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THE FOSSIL MEMBERS OF THE ANT TRIBE LEPTOMYRMECINI (HYMENOPTERA: FORMICIDAE)

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In 1980 Baroni Urbani described *Leptomyrmex neotropicus* from 9 rather poorly preserved specimens clustered in a single piece of Dominican amber and hence presumed to be of Miocene age (the date estimated in Baroni Urbani and Saunders, 1982). The finding is of potential biogeographic importance because *Leptomyrmex*, and hence the very distinctive dolichoderine tribe Leptomyrmecini, is today limited to the Old World, in particular eastern Australia, New Caledonia, New Guinea, the Aru Islands, and the Moluccas. A second genus, *Leptomyrmula*, had previously been described from the Miocene amber of Sicily (Emery, 1891, 1912). It thus appears that an entire tribe was once almost worldwide but has since retreated not only from Europe but the entire Western Hemisphere. Wilson (1985a) doubted Baroni Urbani's tribal placement of the Dominican amber specimens. He found a worker in Dominican amber that superficially resembles *Leptomyrmex*, sharing the same distinctively elongated body form, mesothoracic constriction, petiole, tapered neck, and bulging eyes located toward the rear of the head, but actually belongs to the *Camponotus branneri* group. He suggested that *Leptomyrmex neotropicus* might be the same species. In the meantime, Schlee (1984) published a color photograph of another Dominican amber piece containing four presumed *Leptomyrmex* workers. This example is now preserved in the collection of

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the Museum für Naturkunde, Stuttgart, with the reference number Do-4931-M. He has also provided us with four more workers, in a piece labeled Do-4484-M.

Baroni Urbani was right. The additional, better preserved workers are identical or close to *L. neotropicus*, and prove to belong to the Leptomyrmecini beyond any reasonable doubt. In addition to being so close in overall habitus to the living species of *Leptomyrmex* as to fall easily within the limits of this genus, the material shows the following distinctive traits in common with that Old World genus:

- (1) Slit-shaped anal orifice.
- (2) Masticatory border of mandibles smoothly rounded at the basal angle and lined with more than 15 denticles of uniform size, as opposed to fewer than 10 teeth, usually 5–6, decreasing in size from apex to base in species of *Camponotus*.
- (3) Anteriormost point of antennal socket very close to the posterior clypeal border (in *Camponotus* the two are widely separated).
- (4) Large metapleural gland orifice and prominent bulla (in *Camponotus* bulla small and orifice absent).
- (5) Metathoracic spiracles on dorsum of alitrunk (usually lateral in *Camponotus*).

In addition, Wilson has acquired a male that appears to be a leptomyrmecine, although it possesses at least one trait (absence of the radial cell) that might eventually justify separating it at the generic level from both *Leptomyrmex* and *Leptomyrmula*.

Status of *Leptomyrmex neotropicus* Reexamined

The main features of a well-preserved *Leptomyrmex* are depicted in Figure 1. As noted by Baroni Urbani (1980) for the *L. neotropicus* types and confirmed with the new worker specimens, the habitus of the fossil species is closest to *L. fragilis* (= *L. gracillimus*) of New Guinea, Ceram, and Aru among the living species. This assessment is based on the revision of *Leptomyrmex* by Wheeler (1934) and the examination of large new collections of that genus placed in the Museum of Comparative Zoology during the ensuing fifty years. *L. neotropicus* differs from *fragilis* in its smaller size, even narrower head, projection of the compound eyes beyond the lateral borders of the head, and more concave masticatory borders. In a genus with a relative scarcity of worker characters, the small size is especially notable. The specimen shown in Figure 1 possesses the following

