

Table 1. Mean annual temperature (MAT) estimates for formiciine-bearing fossil localities (Messel, Puryear, Bournemouth) and localities regional to the Farson Fish beds, Wyoming (Little Mountain, Niland Tongue). MAT estimates for Messel were previously published as points on a figure [56], and these values are now stated here, as well as newly published estimates based on both leaf margin analysis (LMA) and the coexistence interval of nearest living relatives of plant fossils [66] (Wilde *et al.* [67] inferred a similar climate for Eckfeld and Messel). A MAT estimate for the Farson Fish Beds has not been reported; values are given for the slightly older Green River Formation Laney Member Little Mountain locality, the regional Wasatch Formation Niland Tongue locality and an unspecified Green River Basin [68]. Values for all sites include both leaf margin analysis and either taxon analogue [66] or isotopic methods [68], except for Bournemouth, which is from isotopic analysis of fossil gastropod shells [24]. An isotopic estimate from the San Juan Basin (SJB) [68] is supplied alongside the LMA-based estimate for Puryear, being of the same palaeolatitude and age [68]. The standard error for LMA values is set at 4.0°C unless the calculated error is greater than 4.0°C, following the recommendation of Peppe *et al.* [69]; for SJB isotope value, it is 5.5°C [68]; error not provided for Bournemouth isotope value [24].

locality	no. of leaf morphotypes	$p_{\text{margin}}(\%)$	MAT
with Formiciinae			
Messel	49	65.0	20.3°C ^a , 21.1°C ^b , 22°C (up to ~24°C) [66]
Puryear	47	91.5	23.9°C [23], 27.7°C ^a , 29.0°C ^b , (27.8°C SJB [68])
Bournemouth	n.a.	n.a.	22°C [24]
Green River Formation			
Little Mountain	49	60.2	19.6°C [22], 18.8°C ^c , 18.3°C [68]
Niland Tongue	14	71.4	23.0°C [22], 22.0°C ^c

^aNew estimates using eqn from Miller *et al.* [25] and data from Greenwood & Wing [23].

^bNew estimates using data and LMA eqn (2) from Greenwood & Wing [23].

^cNew estimates using eqn from Miller *et al.* [25] and data from Wilf [22].

We propose the genus *Titanomyrma* for the new species and transfer the two German species to it, as grouping them within *Formicium* would compound an existing problem that can no longer be avoided.

Lutz [20] recognized the difficulty of defining the genus based on the limited information provided by a single forewing specimen of the type species, *F. brodiei*. He, therefore, used the characters of the new species '*F. giganteum*' and '*F. simillimum*' to form his genus diagnosis and description, effectively employing them as sort of 'functional type species' ('Since Westwood only illustrated the wing, but did not describe it formally, the following new finds from Messel will provide a more detailed diagnosis and description'. p. 182, our translation from the German).

Further, in ant taxonomy generally, because of the variability of wing characters and the small amount of their study compared with those of other insect groups, and by the traditional availability of more commonly collected wingless worker caste specimens, wings are usually ignored or de-emphasized in defining modern species; they are invariably defined by workers.

There appears to be considerable plasticity of wing characters in Formiciinae in particular. Venational morphology of the holotype wings of *F. brodiei* ([20], fig. 1c) and *F. berryi* ([20], fig. 2c) falls within variability between the left and right wings of a specimen of '*F.*' aff. *giganteum* ([21], fig. 95). Further, note the differences between the forewings of this specimen of '*F.*' aff. *giganteum* and the '*F.*' *giganteum* holotype ([19], fig. 3b) and paratype 6 ([19], fig. 5). Also, size differences between males and females of the German species indicate the possibility that smaller and larger wing species could be conspecific [19]. Such examples indicate deep problems in the usefulness of formiciine wings for defining species.

By these reasons, we propose to clarify formiciine taxonomy by considering *Formicium* as a collective genus containing the wing species, which we consider tentative, and erecting the nominal genus *Titanomyrma* to include

the new species and the two German species. As a collective group, *Formicium* would have neither a diagnosis nor a description, but would be defined as including all species of Formiciinae that cannot be placed in a nominal genus owing to lack of sufficient preserved characters. *Formicium brodiei* ceases to be *Formicium*'s type species (a collective genus has none: ICZN Article 67.14 [35]). *Formicium*, however, remains the type genus of Formiciinae, and the subfamily name is not affected.

A team of palaeoentomologists is currently undertaking a major examination of the Formiciinae (T. Wappler 2011, personal communication), with large numbers of new specimens available with which to confidently establish intra- and interspecific variability. We expect that this work will greatly clarify the positions of the wing species. Here, we provide what we recognize is a brief, interim diagnosis and description of *Titanomyrma*, with the understanding that these will soon be established with greater detail by the Wappler team.

(b) *Thermophily, size and the Formiciinae*

To assess the climatic constraints of Formiciinae, we reconstructed the MAT, coldest quarter mean temperature (CQMT) and the MAP of the sites where they have been recovered. Further, we calculated the climate space occupied by the largest living ants to ascertain whether there are common climatic trends associated with great size that are general to ants. Based on analysis of their habitats, the Formiciinae were clearly thermophilic; they are only known from hot climates, with MAT > 20°C (table 1 and figure 4a). This is also supported by their great size, as almost all of the largest modern ant species are restricted to the megathermal climates of the tropics.

The great size of *T. lubei* was only exceeded by that of the largest known ants, *T. giganteum* and *T. simillimum*, the reproductives of which are estimated to have had the mass