is here designated as the type species of the genus, which also includes *Titanomyrma simillimum* comb. nov. and *T. lubei* sp. nov.

(e) Diagnosis: *Titanomyrma*

As provided for *Formicium* by Lutz [20], amended here by: gaster shape variable: ovate or more slender/

cylindrical; A5 width relative to other gaster segments variable; relative lengths of A3–7 variable.

(f) Diagnosis: *Titanomyrma lubei*

Queens separated from other species of *Titanomyrma* most easily by gaster characters: more slender, length/width: 2.14 (*T. giganteum*, 1.40; *T. simillimum*, 1.50); middle half roughly cylindrical (others ovate, A5 widest); A3 length about a quarter width (others about a third); A4 about three times A3 length (others less than twice); A5–6 about half as long as wide (others about a third); A3 not curved around the petiole at joining.

(g) Description: *Titanomyrma*

As provided for *Formicium* by Lutz [20], amended here by change in description of gaster (cf. diagnosis, above).

(h) Description: *Titanomyrma lubei queen*

As in diagnosis; figures 2 and 3*a,d*; immense size, body approximately 51 mm long; head rounded-triangular, approximately 5.5 mm long; approximately 7 mm wide, about a third alitrunk length; antennae, eyes not known; mandibles about a third head length; alitrunk approximately 15 mm long, wing bearing; legs short, tibia III 6 mm; forewing probably in size range of *T. giganteum* queens; waist single segmented, petiole approximately 5.5 mm wide, lacking anterior peduncle; gaster 31 mm long, 14.5 mm wide, without constriction between A3 and A4; spiracles (known on A4–6) long, narrow.

4. DISCUSSION

(a) The status of formiciine species

Titanomyrma is confidently assigned to the Formiciinae by character states unique within Formicidae: extremely large size combined with large, slit-like spiracles [19,20,29], which associate it with *T. giganteum* and *T. simillimum* (early middle Eocene Germany: Messel, and cf. these species from Ekfeld Maar [19–21]), both transferred here to *Titanomyrma* from *Formicium*. *Formicium brodiei* Westwood, *Formicium mirabile* Cockerell [30–32] (both Bournemouth, UK; middle Eocene) and *Formicium berryi* Carpenter [33] (middle Eocene Claiborne Formation, Puryear, TN, USA; incorrectly called Wilcox Formation by Carpenter [33,34]) are only known from forewings, and were grouped with the German species by the similarity of their venations.

The distinctive gaster shape of *T. lubei* is confidently not an artefact of preservation; the tergites are clearly shaped differently than are those of the German species, where A5 is wider than A4 (gaster segments III and II) [20] (figure 3*b,c*). In *T. lubei*, however, these are of similar lengths and maximum widths (figures 2 and 3*a*). Its legs are notably more gracile than those of *T. giganteum* and somewhat more so than those of *T. simillimum*. The mandibles are poorly preserved, but appear smaller than those of the German species (figures 2 and 3*a–c*). Wing length based on the pterostigma in *T. lubei* is about 24 mm, similar to that of the *T. giganteum* holotype queen [20], indicating a forewing length within the range of *T. giganteum*, larger than in *T. simillimum* [20]. However, the body of *T. lubei* is closer in length to the *T. simillimum* holotype, 53 mm [20].