



Figure 4. Climates and distributions of formicini ants and modern ants with any caste over 3 cm in length. (a) Mean annual temperature (MAT) values for the largest living ants (box plots: minimum, 25%, median, 75% and maximum values), the Eocene localities where formicini ants have been recovered and Green River Formation localities comparable with the Farson Fish Beds where *T. lubei* was found (references for fossil site MAT values as in table 1); (b) ranges of modern ant species with any caste over 3 cm in length (locality references in the electronic supplementary material), equator, tropics of Capricorn and Cancer indicated: South America, *Dinoponera* spp.; Africa, *D. wilverthi*; Southeast Asia, *C. gigas*; eastern Australia, *M. brevinoda* (in part, see text).

This is, then, the only modern ant species of this great size that includes part of its range outside of the tropics. The species, as it is currently defined, however, includes those that Clark [52] discussed to be over 3 cm in length as a subset, as well as various groups whose largest individuals (any caste) are recorded only reaching about 24 mm in length. The records of great size appear to be only from Queensland and adjoining northern New South Wales, i.e. the northern part of this range [52]. The range of *M. brevinoda* as a whole has a median MAT of 17.0°C and a CQMT of 11.6°C. The range of Clark's [52] larger form, however, has a nearly megathermal MAT of 19.4°C and a CQMT of 14.3°C.

All of these modern ants inhabit mesic to wet climates, in agreement with MAP estimates for Messel, Puryear (new analyses here) and Green River [22] (see the electronic supplementary material, table S1). The Eocene Arctic was probably a rainforest [15,16], so moisture availability would not have been a barrier.

High temperatures extended well out of the modern tropical belt in the Eocene [15–18,22,23,54–56]. Formicines are exclusively known from climates with an

estimated MAT of about 20°C or greater; MAT of Messel, Puryear and Bournemouth were all megathermal. The climate of the Farson Fish Beds within which *T. lubei* was recovered has not been characterized, but estimates for comparable Green River Formation localities indicate similarly hot conditions (table 1 and figure 4a).

The cooler, microthermal to lower mesothermal [54,55] early Eocene Okanagan Highlands localities of far-western North America bear a number of ant species over 1.5 cm in length—in one case greater than 2.5 cm—but none are known to reach 3 cm [9,57]. A species from the early Eocene Danish Fur Formation is also about 2.5 cm long [9,58]. Ants from the late Eocene cool upland at Florissant, Colorado and from Palaeocene and Eocene ambers (Sakhalin, Baltic, Ukrainian, etc.; indeed, any amber) are not known to reach such sizes (e.g. [59–63]).

### (c) Eocene Arctic climate, hyperthermal events and intercontinental dispersal

Thermophilic organisms face physiological barriers to dispersal outside of the high MAT climate spaces to