New *Technomyrmex* in Dominican amber (Hymenoptera: Formicidae), with a reappraisal of Dolichoderinae phylogeny

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A new species of *Technomyrmex* (*T. caritatis* sp. n.) is described based on workers and larvae from Dominican amber (Oligocene to Lower Miocene). These are preserved with eggs and pupae of the same species and with five other insects in one amber piece found in the Palo Quemado Mine, near Santiago and in two separate amber pieces collected in Carlos Diaz Mine. Both mines are in Cordillera Septentrional. *Iridomyrmex hispaniolae* Wilson is redescribed and transferred to *Technomyrmex*. Most *Technomyrmex* species occur from Africa, east through southern Asia, to Australia. One species transported by human activity is known in the New World and there is only one extant native Neotropical species recorded from Panama. *Technomyrmex* likely represents a case of an Old World ant genus undergoing extinction in the New World. We discuss the affinities of this genus with the extant Dolichoderinae and the phylogeny of the subfamily.

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Introduction

Dominican amber is referred to the lower part of Early Miocene, corresponding to some 20-23 million years B. P. or, less conservatively, to the Oligocene to Lower Miocene – 40 to 15 million years B. P. (Poinar 1992), or else from around mid-Oligocene (circa 30 millions years ago) to the early Miocene (Grimaldi 1996, but see Iturralde-Vinent & MacPhee 1996). Ants represent the numerically dominant group of insects in Dominican amber as they are in most present terrestrial ecosystems (Baroni Urbani & Saunders 1982). After the description of fossil army ants (Wilson 1985b), the Dominican amber fossils span most of the major Recent Formicidae groups. No species preserved in Dominican amber are living today, although they show great similarities with their extant rela-

tives (Baroni Urbani & Saunders 1982). Almost all ant genera found in Dominican amber, however, are extant. Extinct are the myrmicine genera *Ilemomyrmex, Oxyidris,* and a new genus near *Rogeria* (Wilson 1985a, d), and a new genus of Dolichoderinae (De Andrade, in prep.; Baroni Urbani 1995). The Dominican amber genera are not always found today in the Dominican Republic, in the Antilles, or even in the Neotropical Region. For instance, Baroni Urbani (1980) described a Dominican amber Dolichoderinae species, *Leptomyrmex neotropicus,* belonging to a genus confined today to the Indo-Australian region (see Baroni Urbani & Wilson 1987). It is of special interest then to record two *Technomyrmex* species in Dominican amber. *Technomyrmex* is an essentially an Old World genus known in the New World only

from one endemic species (*T. fulvus*) and its sub-species (*T. fulvus sublucidus*), both recorded only from Barro Colorado, Panama. The majority of the species occur from Africa, east through southern Asia, to Australia. There is also one species (*T. albipes*) that is widely distributed by human activity recorded in Florida, California, in the U.K. and in several Pacific Islands (Shattuck 1992a).

Brown (1973) suggested that Myrmicinae is the expanding world-dominating ant taxon at the expenses primarily of the Dolichoderinae, 'which are contracting toward the periphery of the ant-inhabited world. The Formicidae appear to be holding their own'. He pointed out that in Baltic amber (Wheeler 1915) and Florissant ant faunas (Carpenter 1930), the Dolichoderinae represent 64% and 63% of the specimens respectively, whereas the Myrmicinae represent 5% or less. He compared this pattern with the modern distribution, suggesting a massive replacement of the Dolichoderinae primarily by genera of the Myrmicinae in the Northern Hemisphere since the Miocene.

Wilson (1985a, b, c) described several fossil Dominican ant species, including nine Dolichoderinae, and discussed the complete disappearance of several lineages of this subfamily from the Greater Antilles. He suggested that the general decline of Dolichoderinae in North and Central Americas, Europe, and Asia is possibly correlated with the advance of *Crematogaster* as a competitor of *Linepithema, Iridomyrmex* and other smaller genera (Shattuck 1992b).

In one of the above cited papers, Wilson (1985c) described *Iridomyrmex hispaniolae*, based on 46 workers found in 32 Dominican amber pieces from several mines. These specimens were reexamined during study of a piece of amber found in the Palo Quemado Mine that includes part of a dolichoderine colony, as well as several amber pieces from different mines in the Dominican Republic. Results of this study indicate that all of the inclusions belong to *Technomyrmex* Mayr, based on the generic definition proposed by Shattuck (1992a).

The only other part of a fossil ant colony described until now is that of the formicine *Oecophylla leakeyi* (Wilson & Taylor 1964). At least 366 individuals represented by 438 fragments were collected together in a volume of matrix about 2 square feet and several inches thick. This originated from a Lower Miocene Deposit of Mfwangano Island, near Rusinga Isl. in the Kavirongo Gulf neighbourhood of Lake Victoria, Kenya. The sedimentary nature of the matrix did not allow behavioural inferences. In the present case, however, the ant workers were carrying the immatures when caught by the resin. The amber sample contains the first fossil ant eggs and fossil pupae of the Dolichoderinae. Schlee (1990) presented a figure of a Dolichoderinae larva carried by a worker of the same species described as new in this paper and the same picture was reproduced by Grimaldi (1996).

Material and methods

The specimens described in this paper are from an amber fragment known as 'Jorge Caridad' (Fig. 1) belonging to the Museo de la Ciència, Fundació 'la Caixa', Barcelona, Spain. For comparative purposes we studied several other amber pieces, which will be discussed in the appropriate sections.

The amber fragment was found by Jorge Caridad in 1995 in the Palo Quemado Mine, about 10 Km NE of Santiago, Cordillera Septentrional, Republica Dominicana, and includes in a single layer 92 individuals of a dolichoderine species (eggs, larvae, pupae and workers). There are other more badly preserved ant specimens at the boundaries of the piece, presumably of the same species described below. In a different layer there is an alate of an unidentified headless myrmicine ant and the metasoma and hind legs of a worker of another unidentified Myrmicinae. Two wingless Thysanoptera, a badly preserved Mantodea nymph, and a dipteran are also embedded in the same piece.

We tested the hypothesis that our specimens might belong to an undescribed genus because the species we describe below exhibits a previously unrecorded mixture of characters, according to Shattuck (1992a, 1995).

Our task was greatly facilitated by the recent monographic revision of the Dolichoderinae by Shattuck (1992a) and by the phylogenetic analysis of the same group of ants by Shattuck (1995). The characters used for our work are derived nearly exclusively from these two papers.

We made several changes to the coding and weighting of the characters used by Shattuck (1995). In the matrix of Shattuck (1995), all polymorphic characters were coded as unknown. When an unknown character state is encountered by the algorithm searching for the shortest tree(s), it is as-
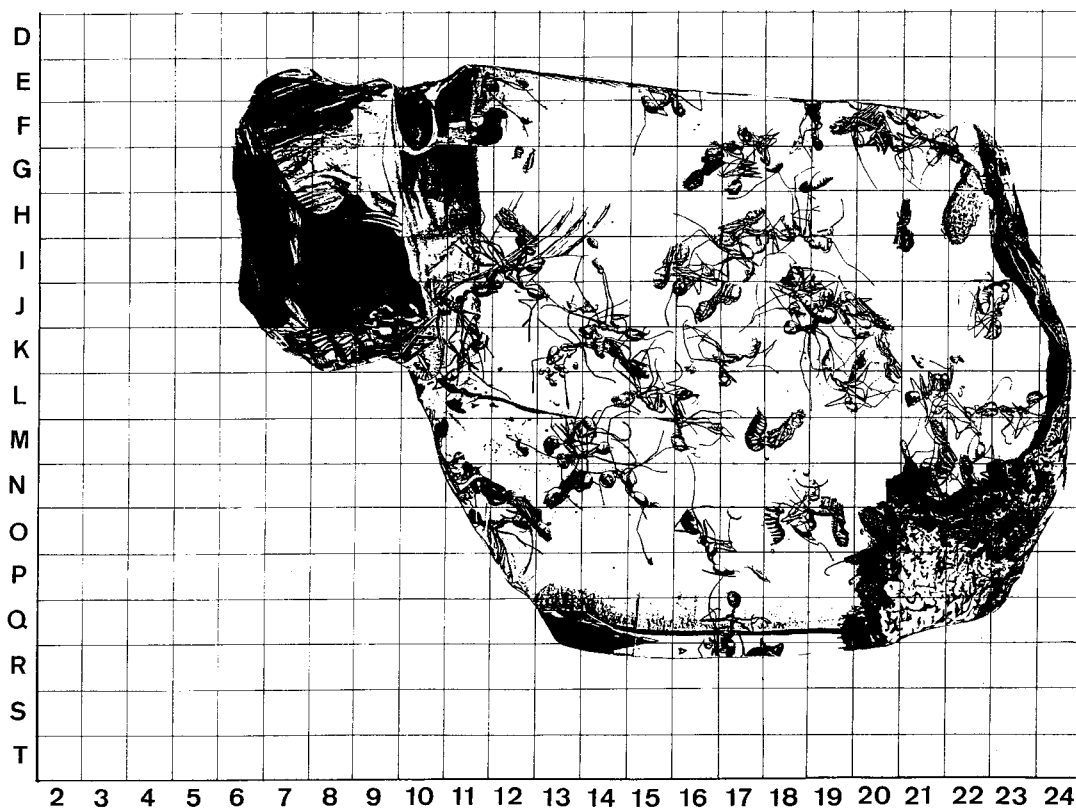
Fig. 1. The 'Jorge Caridad' amber piece fragment MCCB 0060 (Museo de la Ciència, Fundació 'la Caixa', Barcelona, Spain), with the superimposed grid to identify individual specimens.

