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The First Fossil Species of the Australian Ant Genus *Leptomyrmex* in Amber from the Dominican Republic

(Amber Collection Stuttgart: Hymenoptera, Formicidae. III: Leptomyrmecini)

by Cesare Baroni Urbani, Basel

With 6 Figures

Summary

Leptomyrmex neotropicus n. sp. is described on a set of 9 more or less poorly preserved specimens in Dominican amber (Lower Oligocene to Middle Miocene). The new species is related to the Recent ones and particularly to *L. fragilis* (F. SMITH) of New Guinea, Ceram, and Aru islands. This discovery brings additional evidence for the faunal connections between South America and Australia but the common explanations given in the literature cannot account for the *Leptomyrmex* case.

Zusammenfassung

Leptomyrmex neotropicus n. sp. wird anhand einer Serie von 9 mehr oder weniger gut erhaltenen Exemplaren aus dem Dominikanischen Bernstein (unteres Oligozän bis mittleres Miozän) beschrieben. Die neue Art ist mit den rezenten, insbesondere mit *L. fragilis* (F. SMITH) von Neuguinea, Ceram und den Aru-Inseln, verwandt. Dieser Fund erbringt zusätzliches Beweismaterial für die faunistischen Zusammenhänge zwischen Südamerika und Australien, aber die häufig in der Literatur zu findenden Erklärungen sind im Falle dieser *Leptomyrmex* nicht anwendbar.

1. Introduction

The first two papers on Dominican amber ants (BARONI URBANI, 1980 a and b) dealt with the ant genera *Trachymyrmex* and *Anochetus*. The present paper describes a new *Leptomyrmex* species which represents the first fossil record for the genus (see the discussion, chapter 5) and the first record of a non-Neotropical genus among the Dominican amber ant fauna. Although the study of the rich amber material available is far from being concluded, a quick overview on it shows that this is, for the moment, the only case of a genus extraneous to the Recent Neotropical fauna among amber ants of the Dominican Republic.

Despite the fact that all the specimens are rather poorly preserved, we considered it important to spend much time for their investigation, since this is the first fossil record of Leptomyrmecini workers.



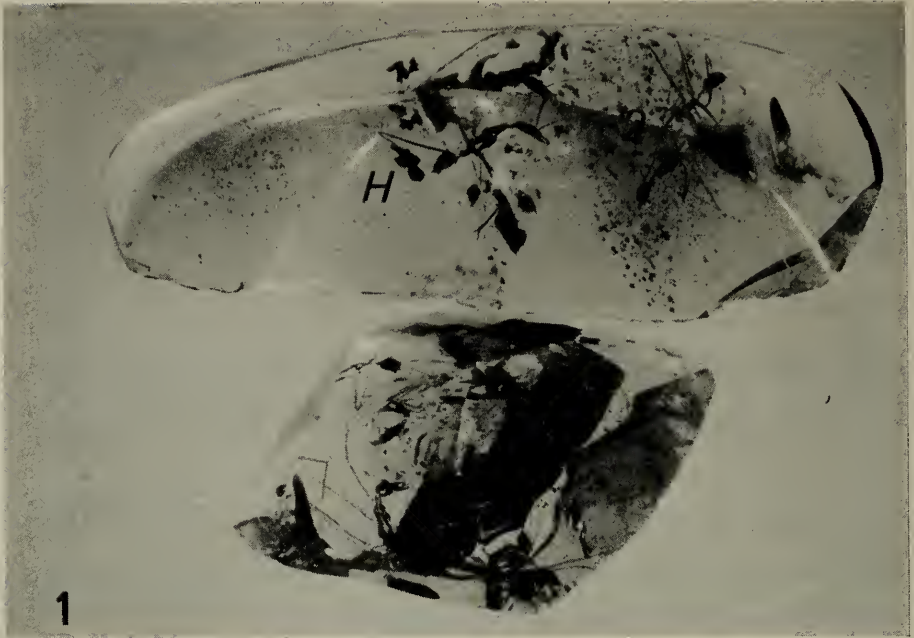


Fig. 1. Two parts of the amber block containing the *Leptomyrmex neotropicus* n. sp. The large one (maximal length 3 cm) with the holotype (H = Do-996-K-1) and one paratype (-2 = Do-996-K-2) with its reflected image. The other piece with additional 7 specimens, of which only a few are visible.