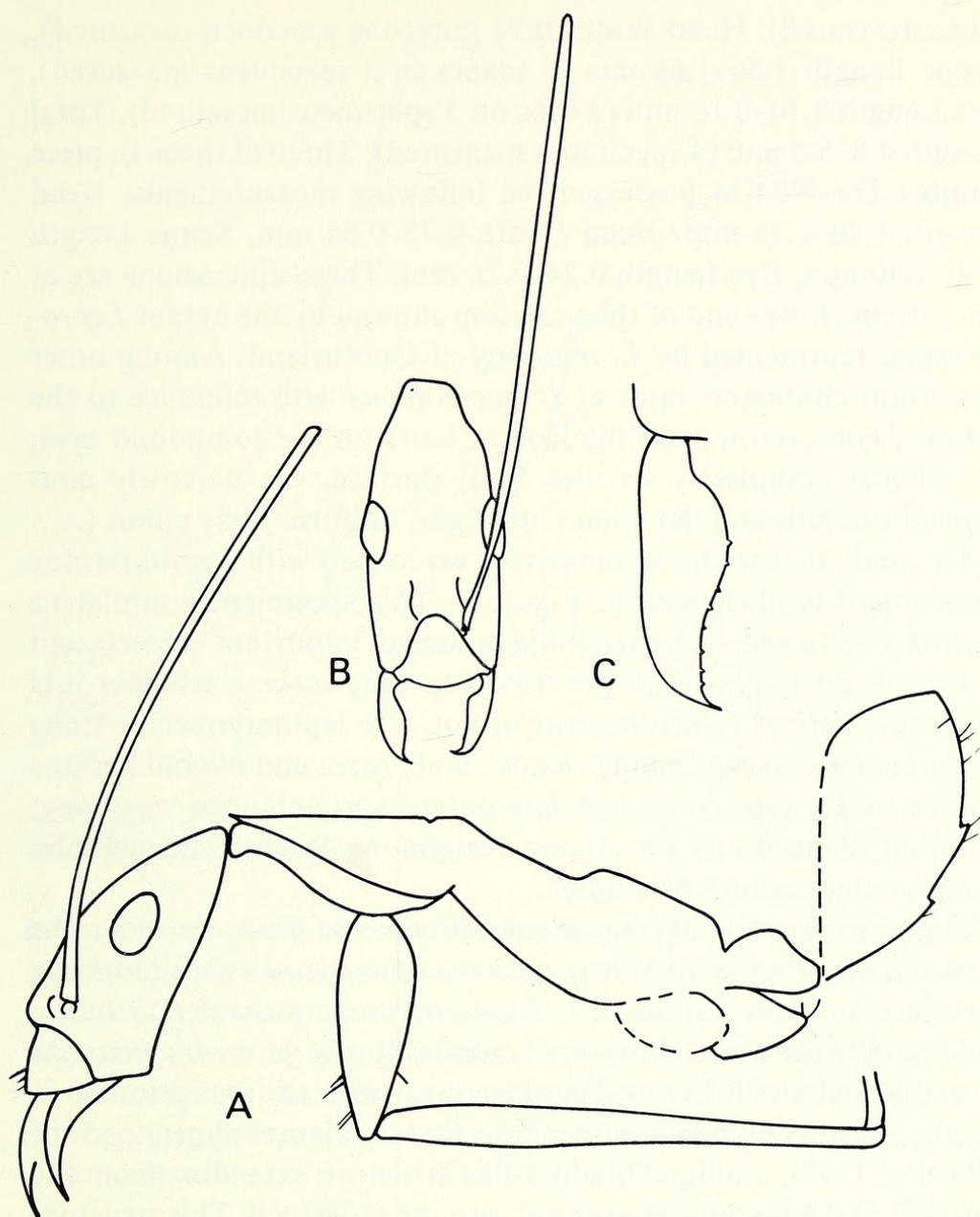


Figure 1. *Leptomyrmex neotropicus* worker from Miocene amber of the Dominican Republic: A, side view of entire body; B, frontal view of head; C, enlarged view of right mandible tilted anteriorly to give a full frontal aspect.

measurements: Head Length (excluding mandibles) 1.50 mm, Head Width (across and including eyes) 0.72 mm, Scape Length 2.48 mm, Eye Length (longest axis) 0.31 mm, total length (including mandibles) 5.6 mm. A second specimen is smaller: Head Length 1.30 mm, total length 4.6 mm. The four Stuttgart specimens embedded in a single amber piece (Museum reference number Do-4931-M) yielded the following measurements: Head Length 0.80–0.83 mm (4 speci-

mens measured), Head Width 0.52 mm (one specimen measured), Scape Length 1.56–1.66 mm (5 scapes in 3 specimens measured), Eye Length 0.14–0.16 mm (3 eyes on 3 specimens measured), Total Length 4.8–5.5 mm (4 specimens measured). Three of those in piece number Do-4484-M possessed the following measurements: Head Length 1.20–1.36 mm, Head Width 0.72–0.84 mm, Scape Length 2.40–2.48 mm, Eye Length 0.24–0.26 mm. These dimensions are at the extreme lower end of the variation showed by the extant *Leptomyrmex*, represented by *L. mjobergi* of Queensland. Among other important character states of *L. neotropicus* with reference to the extant *Leptomyrmex* are the lack of hairs on the compound eyes, the almost completely hairless body surface, the narrowly constricted occiput, and the apparently light, uniform body color.