sumed to be in the most parsimoniously optimized state. We reanalysed the original data matrix and substituted polymorphic states coded as unknown by Shattuck (1995) with the actual polymorphic character states. All the information necessary to make these changes was derived from Shattuck (1992a) and from a few additional references that are cited in the descriptions of the relevant characters. For instance to account for polymorphisms we coded as 1&2&3 when Shattuck (1992a) stated that a character varies from state 1 to state 3, and as 1&3 when the character is either 1 or 3. For the few characters we changed in respect to Shattuck (1992a), we justify the changes in the character description of the appendix. Polymorphism among the outgroups has been assessed by examining the following taxa: *Camponotus (C.) pennsylvanicus* (worker, gynes, male – USA), *C. (Myrmothrix) cingulatus* (w, g, m – Brazil), *C. (Tanaemyrmex)*

lespesii (w, g, m – Brazil), *C. (Myrmobrachys) trapezoideus* (w, g, m – Brazil); *Formica reflexa* (w, g, m – USA) and *F. ciliata* (w, g, m – Mexico); *Melophorus bagoti, M. constans, M. aeneovirens, M. aesopus, M. candidus, M. curtus, M. iridescens, M. ludius, M. pillipes, M. turneri,* and *M. wheeleri* [only workers – several Australian localities (*Melophorus* gynes were not recoded due to the lack of sufficient material, but for *M. constans* Santschi (1928) presented information on characters 33 and 40, both recoded as 3)]; *Paratrechina fulva* (w, g, m – Brazil) and *P. longicornis* (w, g – Mexico).

All 89 characters coded as ordered by Shattuck (1995) were coded as non additive. We do not believe that our understanding of ant evolution is sufficient to trace an evolutionary sequence for these characters. We also included in the analysis *Ecphorella*, which although known from a few speci-

mens, permits coding of most of the characters considered by Shattuck (1995).

For our final analysis, we added three new characters of presumed phylogenetic significance (characters 105-107, see Appendices 1 and 2). In addition, several characters used by Shattuck (1995) to infer the Dolichoderinae phylogeny are used three times, once for workers, once for gynes and once for males. This is the best method to avoid loss of information when a different caste or sex possesses a different character state. However, this results in the characters in question receiving a weight 2 or 3 respectively when two or three castes/sexes are invariant. To counter this difficulty we weighted as 2 all caste/sex dependent-characters, and 6 and 3, respectively, all characters that appeared only once or twice in the original matrix of Shattuck (1995). This has been done because the software we used [PAUP 3.1.1 (Swofford 1993)] does not accept real numbers, and 2, 3 and 6 are the smallest integers satisfying the weighting requirements.

We used *Aneuretus* and four formicine genera as outgroups as did Shattuck (1995). We are aware that this implies an artificial phylogenetic position for *Aneuretus* that does not result from the data on which the trees are computed.

Cladistic analysis

Search for the shortest tree(s), computation of strict consensus tree(s), and comparisons between trees were performed by PAUP 3.1.1 (Swofford 1993). Because of the relatively high number of terminal taxa (27), we used mathematically approximate heuristic methods, which we employed first in the general (default) settings, and then by random addition of taxa (20 replicates), and by branch swapping by tree bisection-reconnection.

Results

We compared individuals in our amber piece with the specimens Wilson (1985c) had described as *Iridomyrmex hispaniolae* and which were transferred to *Linepithema* by Shattuck (1992b). We also compared them with a figure in Schlee (1980, 1990; also Grimaldi 1996), which obviously represents the same or a very close species. The larvae included in the same piece of amber as workers in the Stuttgart sample show a very characteristic trait (the posterior knob) that is unknown in *Line-*

pithema, but present in *Tapinoma, Technomyrmex* and *Aneuretus* (Wheeler & Wheeler 1976; Wilson et al. 1956). The shape of the petiole narrows the assignation of our specimens to *Tapinoma* or *Technomyrmex*. We assign them to *Technomyrmex* based on the presence of five tergites in the gaster of the best preserved specimens.

However, a preliminary cladistic analysis of the extant Dolichoderinae genera with the addition of a presumed new taxon including only these two amber species, and accepting Shattuck's (1995) set of conditions, resulted in 16 trees, rendering Dolichoderinae paraphyletic. Changing the ordination and weighting of characters, but including the two amber species as a presumed new taxon, we obtained three trees where our proposed taxon appeared as the sister genus of *Technomyrmex*. The fossil species share with extant *Technomyrmex* at least two important characters: five visible tergites in the gaster dorsum, and a posterior protuberance on the larvae, as opposed to all other dolichoderines.

We then decided to include these two species in *Technomyrmex* and propose the new combination below.

The amber specimens dealt with in this paper differ from *Technomyrmex* (as defined by Shattuck 1995) in nine generic level characters (see Appendix 1): 4 – anterolateral clypeal margin posterior to mediolateral region (state 1); 5 – anteromedial clypeal margin entire, without a central notch or concavity of any type (1); 13 – apical tooth of mandibles elongate and much longer than the subapical tooth (3); 16 – dorsal face of the propodeum longer than the declivitous face (1); 18 – petiolar scale present (1); 20 – venter of petiole without a lobe (3); 21 – first gastral tergite projecting anteriorly, but not concealing the petiole in dorsal view (3); 22 – first gastral tergite smooth and without a groove or indentation (1); 24 – gastral compression absent (3).

Technomyrmex hispaniolae (Wilson, 1985) comb. n.

(Figs 2, 3)

Iridomyrmex hispaniolae Wilson, 1985c: 33, fig. 10 (in part).
Linepithema hispaniolae (Wilson): Shattuck 1992b (in part).

Type material. – Holotype: Worker in amber sample MCZ 34775, Museum of Comparative Zoology, Harvard
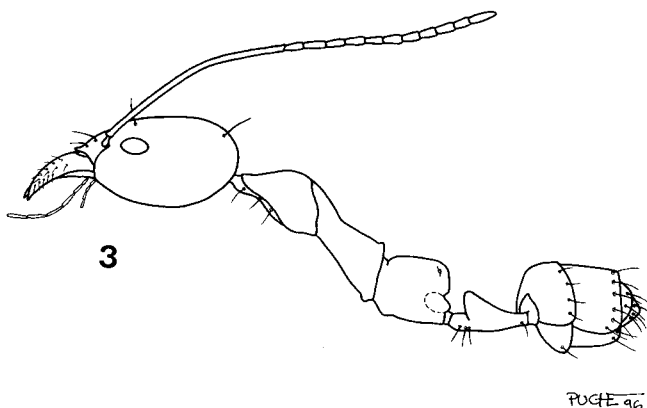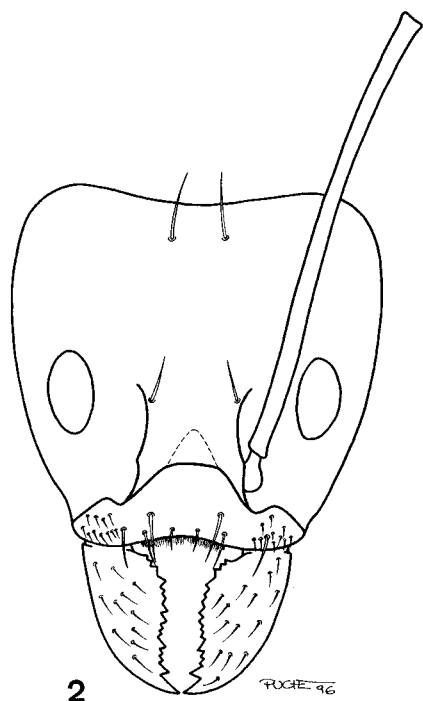
Figs 2-3. *Technomyrmex hispaniolae* (Wilson), holotype worker: (2) head in frontal view, right antenna, left funiculus and palps omitted; (3) head and body in lateral view, right antenna and all legs omitted.