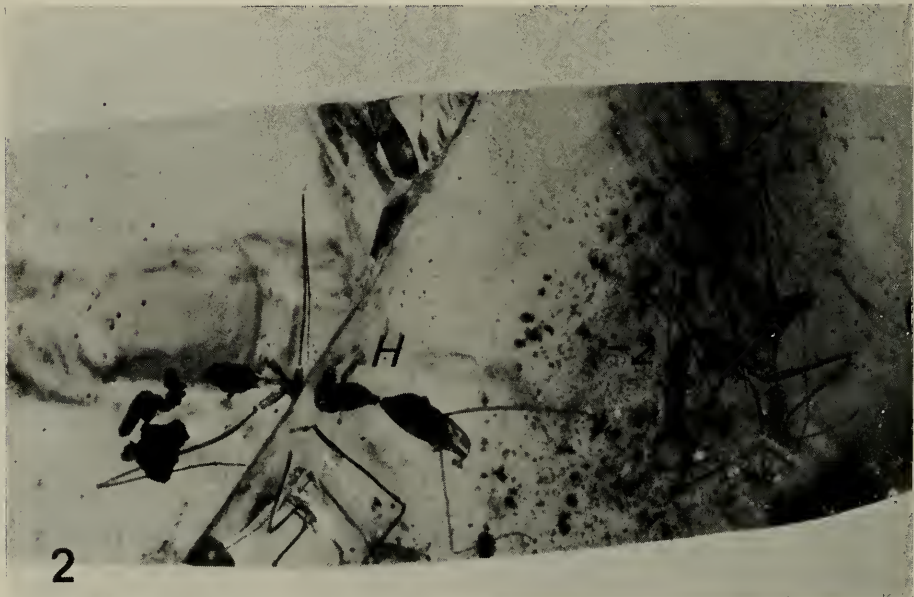


Fig. 2. *Leptomyrmex neotropicus* n. sp., holotype and paratype (see fig. 1) in different view. — Length of the ants 4.8 mm.



Fig. 3. *Leptomyrmex neotropicus* n. sp., two additional specimens (Do-996-K-6 and Do-996-K-7), the presumed pupa (P?), and the beetle (C). — Magnification 10x.

Fig. 4. Parts of the ants (see fig. 3) showing the influence of exposure to heat; this may have occurred under natural conditions (SCHLEE, in preparation). — Magnification 15x.

Acknowledgements

Dr. Dieter Schlee again generously offered to prepare the photomicrographs for this paper as he has done already for the previously published ones on Dominican amber ants. He exercised moreover a keen editorial work on the manuscript and a continuous advising and encouraging function during several discussions and conversations. Without the professional ability and the deep involvement of Armin Coray the drawing of this *Leptomyrmex* species could never be accomplished. Karl Müller and Colette Egger respectively cut and polished the amber sample as they did for several others and Marianne Grauwiler typed the manuscript. Without the help and support from all these persons, the publication of the results of my amber studies would have been greatly delayed if not partly abandoned.

Finally, Gennadij M. Dlussky kindly revised an early draft of this manuscript and allowed me to cite the still unpublished results of his studies on Mesozoic Formicoidea.

2. Material and methods

All the *Leptomyrmex* material available for this study was originally included in a single small suboval piece of Dominican amber of about 3 x 2 cm. It contained at least 9 workers in varying degrees of poor preservation. The colour of the amber is very clear, but one's view is further obscured by one major transversal fissure and by several other inclusions of different nature. The integument of the ant specimens appears nearly always digested, shrunk, fissured, and even collapsed — probably affected by heat treatment after the embedding process (D. SCHLEE, personal communication). The amber piece bears the number Do-996 in the collection of the State Museum of Natural History, Stuttgart, and, apart from the ants, numerous

other inclusions are present. Among others, I tentatively identify the following: 1 wood-louse fragment; 1 very well preserved Scydmenid beetle; several vegetable fragments looking like pollen and fern spores.

The amber block has been cut, to make observations easier, into two parts, which have been partly re-polished. One piece contains two better preserved ants (the holotype, Do-996-K-1, and one other specimen, Do-996-K-2) and several vegetable fragments. The other piece contains the 7 remaining paratypes (Do-996-K-3 to Do-996-K-9), the wood-louse, the beetle and the majority of the plant remains. In both amber pieces the long appendages of the ants (antennae, legs) are situated so close to each other that the ants cannot be separated without damage.