The male that we have tentatively associated with *Leptomyrmex neotropicus* is illustrated in Figure 2. This specimen is similar to *Leptomyrmex* and *Leptomyrmula* in several important respects and is appropriately placed in the tribe Leptomyrmecini, whether it is really the male of *L. neotropicus* or not. The leptomyrmecine traits are as follows: exceptionally slender body form and overall habitus similar to *Leptomyrmex* and *Leptomyrmula*; antennae very long; venation reduced and the stigma vestigial or absent. The genitalia unfortunately cannot be studied.

There are also some important differences. First, consider the venation (see Figure 3). Where extant *Leptomyrmex* species have a peculiarly narrow radial cell, *Leptomyrmula maravignae* has a wider and hence more "ordinary" radial cell, and *L. neotropicus* has no radial cell at all. Living *Leptomyrmex*, with the exception of *L. fragilis*, possess a stigmal appendage ("pterostigmal appendage" of Wheeler, 1934), a unique bladder-like structure extending from the position of the vestigial stigma out into the radial cell. This structure is absent in *Leptomyrmula maravignae* and the putative *Leptomyrmex neotropicus*. In the extant *Leptomyrmex*, the antennae are about 0.7–0.9× as long as the body; in *Leptomyrmula maravignae* they are about 0.5× as long; and in *Leptomyrmex neotropicus* they are about equally long.

The absence of the stigmal appendage and an exceptionally slender body form are shared by the male of *Leptomyrmex neotropicus* with the male of the living *L. fragilis*, but there the resemblance ends. *L. neotropicus* is much smaller than *L. fragilis*, has a

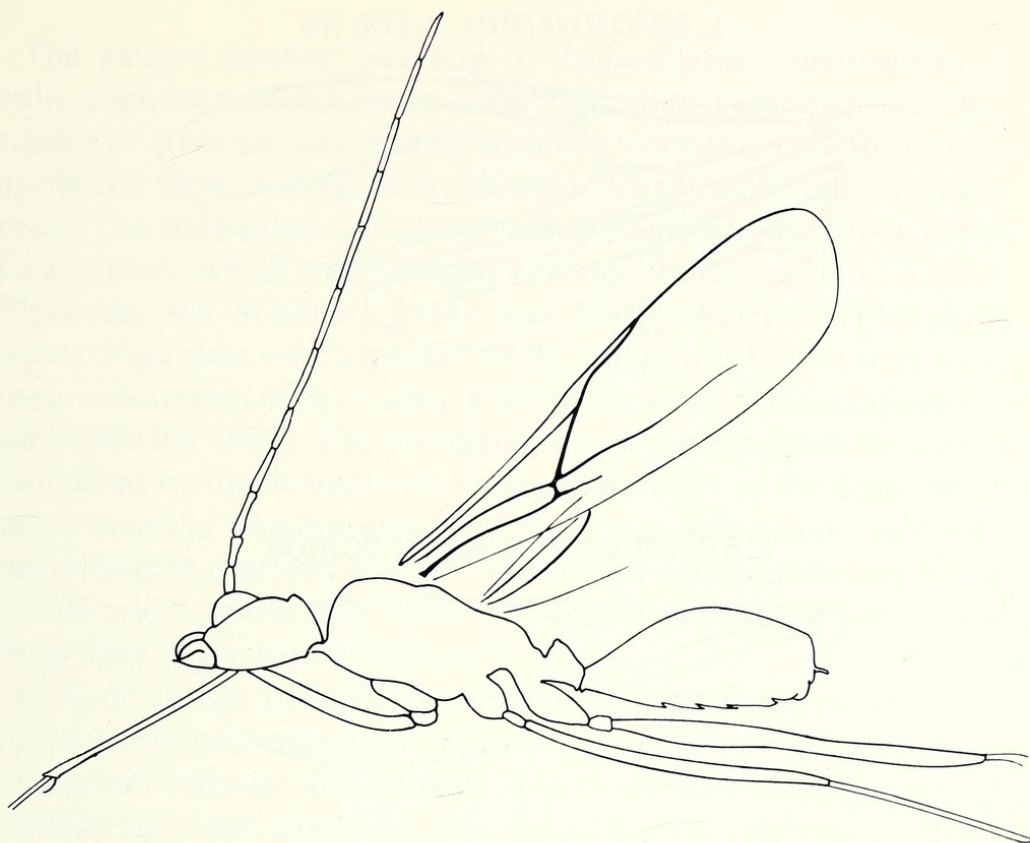


Figure 2. Leptomyrmecine male from the Dominican amber tentatively associated with *Leptomyrmex neotropicus*.

convex (as opposed to concave) prothorax, lacks the radial cell, and has more fully developed, denticulate mandibles. The mandibular form of *L. neotropicus* is shared with *L. erythrocephalus* and *L. nigriventris* among living species. *L. fragilis* has thinner, strap-like, toothless mandibles; this trait is shared by *cnemidatus*, *darlingtoni*, *mjobergi*, *pallens*, *tibialis*, *varians*, and *wiburdi* among the extant *Leptomyrmex*.