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University, Cambridge, USA, from 'Licey Mine, Dom. Rep'. Paratypes: Thirty-one workers in twenty-one amber pieces as follows: Bayaguana Mine ('Valla Guana', sic): four workers in one piece and two workers, in two pieces; Llaroa Mine: one worker in one piece; the Palo Quemado Mine (Santiago Province – Miocene): two workers in one piece and two workers in two pieces; La Toca ('La Tocas', sic), 'midway Santiago-Puerto Plata, Dom. Rep'., R. Harisson: one worker in one piece; Las Cacaos ('Los Cacao', sic) Mine, Dom. R.: one worker in one piece; Dominican Republic amber (no further information): seven workers in seven pieces; eight workers in four pieces (two in each); and three workers in one piece.

Additional material. – In the collection of the American Museum of Natural History, NY, we found several workers identified as *Linepithema hispaniolae* (Wilson, 1985) by P. Ward, preserved in the following pieces (all labelled AMNH): DR-10-162, two workers; DR-10-172, two workers; DR-10-243, two workers; DR-10-175, one worker; DR-187, four workers; DR-10-149, one worker; DR-10-218, one worker; DR-14-1, three workers; PEP-118-26, one worker. All the above individuals match in every detail the description we give for *T. hispaniolae*. Several pieces with isolated males, also identified as *Linepithema* by P. Ward, could not be confidently associated with this species. The piece DR-14-415 contains two workers, one mature larva, and two dolichoderine males, but their position in the amber did not allow specific identification.

In the Staatliches Museum für Naturkunde, Stuttgart, there is an amber piece containing several additional

workers and larvae of this species, as depicted by Schlee (1980, 1990) and Grimaldi (1996: 90) (not examined).

Description. – Worker (Fig. 3). Pilosity: Clypeus with 2 pairs of long (as long as last funicular joint) and flexible setae at the junction of median area and lateral wings, one smaller pair at the median lateral region, and 6 to 7 even smaller hairs at clypeus lateral wings. Antennal carinae with one pair of long hairs. Mandible with 10 to 12 scattered smaller hairs dorsally. Pronotum antero-lateral dorsal region and mesonotum antero-lateral dorsum without hairs. Front legs with 2 pairs on fronto-lateral areas, one on mid legs and 2 on hind legs. Petiole antero-ventral area with two small hairs and 3 near the postero-ventral margin of petiole. Head (Fig. 2): Clypeus anterior margin concavity continuous without angles; side margins interrupting head profile; posterior margin sinuous at the sides. Labial palps apex reaching the apex of second segment of maxillary palps. Antennal carinae protrusion near the clypeus. Scape surpassing vertex 1.3 times its length. Funicular segments almost two times longer than large. Mesosoma: Metanotum dorsal profile straight and smooth. Petiole: Shorter than in *T. caritatis*. Ventral face continuous, without an angle or indentation at the region

posterior to the node. Measurements: See Wilson (1985c).

Larva (not examined, based on Schlee 1980, 1990 and figure in Grimaldi 1996: 90). Segmentation not as distinct as in the species we describe below. The larval shape is very similar to that of *Technomyrmex (= Engramma) lujae* (see Wheeler & Wheeler 1951: 194): short, stout, plump; body slightly curved, profile sigmoid; somites distinct, anterior dorsal profile formed by the enlarged dorsum of prothorax; diameter approximately one third the straight length. Head subpentagonal, moderately large, protruding, ventral, near anterior end; mandibles triangular in frontal view, base broad, apex sharp-pointed; no neck; abdominal segments tapering to a posterior end terminating in a conspicuous knob directed posteriorly; conoid protuberances distributed over the whole body, each with a flexible hair (the base of the hairs interrupts the profile, and are thus called by us protuberances); no bosses; practically hairless; spiracles clearly visible on abdominal segments 1 to 4.

Comments. – Technomyrmex hispaniolae seems to be one of the most common ant species in Dominican amber, being known from several mines in different localities (see above). Among the several pieces on which Wilson (1985c) based his description of *Iridomyrmex hispaniolae*, the two paratype workers from Carlos Diaz mine's have all characters given in the description of the new species below and thus are considered to belong to the new species.

Taylor (1965) described how the workers of the Panamanian *Probolomyrmex angusticeps* (Ponerinae) carry their larva by a doorknob-like structure protruding from the dorsal surface of the last abdominal segment. They also attach the larvae to the roof of the nest in a bat-like manner with an apparently adhesive outer surface of the knob. All *Technomyrmex* workers that are preserved in amber carrying larvae, hold them by non-terminal abdominal segments.

Technomyrmex caritatis Brandão & Baroni Urbani, **sp. n.**

(Figs 1, 4-6)

Iridomyrmex hispaniolae Wilson: Wilson 1985c (in part).
Linepithema hispaniolae (Wilson): Shattuck 1992b (in part).

Type material. – Holotype: Worker in amber fragment MCCB 0060 (piece 'Jorge Caridad'), numbered 16O (co-ordinates identified according the grid superimposed to specimens; Fig. 1), in the Museo de la Ciència, Fundació 'la Caixa', Barcelona, Spain. Collected in February, 1995 in the Palo Quemado Mine, about 10 Km NE of Santiago, Cordillera Septentrional, Republica Dominicana, by Jorge Caridad. Paratypes: Thirty-four workers, 3 groups of eggs, 31 larvae in different stages of development and 18 pupae, all in the same amber sample as the holotype, preserved in the same amber layer (out of 10 layers recognisable in the sample).

Additional material. – Two workers (paratypes of *Iridomyrmex hispaniolae* Wilson) preserved in 2 amber pieces from Carlos Diaz Mine, near Tamboril, Dominican Republic (see Comments above).

Etymology. – This species is named after Jorge Caridad, the Dominican miner who found the amber piece and also from the Latin *caritas* (= charity) to record the behaviour of the workers embedded in amber, that were most probably taking the colony immatures away from a peril.

Description. – Note: For the reconstruction drawing we used the head profile and gaster of several workers; for the trunk we used the anterior part of 16J (Fig. 1) and the posterior of 18G; for the petiole we used individuals 18N and 16O. Although the specimens are very well preserved only some workers are in a position that afford precise measurements, that is, for which there is no apparent distortion and that have head and trunk axes perpendicular to the amber surface. We used the same grid as above to identify measured specimens, and even then not all measurements were taken from all chosen specimens. Abbreviations and definitions are the standard ones in ant studies, unless stated otherwise.

Worker (Fig. 5). Pilosity: Clypeus with a pair of long (as long as last funicular joint) and flexible setae at the junction of median area and lateral wings, 2 smaller pairs at the median lateral region, and 3 to 4 even smaller hairs at clypeus lateral wings. Antennal carinae with 2 pairs of long hairs. Four to 5 scattered smaller hairs on mandible dorsum. One pair of long on vertex; one on the anterolateral dorsal region of pronotum and one on the antero-lateral dorsum of mesonotum; 3 pairs on fronto-lateral areas of fore legs, one on mid legs and 2 on hind legs. Head (Fig. 4): Clypeus anterior margin concavity marked by angles; side margins not interrupting head profile; posterior margin evenly concave at the sides. Labial palps apex reaching the apex of third segment of maxillary palps. Antennal carinae with a protrusion near the