The drawings of the new *Leptomyrmex* needed particular care because of the previously mentioned poor conservation of the specimens. They are based on a long reconstruction work by ARMIN CORAY and have been obtained by comparing the same parts in different specimens, the presumed original dimensions being produced by partial extrapolation. At least one detail, i.e. the opening of the metapleural gland, has not been seen clearly enough in the fossil material and has been copied from Recent species. Altogether, I believe that a good level of credence can be given to the final drawing. A comparison between the drawing and the photographs accompanying this paper should prove, in my opinion, not only the large amount of work needed to prepare the reconstruction but also that the result was worth of it.

Mr. ARMIN CORAY, who so skillfully prepared the reconstruction, has asked to add a small paragraph to explain in more detail, as justification for the method, how the published final drawing has been obtained. I think it interesting to literally reproduce here his explanations: „Das vorhandene Material von *Leptomyrmex* zeigt sich durchwegs im Zustand mehr oder weniger starker Zersetzung, wodurch die Proportionen der einzelnen Tiere vielfach empfindlich gestört und verändert sind. Um eine Zeichnung zu erstellen, war ich somit gezwungen, von den vorhandenen 9 Exemplaren so viel Informationen wie möglich zu gewinnen, was durch Messungen und Zeichnungen der brauchbaren Teile geschah. Anhand der Daten wählte ich ein Tier, von dem wichtige Teile verwendbar waren, als ‚Hauptexemplar‘ aus und setzte es als Maßstab all meiner Ergänzungen ein. Mit Hilfe vergleichbarer Exemplare konnte ich einige Teile hinzufügen; aber vielfach waren zwischen den Tieren doch gewichtigere Größenunterschiede festzustellen, was es notwendig machte, mehrere Stücke im Größenverhältnis verändert für die Rekonstruktion zu verwenden. In diese Rekonstruktionszeichnung sind schließlich die Maße und (oder) Proportionen von mehr als der Hälfte der vorhandenen Exemplare eingegangen.“

3. Description

Leptomyrmex neotropicus n. sp.

Holotypè: Worker in amber fragment Do-996-K-1, the specimen in the middle and clear portion of the amber block (with the trunk crossed by a transversal fissure), in the collection of the State Museum of Natural History (Dept. of Phylogenetic Research), Stuttgart.

Paratypes: 8 workers, one in the same amber block as the holotype (the specimen in the obscured part of the amber piece) and the other seven partly damaged and partly incomplete in the other amber fragment, in the same collection as the holotype. Some of the paratypes miss a part of the appendages and/or of the body and some show big deformations of the integument. One of them might be a pupa, although the preservation conditions do not allow a sure decision.

Derivatio nominis: „Neotropicus“ is a barbarism employed to designate the provenance from the Neotropical region and used here to underline the totally unexpected presence of a member of the genus *Leptomyrmex* on the American hemisphere.