DISCUSSION

The leptomyrmecine male, whether *Leptomyrmex neotropicus* or not, may be sufficiently different from the living *Leptomyrmex* and Sicilian amber *Leptomyrmula* to warrant separation as a distinct genus. However, we do not believe it prudent to take this step until enough material has accumulated to make the worker-male association more probable, and to better estimate the extent of variation in both castes.

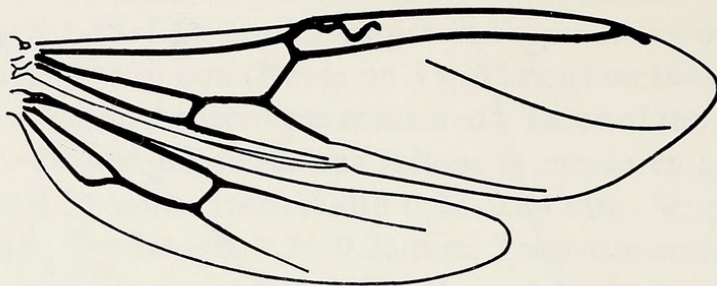
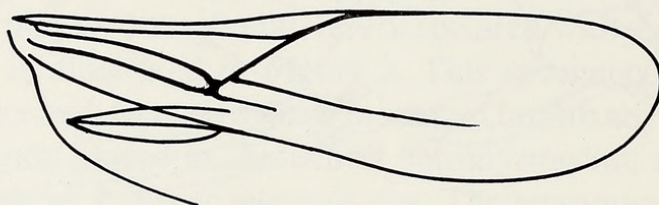
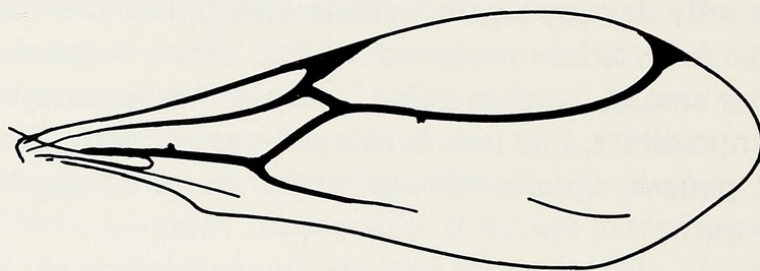
Leptomyrmex tibialis*Leptomyrmex neotropicus**Leptomyrmula maravignae*

Figure 3. Wings of males of the living *Leptomyrmex tibialis* of Australia (Wheeler, 1934), *Leptomyrmula maravignae* of the Sicilian amber (Emery, 1891), and the putative *Leptomyrmex neotropicus*.

The picture remains puzzling. If *Leptomyrmex neotropicus* is really cognate with the living Indo-Australian *Leptomyrmex*, that is, derived from an immediately common ancestor, then the Leptomyrmecini have undergone a dramatic retreat since later Tertiary times. The only other ant group with a comparable history is the Aneuretinae, which once ranged through Europe (Baltic amber, Oligocene; see Wheeler, 1914) and North America (Florissant shales, Oligocene; see Carpenter, 1930), but now is known only from *Aneuretus simoni* of Sri Lanka in the living world fauna (Jayasuriya and Traniello, 1985). The peculiarity of the leptomyrmecine case is heightened by the distinctively modern character of the Dominican amber fauna in which it occurs: of 37 genera and well-defined subgenera of ants recorded to date, 34 have survived somewhere in the New World tropics; only three are absent, and these are extinct everywhere in the world (Wilson, 1985b).

It is of course possible that *Leptomyrmex neotropicus* represents a wholly convergent line to the Old World "true" Leptomyrmecini, but we consider that unlikely. The character states possessed in common seem too numerous and detailed to be convergent. However, the matter will be settled with confidence only with the acquisition and study of larger series.

SUMMARY

Additional specimens have confirmed the existence of the ant tribe Leptomyrmecini in Miocene amber of the Dominican Republic. The workers of the species, *Leptomyrmex neotropicus*, are not distinguishable at the generic level from the living *Leptomyrmex* of Australia and Melanesia, but the male tentatively associated with the workers has peculiarities in wing venation that may eventually justify a separation from *Leptomyrmex* as well as from *Leptomyrmula* of the Miocene Sicilian amber. This is the only higher ant taxon other than the subfamily Aneuretinae known to have gone extinct in the New World while surviving in the Old World.

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