Figs 4-6. *Technomyrmex caritatis* sp. n., holotype worker and mature larva: (4) head in frontal view, right antenna, left funiculus and palps omitted; (5) habitus in lateral view, right antenna and right legs omitted; (6) mature larva in lateral view.
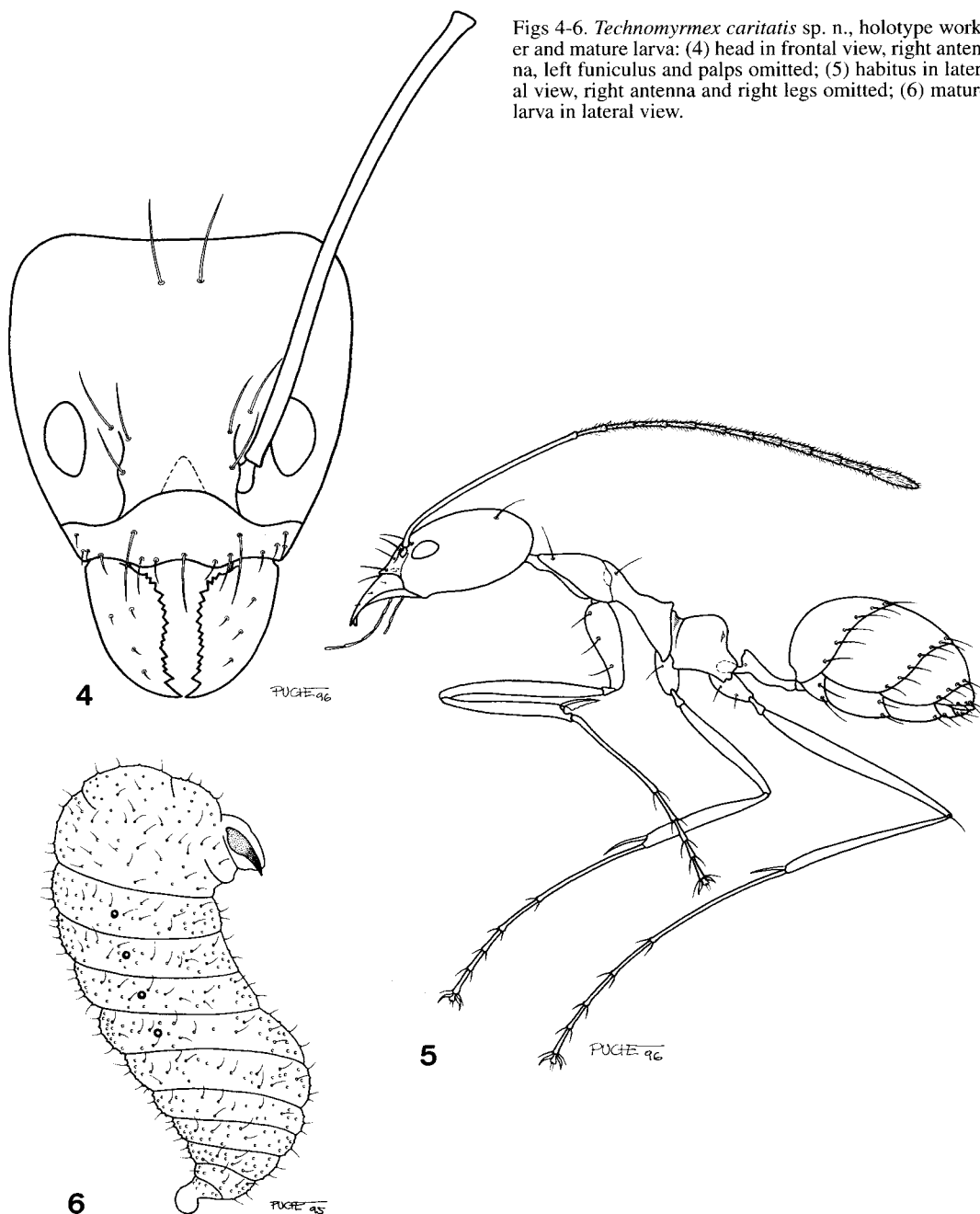
apex. Scape surpassing vertex 1.5 times its length. Funicular segments almost 4 times longer than large. Mesosoma: Metanotum dorsal profile sigmoid, longitudinally striate. Petiole: Very long and slender posteriorly. Ventral face with an angle or indentation at the region posterior to the node. Measurements (in millimetres; codes in parentheses refer to the individual measured; averages are followed in parentheses by the number of individuals measured):
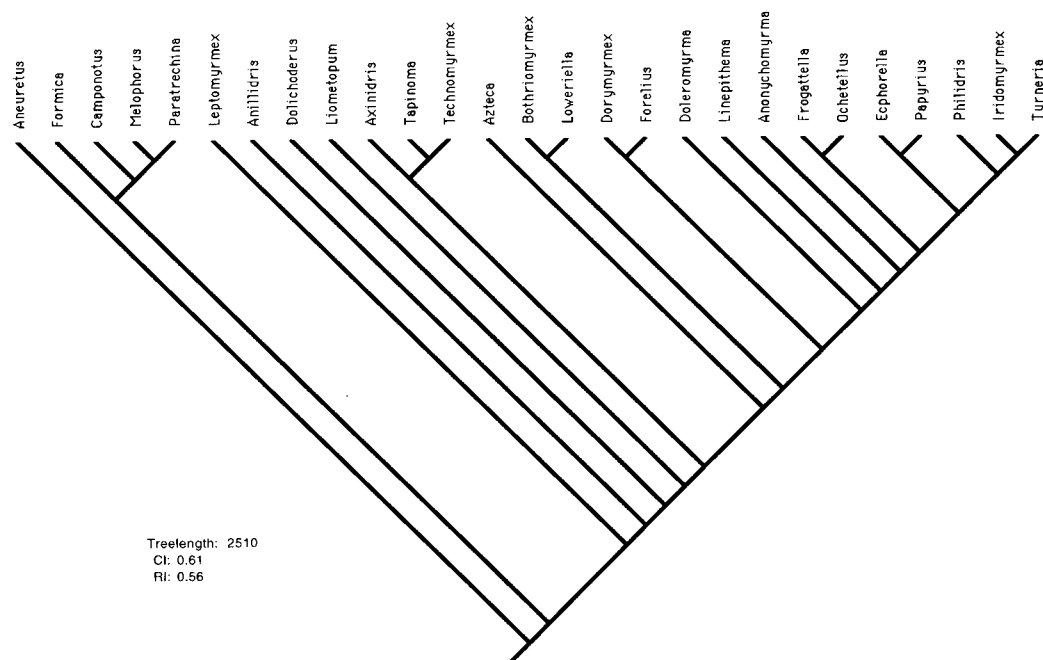
Fig. 7. Unique tree (TL 2510, CI 0.61, RI 0.56) resulting from a reanalysis of all extant genera of Dolichoderinae (incl. *Ecphorella*) and combining data from extant *Technomyrmex* and the presently described Dominican fossils (see Material and methods).

HW – 0.55 (11J); 0.54 (23K). Average 0.55 (2)
HL – 0.55 (11J); 0.73 (16O); 0.51 (16J); 0.62 (19K). Average 0.60 (4)
SL – 0.84 (23K); 0.90 (16O); 0.78 (16J); 0.85 (19K). Average 0.84 (4)
WL – 1.14 (23K); 1.04 (16O); 0.84 (16J); 0.90 (19K). Average 0.94 (4)
MtL (midtibial length) 0.95 (23K); 0.67 (16J); 0.61 (19K). Average 0.74 (3)

Larva (Fig. 6). Segmentation very distinct, particularly in the first seven abdominal segments. Profile marked by 4 – 6 conoid protuberances per segment, apparently more common on dorsal and ventral faces than on the lateral ones; the protuberances are in a straight line in the lateral areas of some segments, whereas in others they are in zig-zag.

Comments. – A group of eggs, a group of small larvae, a large larva or a pupa can be assigned to each worker in 'Jorge Caridad's amber piece. This strongly suggests that the workers were all carrying immatures when trapped in resin. It is also possible to see that mature larvae and pupae were carried either with the anterior end upwards or downwards. This may reflect of course the rush in face of peril (see Wagensberg et al. 1996, 1997).

Technomyrmex caritatis is distinguished from *T. hispaniolae* by the longer funicular segments and by the shapes of the clypeus and petiole. *T. caritatis* is more slender in all characters studied, in special the mesal segment 'waist', that is, seen from the side, *T. caritatis* trunk is much slender and narrower in lateral view than that of *T. hispaniolae*.

Considerations on dolichoderine phylogeny

At a first stage of our study we tried to follow as much as possible the research model of Shattuck (1995). As explained before, we included in the analysis *Ecphorella*, that had been excluded by Shattuck (1995), because he knew of only a single worker. A search for the shortest tree(s) using the modified data matrix that takes into account character polymorphisms, assuming all characters to be nonadditive, giving equal weight to the characters (see Material and methods), and including three new characters and the fossil species described in the present paper, resulted in one tree

(TL 2510, CI 0.61, RI 0.56) (Fig. 7). The ingroup taxa were supported as monophyletic by the following synapomorphies: secondary loss of ocelli, and the petiolar scale inclined posteriorly in the workers, the larvae with reduced neck, sparse hairs, lightly sclerotized mandibles, reduced maxillary palp and galea, and small sericteries, and pupae not enclosed by cocoons. This tree displayed also genus-level phylogenetic relationships closer to the one originally obtained by Shattuck.

Discussion

This paper presents the first record of *Technomyrmex* in Dominican amber and the second fossil record for the genus. The previous record of fossil *Technomyrmex* is from Miocene amber from Sicily (Emery 1891). This genus is common in the Old World tropics but is known from only one rare native species in the New World. The addition of two fossil species in Dominican amber, based on several samples, suggests that the genus was much more common in the Neotropics during the Oligocene-Miocene. To the numerous Old World genera currently extinct in the Neotropical fauna, but recorded in amber, recently listed by Baroni Urbani (1995), the records presented in this paper are likely to suggest that *Technomyrmex* is on the way to extinction in the Neotropics.

Ten out of 31 taxa of Dolichoderinae genera (31%) are extinct. Another 10 (31%) extant genera, with the addition of *Technomyrmex*, are represented in the fossil record. Of the 176 described Myrmicinae genera, only 21 (12%) are extinct and only 18 (10%) extant genera are represented in the fossil record (Bolton 1995). Brown (1973) stated that the Dolichoderinae seem to be retracting from their former dominant status. If we include the very closely related *Aneuretus* with Dolichoderinae in comparison with Myrmicinae, this impression becomes even stronger because only *Aneuretus* is extant, the other four aneuretine genera are extinct.