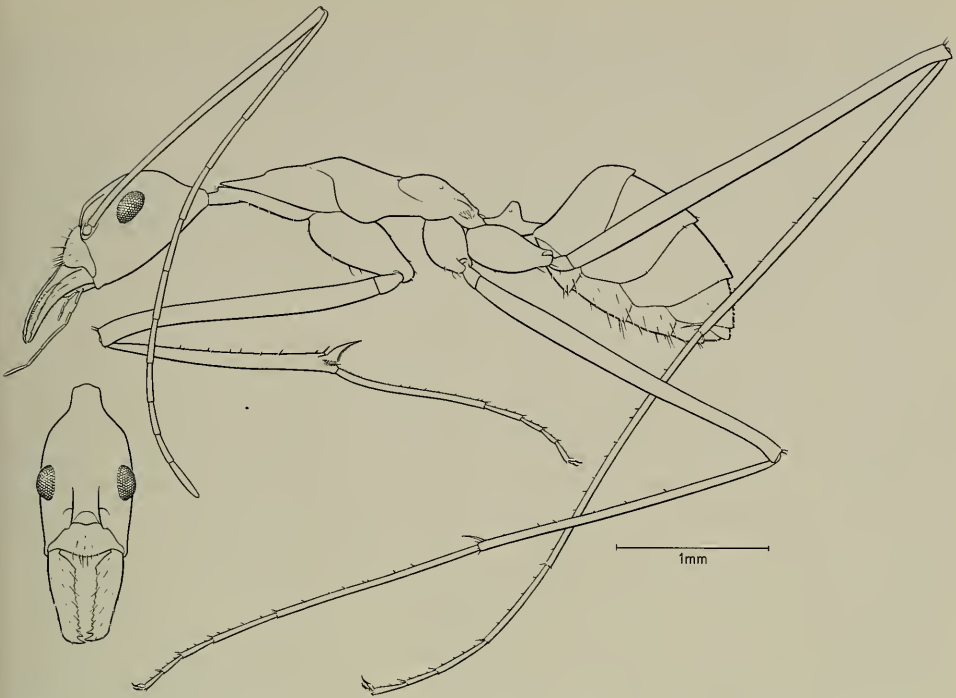


Fig. 5. *Leptomyrmex neotropicus* n. sp. Schematic profile of the whole body and head in frontal view. Reconstruction by ARMIN CORAY. See text chapter 2.

Diagnosis: Worker. A relatively polymorphic *Leptomyrmex* recalling members of the *fragilis* species group, with large eyes very prominent on the sides of the head, and a very constricted occipital region.

Measurements (in mm): Total length, holotype 4.84, paratypes 4.16—4.81. Head length on the sagittal plane (mandibles excluded), holotype 1.30, paratypes 0.74—1.20. Maximum head width (eyes excluded), holotype 0.60, paratypes 0.83—1.00. Maximum eye width, holotype 0.16, paratypes 0.10—0.24. Scapus length, holotype 2.30, paratypes 2.03—2.54. Posterior tibia length, holotype 2.44, paratypes 1.84—2.34.

Worker (fig. 5). Head, excluding the mandibles, nearly twice as long as broad, with the eyes slightly before the cephalic midline. Cephalic sides nearly parallel and following the cheeks for about 4/5 of the whole length, strongly constricted in the neck-like shaped posterior 5th. Clypeus anteriorly feebly pronounced and bluntly carinated in the middle. Eyes large and suboval, their maximum diameter longer than the maximum frons width. Mandibles long and slender, dorsoventrally compressed, with a row of 17—20 small, irregular denticles on the masticatory margin and no visible teeth on the basal border. Antennae very long and slender with the scapus nearly twice as long as the head without mandibles and the funiculus more than three times as long as the head. Funicular joints gradually decreasing in length from the basal to the preapical, with the terminal one longer, comparable in length to the antennal joint IX. Most specimens show a small inflation on the articulation between two consecutive joints, although this is likely to be an alteration due to the poor preservation of this material as it is surely the case for the thickening of the scapus in two paratype specimens. Maxillary palps longer than the mandibles, 6-jointed, with the 4th joint longer than joints 1—3 together. Labial palpi 4-jointed and much shorter, slightly shorter, as a whole, than maxillary joint 4th.

Trunk long and slender, slightly prominent in correspondence with the mesonotum and propodeum. Maximum width at the level of the humeri. Pronotum, mesonotum, and propodeum subequal in length. Propodeum rounded in profile, with the declivity about twice as long as the base. Petiole small and rounded in profile; its width about $\frac{1}{3}$ of the maximum propodeal width. Gaster elliptical.

Legs extremely slender and elongated. The fore tibia bears a well developed pectinate spur opposite to a tiny pectinate area on the first tarsal segment, like in most ants. Only, a second smaller pectinate area is present on the tibia itself between the apex and the spur (see fig. 5). This structure, to my knowledge, has never been described before, but, although less visible, it is present also in all the Recent species of the genus which I have been able to see.

Integument, colour, pilosity. These three characters are extremely difficult to see and to evaluate because of the poor preservation of the available specimens. Most of the body surfaces appear folded or fissured, in some instances to such an extent even that the whole outline of a part is affected, as with the previously mentioned case of the antennal scapi and, in another specimen, the legs. My impression is that, before alteration, the integument should have been uniformly smooth and opaque on the whole body. The colour of these amber specimens appears to be light brown with darker head and gaster. Most of the body appears glabrous except the inferior and posterior surfaces of the gaster, the coxae, and the oral region which bear a considerable amount of erect or suberect short hairs. A few subdecumbent and short hairs on the prosternum and on the ventral face of the coxae. Tibiae and tarsi with rare short bristles on the internal margins. It is likely that the minute pruinose pubescence covering the whole body of the Recent species is present also in the fossil one, although, in the available material, it is easily detectable only on the antennal scapi of one specimen.