The consensus tree obtained in our analysis is different in several respects with the phylogeny proposed by Shattuck (1995). Comparing the consensus between our hypothesis and that of Shattuck (1995), *Leptomyrmex* appears as the basal taxon of Dolichoderinae in both analyses, and the following clades appear in common (*Axinidris* (*Tapinoma* + *Technomyrmex*)), (*Bothriomyrmex* + *Loweriella*), (*Dorymyrmex* + *Forelius*) plus the

Formicinae outgroups. We refrain from detailed comparisons of the relative topologies of the two trees because we are convinced that the discrepancies between our results and those of Shattuck are better assessed by considering different or additional characters of presumable phylogenetic relevance.

Acknowledgements

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Appendix 1. List of characters. These are basically the characters used by Shattuck (1995). Changes to some characters have been introduced in all cases of polymorphisms. Other changes to their original definitions and/or coding are explained and preceded by an asterisk (*).

Worker characters

1. Compound eyes (1) absent, (2) with 10-50 ommatidia, (3) with more than 50 ommatidia.
2. Compound eyes (1) relatively posterior on head, (2) relatively anterior on head (coded as unknown ('?') when eyes absent (character 1, state 1).
3. Ocelli (1) present, (2) absent.
4. Anterolateral clypeal margin (1) posterior to the mediolateral region, (2) even with the mediolateral region, (3) with the corners expanded slightly anterior of the mediolateral region.
5. Anteromedial clypeal margin (1) entire, without a central notch or concavity of any type; (2) with a broad, shallow concavity; (3) with a distinct central notch; (4) with a central projection, either pointed or rounded (sometimes only feebly projecting).
*6. Anterior clypeal setae (0) absent, (1) short, less than twice the maximum scape diameter; (2) about the same length as the closed mandibles; (3) long and surpassing the distal edge of the closed mandibles. State 0 added for the Dominican fossil and for some *Tapinoma*, coded then as polymorphic (Shattuck 1992a).
*7. Anterior clypeal setae (1) straight, (2) moderately curved ventrally, (3) strongly curved ventrally (coded as unknown ('?') when setae absent (character 6, state 0), as Shattuck 1995 did for character 2).
8. Posterior clypeal margin (1) even with or anterior to the anterior surface of the antennal condyle, (2) between the anterior and posterior surface of the antennal condyle, (3) even with or posterior to the posterior surface of the antennal condyle.
9. Medial hypostoma (1) entire, (2) notched, (3) absent.

10. Palp formula (1) 6:4, (2) < 6:4.
11. Number of mandibular teeth (1) ≤ 4, (2) 5-10, (3) > 10.
12. Number of mandibular denticles (1) ≤ 3; (2) 4-5; (3) > 5, uniformly distributed along margin; (4) >5, grouped in subsets along margin.
13. Apical tooth of mandible (1) subequal in length to the subapical tooth, (2) slightly longer than the subapical tooth, (3) elongate and much longer than the subapical tooth.
*14. Basal angle of mandible (1) distinct, with a well-developed tooth or angle separating the masticatory and basal margins; (2) weakly defined by a denticle; (3) indistinct, with a relatively uninterrupted curve between the two margins. *Anonychomyrma* and *Doleromyrma* coded as 1 and not as ? (Shattuck, 1992a).
15. Basal margin of mandible (1) smooth and without teeth or denticles; (2) denticulate distally, smooth proximally; (3) denticulate along entire surface.
16. Dorsal face of propodeum (1) longer than the declivitous face, (2) subequal in length to the declivitous face, (3) shorter than the declivitous face.
17. Propodeal spiracle (1) lateral and ventral of the propodeal dorsum, (2) dorsal and medial along the basal propodeal face, (3) dorsal and posterior, near the propodeal angle.
18. Petiolar scale (1) present, (2) reduced, (3) absent.
19. Petiolar scale (1) vertical and not inclined anteriorly, (2) moderately inclined anteriorly but with the anterior and posterior faces approximately the same length, (3) strongly inclined anteriorly and with the anterior face much shorter than the posterior face (coded as 3 when scale absent (character 18, state 3)).
20. Venter of petiole (1) with a well-developed lobe, (2) with a slight or weakly developed lobe, (3) without a lobe.
21. First gastral tergite (1) elongate posteriorly; (2) vertical and not concealing the petiole in dorsal view; (3) projecting anteriorly, but not concealing the petiole in dorsal view; (4) projecting anteriorly and concealing the petiole in dorsal view.
22. First gastral tergite (1) smooth and without a groove or indentation, (2) with a groove or indentation for the reception of the basal portion of the petiole, (3) with a groove or indentation for the reception of the entire height of the petiole.
23. Anterior tergosternal suture of the first gastral segment (1) extending laterally from the helcium, without or with at most a very weak dorsal arch; (2) extending laterally from the helcium in a distinct dorsal arch which has approximately the same height as the helcial dorsum; (3) extending laterally from the helcium in a distinct arch which extends dorsally of the dorsal helcial surface; (4) very weakly developed immediately lateral of the helcium and forming a distinct arch which extends dorsally of the dorsal helcial surface; (5) absent immediately lateral of the helcium and with the lateral section of the suture terminating immediately above the helcium; (6) absent immediately lateral of the helcium and with the lateral section of the suture extending anterodorsally and terminating near the dorsal surface of the gaster.
24. Gastral compression (1) lateral, (2) dorsoventral, (3) absent (gaster circular in cross section).
25. Fourth gastral sternite (1) keel-shaped posteriorly, (2) flat across entire posterior border.
26. Proventricular cupola (1) narrow relative to bulb, (2) slightly broader than bulb, (3) much broader than bulb.
27. Proventricular cupola (1) with long pile, (2) with short pile, (3) without pile.
28. Proventricular cupola (1) with very small phragma; (2) with narrow phragma; (3) with short, lateral phragma; (4) without phragma.
29. Proventricular bulb (1) exposed in lateral view, (2) partially hidden by cupola in lateral view, (3) completely hidden by cupola in lateral view.
30. Proventricular longitudinal muscle No. 1 (1) present, (2) absent.
31. Proventricular occlusory tract (1) present, (2) absent.

Gyne characters

32. Anterolateral clypeal margin (1) posterior to the mediolateral region, (2) even with the mediolateral region, (3) with the corners expanded slightly anterior of the mediolateral region.
33. Anteromedial clypeal margin (1) entire, without a central notch or concavity of any type; (2) with a broad shallow concavity; (3) with a distinct central notch; (4) with a central projection either pointed or rounded (sometimes only feebly projecting).
34. Anterior clypeal setae (1) short, less than twice the maximum scape diameter; (2) about the same length as the closed mandibles; (3) long and surpassing the distal edge of the closed mandibles.
35. Anterior clypeal setae (1) straight, (2) moderately curved ventrally, (3) strongly curved ventrally.
*36. Posterior clypeal margin (1) even with or anterior to the anterior surface of the antennal condyle, (2) between the anterior and posterior surfaces of the antennal condyle, (3) even with or posterior to the posterior surface of the antennal condyle. Based on figures in Shattuck (1992a) we coded *Anonychomyrma* as state 3 (fig. 10), *Axinidris* as 2 (fig. 18), *Iridomyrmex* as 2 (fig. 91) *Tapinoma* as 3 (fig. 144), and *Technomyrmex* as 1 (fig. 152).
37. Palp formula (1) 6:4, (2) < 6:4.
38. Number of mandibular teeth (1) ≤ 4, (2) 5-10, (3) > 10.
39. Number of mandibular denticles (1) ≤ 4; (2) > 4, uniformly distributed along margin; (3) > 4, grouped in subsets along margin.
40. Apical tooth of mandible (1) subequal in length to the subapical tooth, (2) slightly longer than the subapical tooth, (3) elongate and much longer than the subapical tooth.
41. Basal angle of mandible (1) distinct, with a well-developed tooth or angle separating the masticatory and basal

margins; (2) weakly defined by a denticle; (3) indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle.

42. Basal margin of mandible(1) smooth and without teeth or denticles; (2) denticulate distally, smooth proximally; (3) denticulate along entire surface.
43. Episternal suture (1) complete, (2) complete bur weakly developed anteriorly, (3) weak, nearly absent.
44. Axilla (1) parallel, (2) constricted medially, (3) absent dorsally.
45. Axilla (1) entire, (2) with a suture medially.
46. Anterior axillar suture (1) straight, (2) angular medially.
47. Dorsal face of propodeum (1) longer than the declivitous face, (2) subequal in length to the declivitous face, (3) shorter.
48. Radial cell (1) closed, (2) open.
49. Number of forewing cubital cells (1, 2).
50. Number of forewing discoidal cell, (0, 1, 2).
51. Number of hindwing cells (0, 1, 2, 3).
52. Petiolar scale(1) present, (2) reduced.
53. Petiolar scale (1) vertical and not inclined anteriorly, (2) moderately inclined anteriorly but with the anterior and posterior faces approximately the same length, (3) strongly inclined anteriorly and with the anterior face much shorter than the posterior face.
*54. Petiole (1) with a well-developed, rounded lobe, (2) with a slight or weakly developed lobe, (3) without a lobe, (4) with a well-developed, angular lobe. Based on figures in Shattuck (1992a) we coded *Dorymyrmex* as 1&2 (fig. 68), *Iridomyrmex* as 1&2 (fig. 94, female), and *Tapinoma* as 1&2 (fig. 145).
55. First gastral tergite (1) elongated posteriorly; (2) vertical and not concealing the petiole in dorsal view; (3) projecting anteriorly, but not concealing the petiole in dorsal view; (4) projecting anteriorly and concealing the petiole in dorsal view.
56. First gastral tergite (1) smooth and without a groove or indentation, (2) with a groove or indentation for the reception of the basal portion of the petiole, (3) with a groove or indentation for the reception of the entire height of the petiole.