4. Relationships

Despite the poor preservation of most of the material, the head and petiolar shape, etc., do not leave any doubt about the attribution of this species to the genus *Leptomyrmex*. The narrow head and the elongated occipital constriction indicate a close relationship with *L. fragilis* (F. SMITH) presently living in New Guinea, Aru Islands, and Ceram. But the much smaller size (maximum total length of *neotropicus* 4.8 mm; minimum length of *fragilis* 6.5 mm), the eyes projecting out from the sides of the head in dorsal view, and the superior outline of the trunk, represent important characters largely justifying the erection of a new species for the amber material.

However, one cannot categorically exclude that the new species belongs to the fossil genus *Leptomyrmula*, known on one single male from Sicilian amber. The most consistent difference between *Leptomyrmex* and *Leptomyrmula* lies in the wing venation which is unknown in *L. neotropicus*, but I cannot detect, in the Dominican fossil, a single character which could even suggest the opportunity of a generic separation from the Recent members of the genus *Leptomyrmex*.

5. Discussion

Phylogeny: The genus *Leptomyrmex* comprises 14 species and a high number of infraspecific forms mostly based on chromatic characters. The genus has been reviewed by WHEELER (1934) and very little information has been added to our knowledge since this date. The members of this genus are morphologically very homogeneous because, like most Dolichoderinae, although perhaps more so in this

genus, these ants lack peculiar integumental structures enabling an easy species discrimination. These species constitute a small and very compact group within the Dolichoderinae where they represent the only living members of the tribe Leptomyrmicini. In fact, their sole known relative is a unique fossil male from Sicilian amber (Middle Miocene) described by EMERY (1891) as *Leptomyrmex maravignae*. Later on, EMERY (1911) erected a new genus, *Leptomyrmula*, for this same specimen, on the basis of a peculiarity of the wing venation (a marked trace of Rsf1, entirely missing in *Leptomyrmex*). Both genera, *Leptomyrmex* and *Leptomyrmula*, constitute the tribe Leptomyrmicini which is highly characteristic because of the wing venation of the male and the elongated and slender body constitution. Also, *Leptomyrmex* shows other peculiarities, such as apterous queens (a rare situation in ants and unique among Dolichoderinae), a peculiar proventricular morphology, and several particulars of the larval morphology (head violin-shaped, vestigial mandibles, body hairs very reduced or absent, etc.). Of course, these peculiarities of the females and larvae could not be observed in *Leptomyrmula*, being represented only by one male specimen. Thus, it remains unsettled at the present, if these peculiarities mentioned above, represent autapomorphies of the genus *Leptomyrmex*, or synapomorphies of *Leptomyrmex* plus *Leptomyrmula*, i.e. for the tribe Leptomyrmicini. The same is true for some behavioural peculiarities (see below).

Actually, apart from the previously mentioned presence of Rsf1, the male of *Leptomyrmula* does not significantly differ (at least as far as the preservation of the specimen allows to see) from other *Leptomyrmex* males.

The old idea of EMERY, later accepted by all the authors who dealt with these ants, although with different interpretations of the wing venation, is that *Leptomyrmula* represents a direct ancestor of the Recent Leptomyrmicini which have entirely lost the Rsf1 in the course of evolution.

If the presumed age of the Sicilian amber (Middle Miocene) can be confidently accepted, the presence now of another fossil in Dominican amber (which should be contemporary or older than Simetite), allows the following hypotheses:

1. The present trace of Rsf1 is the only morphological structure characterizing the genus *Leptomyrmula*. *Leptomyrmex neotropicus*, the wing of which is unknown, either can or does not belong to *Leptomyrmula*.
2. With the presence of a true *Leptomyrmex* contemporary with or older than *Leptomyrmula*, the latter cannot be interpreted as an ancestor of the former; it can only represent a sister group. The presupposition for this conclusion is that the worker of *Leptomyrmex* can be recognized as „true *Leptomyrmex*“, and can be separated from *Leptomyrmula* workers.

Though these *Leptomyrmula* workers are still unknown, I am inclined to accept the second hypothesis.

WHEELER (1934) already noted how most Recent *Leptomyrmex* species show a great colour variation which is constant at least within a single nest or population and which, in the classical myrmecological literature, received often infrasubspecific names. WHEELER raised all these forms to subspecific rank, added several new ones, and justified his point of view by attributing an important evolutionary meaning to the colour patterns. According to his views, the most primitive forms live in tropical rain forests and are constantly melanic. In the course of evolution, these ants adapted to xerophyllous forests by progressively losing the black pigment and some of them, showing an entirely yellowish colour pattern, adapted to the bush and probably shifted to a nocturnal or crepuscular behaviour.

The pale colour of *L. neotropicus* from Dominican amber probably fits this idea. It has been concluded (SCHLEE, personal communication) that the small percentage of water insects and moist-habitat groups among the total fauna of the Dominican

amber, together with the high percentage of Grylloidea, Hymenoptera, Termites, etc., indicate a hot and relatively dry climate.

Behaviour: Very scanty is the information we have on the behaviour of *Leptomyrmex*, but the few published accounts allow us to suppose a set of ethological peculiarities at least as important as the morphological ones. According to WHEELER (1915; 1934), these ants do not excavate a nest, like other ants, but use preformed large cavities such as abandoned nests of lizards or of small marsupials. At least some species have a special worker subcaste functioning as honey-storers, a unique feature among Dolichoderinae. Moreover, these ants walk bearing the gaster bent forward over the trunk and they never leave the nest in files, only individually.

If we can assume that the *L. neotropicus* specimens were not embedded by resin into the nest, the presence of so many individuals (9) into such a small volume of amber (the original amber piece measured less than 10 cm³ and the ants occupied only the superior part of it), forces us to postulate the existence of some kind of column or trail on which the insects have been covered together by resin. I already mentioned (see p. paratypes) the possible presence of a pupa among the available specimens and this fact could account for a nest migration behaviour during which, of course, several workers run together around the brood.

Biogeography: The known distribution of *Leptomyrmex* is given in Fig. 6. It is easy to see that all the living species are confined to the Papuan, New Caledonian, and Queensland coastal biogeographic provinces (nomenclature according to UD-VARDY, 1975). There is no doubt that at least the Australian populations of the genus represent a very old settlement as is proved by the presence, in Queensland, of a species of spider which mimics *L. erythrocephalus* by curving its abdomen upwards and forwards exactly as the ants do with their gaster (TURNER, 1898). Moreover, in New South Wales, RAINBOW (1898) reports a Misumenine spider specialized in feeding only on *L. erythrocephalus*.

WHEELER (1915: 262) already postulated a very wide former distribution of the Leptomyrmicini, probably with many different genera, in the Old World. Now we can extend this past distribution to the New World, too, but the fossils still indicate a high morphological uniformity.

On the other hand, it is less clear if the Australian region is really the centre of origin of the Leptomyrmicini as WHEELER supposed. By having apterous queens, *Leptomyrmex* species are less subject to passive dispersal than other ants. This had already been noted by WHEELER (l. c.) who added that „the genus could only have reached its present distribution at a time when land connections existed between New Guinea, Australia and New Caledonia“. Now, however, by adding the Caribbean area to this list of formerly connected lands, will force us to date back the origin of *Leptomyrmex* to a time possibly anterior to the origin of the whole family Formicidae. It is much safer to postulate a cosmopolitanism or tropicopolitanism until Miocene times and a postmiocenic contraction of the distribution. Hence, even the Australian origin of the genus remains doubtful (see below).

The Leptomyrmicini have no close relatives among other known fossil or Recent Dolichoderinae, but, eventually, the Neotropical *Dolichoderus* s. str. are better comparable with them than any other ant for their elongated trunk and appendages.

The Recent Dolichoderinae comprise 22 genera (by excluding *Aneuretus* and considering *Hypoclinea* as a good genus) and the highest generic concentration is in the Neotropical and Australian regions with 10 genera each. Now, with the discovery of *L. neotropicus*, the total number of Neotropical Dolichoderinae genera amounts to 11 and the Australian region loses the exclusiveness of one of its more