Male characters

57. Scape length (1) shorter than the length of funicular segments 2 + 3, (2) at most only slightly longer than the length of funicular segments 1 + 2 + 3, (3) much longer than the length of funicular segments 1 + 2 + 3 but not exceeding the occipital border, (4) much longer than the length of funicular segments 1 + 2 + 3 and exceeding the occipital border.
58. First funicular segment (1) cylindrical or cone-shaped, (2) barrel-shaped.
59. Second funicular segment (1) straight, (2) with a lateral bent.
60. Anteromedial clypeal margin (1) entire, without a central notch or concavity of any type; (2) with a broad, shallow concavity; (3) with a distinct central notch; (4) with a central projection, either pointed or rounded (sometimes only feebly projecting).
61. Anterior clypeal setae (1) short, about as long as the maximum diameter of the scape; (2) about the same length as the closed mandibles; (3) long and surpassing the distal edge of the closed mandibles.
62. Posterior clypeal margin (1) even with or anterior to the anterior surface of the antennal condyle, (2) between the anterior and posterior surfaces of the antennal condyle, (3) even with or posterior to the posterior surface of the antennal condyle. Based on figures in Shattuck (1992a) we coded *Dolichoderus* as 2 (fig. 53), *Linepithema* as 1 (fig. 108), and *Ochetellus* as 2 (fig. 125).
63. Palp formula (1) 6:4, (2) < 6:4.
64. Number of mandibular teeth (1) ≤ 4, (2) 5 – 10, (3) > 10.
65. Number of mandibular denticles (1) ≤ 5, (2) > 5.
66. Apical tooth of mandible (1) absent (tip of mandible rounded and without a differentiated tooth), (2) distinct and shorter than subapical tooth, (3) subequal in length of subapical tooth, (4) slightly longer than subapical tooth, (5) elongate and much longer than subapical tooth.
67. Basal angle of mandible (1) distinct, with a well-developed tooth or angle separating the masticatory and basal margins, (2) weakly defined by a denticle, (3) indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle.
68. Basal margin of mandible (1) smooth and without teeth or denticles, (2) denticulate distally, smooth proximally, (3) denticulate along entire surface.
69. Axilla (1) parallel or subparallel, (2) constricted medially, (3) absent dorsally.
70. Axilla (1) entire, (2) with a suture medially.
71. Anterior axillar suture (1) straight, (2) angular medially.
72. Dorsal face of propodeum (1) longer than the declivitous face, (2) subequal in length to the declivitous face, (3) shorter.
73. Radial cell (1) closed, (2) open.
74. Number of forewing cubital cells (0, 1, 2).
75. Number of forewing discoidal cells (0, 1, 2).
76. Number of hindwing cells (0, 1, 2).

77. Petiolar scale (1) vertical and not inclined anteriorly, (2) strongly inclined anteriorly and with the anterior face much shorter than the posterior face.
78. Venter of petiole (1) with a well developed lobe, (2) with a slight or weakly developed lobe, (3) without a lobe.
79. Attachment of petiole to gaster (1) narrow, (2) intermediate, (3) broad.
80. First gastral tergite (1) elongated posteriorly, (2) vertical and not concealing the petiole in dorsal view, (3) projecting anteriorly, but not concealing the petiole in dorsal view, (4) projecting anteriorly and concealing the petiole in dorsal view.
81. First gastral tergite (1) smooth and without a groove or indentation, (2) with a groove or indentation for the reception of the basal portion of the petiole, (3) with a groove or indentation for the reception of the entire height of the petiole.
82. Pygostyles (1) present; (2) present, reduced; (3) vestigial or absent.
83. Posterior margin of subgenital plate (1) convex, (2) even across entire width, (3) concave, (4) with a 'V'-shaped notch.
84. Paramere (1) divided by a membranous region, (2) entire.
85. Digitus (1) linear, without a down-turned tip; tip sometimes slightly swollen; (2) linear, with a slight ventral arch; (3) with a down-turned tip.
86. Cuspis (1) parallel with digitus, (2) ventral of digitus, (3) absent.
87. Ventral lobe of volsella (1) present as a swelling, (2) present as concave lobe, (3) absent.
88. Aedeagus (1) with teeth ventrally, (2) without teeth ventrally.

Subfamily-level characters
(defined as such by Shattuck 1995)

89. Worker. Hind coxal cavities (1) open, (2) closed. *Aneuretus* coded as 1&2 as in Baroni Urbani et al. (1992).
90. Worker. Anterodorsal margin of helcium (1) excised, (2) entire.
91. Worker. Lateral regions of helcium sternite (1) retracted posteriorly relative to lateroventral helcium tergite and with sternite and tergite fusion occurring for a length less than one half tergite length, (2) approximately the same length as lateroventral helcium tergite and with sternite and tergite fusion occurring for a length greater than one half tergite length.
*92. Worker. Pygidial (= anal) gland (1) present, (2) absent. Coded as '?' for *Ecphorella*, as the holotype and unique specimen has never been dissected (Shattuck 1992a).
*93. Worker. Cyclopentanoid monoterpenes (1) present, (2) absent. Recoded after Attygalle & Morgan (1984), but for *Aneuretus* (Wilson et al. 1956) and *Bothriomyrmex* (Forel 1878: 381 'Contenu des vessies anales inodore et ne changeant pas à l'air').
94. Worker. Acidopore (1) present, (2) absent.
95. Worker. Formic acid production (1) present, (2) absent.
*96. Worker. Sting (1) fully developed, (2) reduced and non-functional. Coded as '?' for *Ecphorella*, as the holotype and unique specimen has never been dissected (Shattuck 1992a).
*97. Worker. Furcula (1) free from sting base, (2) fused with sting base. Coded as '?' for *Ecphorella*, as the holotype and unique specimen has never been dissected (Shattuck 1992a).
*98. Larval neck (1) well-defined, (2) reduced. Coded as '?' for *Anillidris*, *Axinidris*, *Ecphorella* and *Loweriella*, as the larvae are unknown, and *Doleromyrma* larvae were not examined (Shattuck 1992a).
*99. Larval hairs (1) abundant, (2) sparse. Coded as '?' for *Anillidris*, *Axinidris*, *Ecphorella* and *Loweriella*, as the larvae are unknown, and *Doleromyrma* larvae were not examined (Shattuck 1992a).
*100. Larval mandibles (1) heavily sclerotized, (2) lightly sclerotized. Coded as '?' for *Anillidris*, *Axinidris*, *Ecphorella* and *Loweriella*, as the larvae are unknown, and *Doleromyrma* larvae were not examined (Shattuck 1992a).
*101. Larval mandibles with (1) three teeth, (2) less than three teeth. Coded as '?' for *Anillidris*, *Axinidris*, *Ecphorella* and *Loweriella*, as the larvae are unknown, and *Doleromyrma* larvae were not examined (Shattuck 1992a).
*102. Larval maxillary palp and galea (1) paxilliform, (2) reduced to sensilla. Coded as '?' for *Anillidris*, *Axinidris*, *Ecphorella* and *Loweriella*, as the larvae are unknown, and *Doleromyrma* larvae were not examined (Shattuck 1992a).
*103. Larval sericteries (1) wide, (2) small. Coded as '?' for *Anillidris*, *Axinidris*, *Ecphorella* and *Loweriella*, as the larvae are unknown, and *Doleromyrma* larvae were not examined (Shattuck 1992a).
*104. Pupal cocoons (1) present, (2) absent. Coded as '?' for *Anillidris*, *Axinidris*, *Ecphorella* and *Loweriella*, as the pupae are unknown, and *Doleromyrma* pupae were not examined (Shattuck 1992a).

New characters added for this analysis

105. Larval segmentation well marked (1), or superficial and poorly visible (2). Most larvae coded after Wheeler & Wheeler (1951, 1966, 1976) and Wilson et al. (1956). Coded as '?' for *Anillidris*, *Axinidris*, *Ecphorella* and *Loweriella*, as the larvae are unknown, and *Doleromyrma* larvae that were not examined (Shattuck 1992a).
106. Posterior or posterodorsal larval knob absent (1) or present (2). Most larvae coded after Wheeler & Wheeler (1951, 1966, 1976) and Wilson et al. (1956). Coded as '?' for *Anillidris*, *Axinidris*, *Ecphorella* and *Loweriella*, as the larvae are unknown, *Doleromyrma* larvae were not examined, and *Dorymyrmex* coded '?' since it has a posterior subcone but no true knob (Shattuck 1992a).
107. Worker. Gaster with 4 apparent tergites (1), or 5 apparent tergites (2).

Appendix 2. Matrix of characters (see Appendix 1) for all genera considered by Shattuck (1995), and four Formicinae genera, including the weighting of characters as explained in Material and methods.

character weights	6	6	6	3	2	2	3	2	6	2	2	2	2	2	2	2	6	6	2	2	2
taxa/characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Aneuretus	3	2	1	2	2	1	?	3	1	2	2	4	2	1	1	3	1	1	1	3	2
Camponotus	3	1	1	1&2	1&2&4	1	1&2	1	1	1	2	1	2	1	1	1	1	1	1	2&3	2
Formica	3	1	2	1	1	1	1	1	1	1	2	1	1	1	1	2	1	1	1	2	2
Melophorus	3	1	1&2	1&2	1	2	3	1	1	1	2	1	3	1	1	3	1	1	3	2	2
Paratrechina	3	2	1	1	1	2	2	1	1	1	2	1	2	1	1	3	1	1	3	2	4
Anillidris	1	?	2	2	1	1	2	3	2	2	1	1	1	1	1	2	1	1	3	2	?
Anonychomyrma	3	2	2	1&2	1	1	1	2	1	1	2	1&2	2	1	3	1&2	2	1	1&2	1&2&3	2
Axinidris	3	2	2	2	3	2	2	2	1	1	2	1	1	3	3	1&2	1	1	3	3	3
Azteca	3	2	1	2&3	1	2	1	2	1	1&2	2	1	1	1	1&2&3	1	2	1	3	1	2
Bothriomyrmex	2	2	2	2	1&2	2	2	1	3	2	2	1&2	2	1	3	3	1	1	2&3	1	4
Doleromyrma	3	2	2	2	1	1	2	2	1	1	1&2	2	2	1	2	3	1	1	2	1	3
Dolichoderus	3	1&2	2	1&2	1&2	1	1	3	1	1	3	1	1	2&3	3	2	1	1	2	3	2
Dorymyrmex	3	2	2	2	1	3	3	2	1	1	2	1	3	1	1&2&3	1&2&3	1	1&2	2&3	2	2
Ecphorella	3	2	3	3	1	1	1	2	1	2	2	1	3	?	?	2	3	1	3	1	2
Forelius	3	2	2	2	1	2	2	2	1	1	2	1	1&2&3	1	1	1&3	1	1&2	3	1	4
Froggattella	3	2	2	1	4	1	1	3	1	1	2	1	1	2	2	1	3	1	3	2	2
Iridomyrmex	3	1	2	1	4	1	1	2	1	1	2	1&2	2&3	1&2&3	2	1&2	1	1	3	1&3	2
Leptomyrmex	3	2	2	2	1	1	1	1	2	1	2&3	3	2	2	2	1	1	1	3	2&3	1
Linepithema	3	2	2	2	2	1	1	2	1	1	2	4	3	1&2	2	2	1	1	2&3	1&2	2
Liometopum	3	2	1	3	2	1	1	3	1	1	2	1	1	3	3	2	1	1	1	2	2
Loweriella	2	2	2	2	1	2	1	1	3	1	2	1&2	3	2	1	3	1	1	3	1	3
Ochetellus	3	2	2	2	2	1	1	3	1	1	2	1	2	1	2	3	1	1	1	2&3	2
Papyrius	3	2	2	1	2	1	1	2	1	2	3	1	3	2	1	2	1	1	3	1	2
Philidris	3	2	1	1	4	1	1	2	1	1	3	1	2	2	2	2	1	1	3	1	2
Tapinoma	3	2	2	2	1&2&3	0&1&2	1&2	2	1	1	1&2	3	1&2	3	2&3	3	3	1	3	2	4
Technomyrmex	3	2	2	2	2&3	0&1&2	1	1&3	1	1&2	1&2	1&2&3	1&2	2&3	1&2&3	2&3	1	1&2&3	3	2&3	3&4
Turneria	3	1	2	1&3	1&2	1&2	1	2	1	1	2	3	2	2	3	1&2	3	1	3	1	2

taxa/characters	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
character weights	6	6	6	6	6	6	6	6	6	6	3	2	2	3	2	2	2	2	2	2	2	6
Aneuretus	1	1	2	1	1	3	4	1	1	2	2	2	1	1	3	?	2	3	2	1	1	1
Camponotus	1	1	3	2	1	1	4	1	1	1	1&2	1&2&4	1	1	1	1	2	1	2	1	1	1
Formica	1	1	3	2	1	1	4	1	2	1	1	—	1	1	1	1	2	1	2	1	1	1
Melophorus	1	1	2	2	1	1	4	1	1	1	1	3	2	3	2	1	2	1	3	1	1	1
Paratrechina	3	5	3	2	1	?	4	1	?	?	1	1	1	1	1	1	2	1	2	1	1	1
Anillidris	?	?	?	?	?	?	?	?	?	?	2	1	1	1	3	2	2	1	2	1	1	1
Anonychomyrma	2	1	3	1	3	2	3	3	?	2	3	1	1	1	3	1	2	1	2	1	2	2
Axinidris	2	5	2	2	?	?	?	?	?	?	2	3	1&2	1	2	1	2	1	2	?	?	1
Azteca	2	1&2&3	1&2&3	1	2	2	4	1	1	1	2&3	1&2	1&2	1	2	1&2	2	1	1&2	1	1&2&3	1
Bothriomyrmex	3	1&2	2	2	?	?	?	?	?	?	2	1&2	1&2	2	2	2	1&2	2	3	1	1	1
Doleromyrma	3	3	3	2	?	?	?	?	?	?	2	1	1	1	2	1	2	2	2	2	1	1
Dolichoderus	1&2	1	1&2	1	1	2	4	1	1	2	2&3	1	1	1	?	1	3	2	1	1	3	3
Dorymyrmex	2&3	2&3	1	1	3	2	?	2	2	2	2	?	3	3	2	?	2	1	3	1	1&2	1&2&3
Ecphorella	2	3	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Forelius	3	3	2	1	3	2	3	2	2	2	1	1	2	2	2	1	2	1	2	1	1	1
Froggattella	2	4	2	2	3	2	2	3	2	2	1	4	1	1	3	1	2	1	1	2	2	2
Iridomyrmex	2	3	1&3	2	3	2	2	3	2	2	2	4	1	1	2	1	2	2	3	1	2&3	3
Leptomyrmex	1	1	1	1	1	1	4	1	1	1	2	1	1	1	2	1	2	2	3	3	2&3	1
Linepithema	2&3	2	3	1	3	2	3	3	?	2	2	1	1	1	3	1	2	3	3	1&2	2&3	1
Liometopum	2	3	3	1	3	1	4	1	1	1	2	2	1	1	2	1	2	1	2	3	2	1
Loweriella	3	2	3	1	?	?	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?
Ochetellus	2&3	3	2	2	3	2	2	3	2	2	1	2	1	1	2	1	2	1	2	1	2	2
Papyrius	3	3	2	2	3	2	2	3	2	2	2	1	1	1	2	2	2	1	2	1	1&2	3
Philidris	2	3	3	2	3	2	1	3	?	2	1	1&4	1	1	3	1	2	1	1	1	2	2&3
Tapinoma	3	6	1&2&3	2	2	2	4	1	1	2	2	1&2&3	1&2	1&2	1	1	2	1&2	2	3	2&3	1
Technomyrmex	1&3	6	1&2&3	2	3	2	4	2	2	2	2	1&2&3	1&2	1	1	1	1&2&3	1&2	1&2	3	2&3	1
Turneria	2&3	5	3	2	3	2	2	3	2	2	3	1	1	1	2	1	2	1	1	2	3	1&2&3