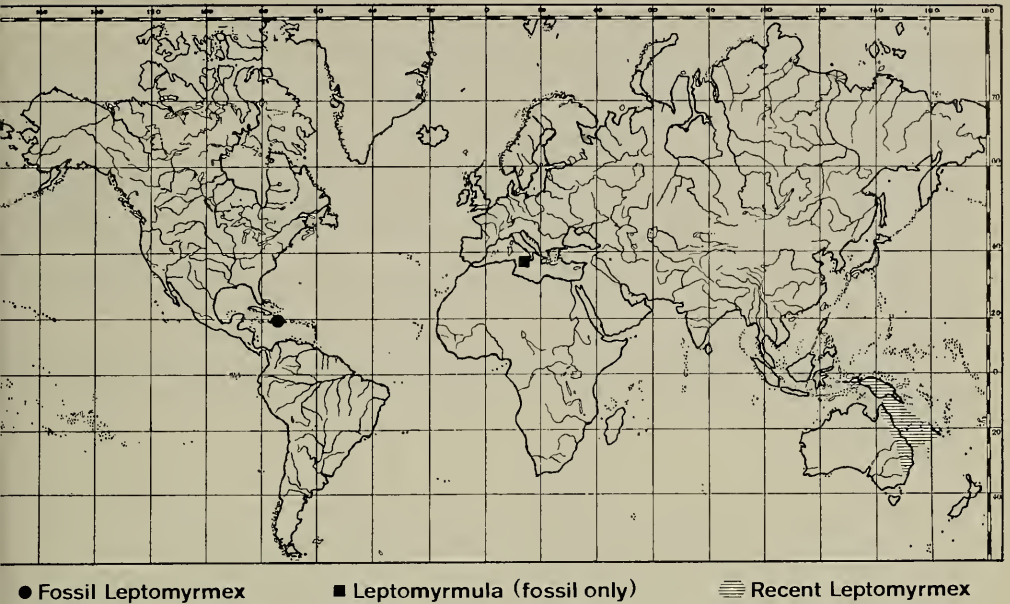


Fig. 6. Known distribution of Recent and fossil Leptomyrmecini.

spectacular peculiarities. Although drawing a concluding statement on this matter would be premature, the Neotropical region shows at least three indications for being the potential center of origin for the Leptomyrmecini: 1. The oldest known fossil for the whole tribe (*L. neotropicus*). 2. The presence of the most probable closest living relative of *Leptomyrmex* (i.e. *Dolichoderus*). 3. The highest generic diversity of *Dolichoderinae*.

This record of *Leptomyrmex* in the Neotropical region brings additional evidence for a faunal relationship between South America and Australia. At least in ants such a relationship is quite evident in the Recent fauna. For instance, of the 146 genera present in the Neotropical fauna according to KEMPF (1972), 37 live in Australia, too. Four of these genera (*Heteroponera*, *Rogeria*, *Rhopalothrix*, and *Glamyromyrmex*) are known only from Australia and South America. On the contrary, for instance, only 29 genera are common to the Neotropical and Afrotropical¹⁾ regions and none of them is known only from these two regions. *Leptomyrmex neotropicus* gives additional weight to this distributional pattern, although it does not help in explaining it.

In fact, such distributions are not uncommon among other animals, and JEANNEL (1942) gives a list of several insect groups showing them. MÜLLER (1977) adds other examples and SCHMINKE (1974), on the basis of Bathynellia crustacea, reaches the same conclusion of JEANNEL, i.e. that such a distribution pattern could have been attained only during Lower Cretaceous times. However, although I am unable to give a better explanation, the ant case cannot endorse the JEANNEL-SCHMINKE hypothesis. In fact, the oldest known fossil Formicoidea date back to Upper Cretaceous and none of them belongs to the Family Formicidae or, at least, to the living subfamilies included in it (DLUSSKY in RASNITSYN, 1975, and DLUSSKY, paper in preparation). According to a still unpublished phylogenetic reconstruction of the

¹⁾ The term Afrotropical is used here in the same sense as Africotropical of UDVARDY (1975) and preferred to the latter for purely euphonic reasons.

Formicidae evolution kindly provided by Dr. G. M. DLUSSKY and on which I largely agree, the sole known Mesozoic Formicidae belong to the extinct subfamily Aidomyrmicinae DLUSSKY, while the Sphecomyrminae are not the stem group of Recent Formicidae. It is quite clear, hence, that *Leptomyrme* cannot have attained its distribution prior to the appearance of its direct ancestor.

The distribution of *Leptomyrme* is paralleled by that of chelyid turtles which occur only in the fresh waters of South America and Australia and by the distribution of meiolaniid turtles, extinct giant land turtles known from South America (late Cretaceous and Eocene) and eastern Australia, Lord Howe, and Walpole islands (Pleistocene). These distributions have been commented on by several students (see, among others, SIMPSON, 1943) who have been forced to postulate that some unknown way of passive dispersal must be responsible for them.

If transoceanic dispersal can account for such disjunct distributions of heavy fresh water and land turtles, the same explanation can surely fit the case of the tiny *Leptomyrme*, too.

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