taxa/characters	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67
character weights	6	6	6	2	6	6	6	6	6	2	2	2	6	6	6	6	2	2	2	2	2	2	2	2
Aneuretus	1	1	1	2	1	2	1	2	1	1	3	1	1	1	2	1	1	1	1	2	2	1	5	1
Camponotus	1	1	1	3	1	1	0	3	1	1	2	2	1	1	1	1	1	2	1	1	1	1	5	3
Formica	1	1	1	3	1	1	1	2	1	1	1&3	2	1	4	1	1	1	2	2	1	1	1	5	3
Melophorus	3	1	1	3	1	1	0	2	1	1	1	2	1	4	1	1	1	2	2	1	1	1	5	1
Paratrechina	1	1	1	3	1	1	0	2	1	3	2	4	3	4	1	1	1	2	1	1	1	1	4	3
Anillidis	1	1	1	2	1	2	1	2	1	1	2	2	2	1	2	1	1	1	2	1	2	1	4	1
Anonychomyrma	1&2	1&2	1	1	1	1&2	1	2&3	1	1&3	1&3	2	?	1	1	1	1	1	2	1	2	1	4	1
Axinidris	3	?	?	1	1	1	1	0	1	3	3	3	2	1	1	1	3	1	2	1	3	1	4	?
Azteca	1&2&3	1	1&2	2	1&2	1	1&2	2	1	3	1	2	3	3	2	1	1	1	2	1&2	1	1	4&5	3
Bothriomyrmex	2&3	1	?	3	1	1	0&1	1&2	1	2&3	1	4	3	3	1	1	1	1	2	2	1	1	5	3
Doleromyrma	1	1	1	2	1	2	1	2	1	2	1	3	3	1	2	1	1	1	?	1	2	1	5	1
Dolichoderus	1&2	1	1	2	1	2	1	2	1	1&2&3	3	2	?	2	1	1	1	1	2	1	3	1	4&5	3
Dorymyrmex	1	1	1	?	2	1&2	0&1	1&2	1	2	1&2	4	3	2	1	2	1	2	2	1	1	1	5	1
Ecphorella	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Forelius	1	1	1	2	2	1	0	1	1	1	1	2	3	2	1	2	1	2	2	2	1	1	5	1&3
Froggattella	1	1	1	1	1	2	1	2	1	3	3	1	1	1	2	1	1	1	2	1	1	1	1	3
Iridomyrmex	1	1&2	1	2	1	1&2	1	2	1	1&2	1&2	2	?	1	?	1	1	1	1	1	1	1	2	3
Leptomyrmex	2	1	1	1	?	?	?	?	1	2	1	2	1	1	1	1	1	1	1	1	1	1&2	1&5	2&3
Linepithema	1	2	1	2	1	2	1	2	1	1	2	2	3	1	2	1	1	1	1	1	1	2	3&4&5	2
Liometopum	1	1	1	2	1	2	1&2	2	1	1	4	2	2	2	1	1	1	2	2	1	2	1	4	1
Loweriella	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?
Ochetellus	1	1	2	1&3	1	2	1	2	1	2	1	2	3	1	2	1	1	1	2	1	1	1	2	3
Papyrius	1	1	1	2	2	1	1	2	1	1	1	2	2	1	2	1	1	1	2	2	1	1	2	1
Philidris	1	1	1	2	1	2	1	2&3	1	1&2&3	1	2	2	1	2	1	1	1	2	1	1	2	3&4	3
Tapinoma	1&2	1	1	3	1	1&2	0&1	1&2	2	3	1&2	4	3	4	1	1	1&3	1&2	2	1	2&3	1	4	3
Technomyrmex	1&2	1	1	3	1	1	0&1	0	2	3	2&3	4	2	1	1	1	2	1&2	1	1&2	3	1	4	3
Turneria	1	1	1	2	1	2	1	2	1	3	3	2	2	1	2	1	1	1	1	1	1	1	1	3

character weights	2	6	6	6	2	6	6	6	6	2	2	6	2	6	6	6	6	6	6	6	6	6	6	6	6
taxa/characters	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92
Aneuretus	1	1	1	1	2	2	2	1	2	1	2	2	1	1	1	2	2	2	1	1	2	1&2	2	2	1
Camponotus	1	3	1	1	3	1	1	0	2	1	2	1	2	1	1	2	2	2	1	1&2	1	2	1	1	2
Formica	1	1	1	1	3	1	1	1	2	1	3	1	2	1	1	1	2	3	1	2	1	2	1	1	2
Melophorus	1	3	1	1	3	1	2	0	2	1	1	1	2	3	3	3	2	2	1	2	1	2	1	1	2
Paratrechina	1	3	1	1	3	1	1	0	1	2	2	1	2	3	3	3	2	1	?	?	2	2	1	1	2
Anonychomyrma	3	1	1&2	1&2	?	1	1	1	2	1	1&3	3	2	1	1	3	1	3	1	2	1	2	1	1	1
Axinidris	?	2	1	1	2	1	1	1	0	2	3	.1	3	2	1	4	2	3	2	1	2	2	1	1	1
Azteca	1	1&2	1	1	2	1	1	1&2	2	1	1	3	2	3	3	1&2	2	1	3	1	1	2	1	1	1
Bothriomyrmex	1	2&3	1&2	1	2	1&2	1	0&1	1&2	1	1	2	2	3	3	1	2	3	3	3	2	2	2	1	1
Doleromyrma	1	1	1	1	1	1	1	1	2	1	1	3	2	1	1	3	1	3	3	2	1	2	1	1	1
Dolichoderus	3	2	1	1	2	1	2	1	2	1	3	1	?	1	1	3&4	2	3	1	2	2	2	1	1	1
Dorymyrmex	1	1	1	1	2	2	0	0	2	1	2	3	?	1	2	1	2	1&3	3	2	1	2	1	1	?
Ecphorella	?	?	?	?	?	?	?	?	?	?	?	?	?	1&2	2	?	?	?	?	?	?	2	?	?	?
Forelius	1	1	1	1	1&2	2	0&1	0	0	1	2	3	2	1	3	?	?	2	3	2	1	2	1	1	1
Froggattella	1	1	1	1	?	1	1	1	2	1	2	3	2	1	3	3	1	3	1	2	1	2	1	1	1
Iridomyrmex	1	1	1	1	1	1	1	1	2	1	2&3	2&3	2	1	1	4	1	2	1	3	2	2	1	1	1
Leptomyrmex	1	3	?	1	1	1	0&2	0&1	2	1	2	1	1	1	1	1&2	1	3	1	2	1	2	1	1	1
Linepithema	?	1	1	1	1	1	2	1	2	1	3	1	1	1	1&2	3	1	3	3	1&2	1	2	1	1	1
Liometopum	2	2	1	1	2	1	2	1	2	1	1	1	2	3	1	3&4	2	3	2	2	1	2	1	1	1
Loweriella	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?	?	?
Ochetellus	1	1	1	2	?	1	1	1	2	1	2	3	1	1	1	2	1	3	3	3	1	2	1	1	1
Papyrius	1	1	1	2	3	2	1	1	2	1	2	3	1	3	3	3	1	3	1	2	1	2	1	1	1
Philidris	1	1	1	1	?	1	1	1	2	1	1	3	1	1	1	3	1	2	1	2	1	2	1	1	1
Tapinoma	1	1&2	1	1	3	1	1	0&1	0&1&2	2	2	1	4	3	3	3	1	3	3	2	1	2	1	1	1
Technomyrmex	3	1&2	1	1	3	1	1	0	0	2	2	1	4	3	1	3&4	2	3	2	3	1	2	1	1	1
Turneria	1	1	1	1	2	1	1	1	2	1	1	3	1	1	1	3	1	2	2	1	2	2	1	1	1

taxa/characters	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107
character weights	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
Aneuretus	2	2	2	1	2	1	1	1	1	1	1	1	2	2	1
Camponotus	2	1	1	2	1	1	1	1	2	1	1	1	1	1	1
Formica	2	1	1	2	1	1	1	1	2	1	1	1	1	1	1
Melophorus	2	1	1	2	1	1	1	1	2	1	1	1	1	1	1
Paratrechina	2	1	1	2	1	2	1	1	2	?	1	2	1	1	1
Anillidis	1	2	2	2	2	?	?	?	?	?	?	?	?	1	1
Anonychomyrma	1	2	2	2	2	2	2	2	2	2	2	2	1	1	1
Axinidris	?	2	2	2	2	?	?	?	?	?	?	?	?	1	1
Azteca	1	2	2	2	2	2	2	2	2	2	2	2	1	1	1
Bothriomyrmex	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1
Doleromyrma	?	2	2	2	2	?	?	?	?	?	?	?	?	?	1
Dolichoderus	1	2	2	2	2	2	2	2	2	2	2	2	1	1	1
Dorymyrmex	1	2	2	2	2	2	1	2	2	2	2	2	1	?	1
Ecphorella	?	2	?	?	?	?	?	?	?	?	?	?	?	1	1
Forelius	?	2	2	2	2	2	2	2	2	2	2	2	1	1	1
Froggattella	?	2	2	2	2	2	2	2	2	2	2	2	1	?	1
Iridomyrmex	1	2	2	2	2	2	2	2	2	2	2	2	1	1	1
Leptomyrmex	?	2	2	2	2	2	2	2	2	2	2	2	1	1	1
Linepithema	1	2	2	2	2	2	2	2	2	2	2	2	1	1	1
Liometopum	?	2	2	2	2	2	2	2	2	2	2	2	1	1	1
Loweriella	?	2	2	2	2	?	?	?	?	?	?	?	?	1	1
Ochetellus	?	2	2	2	2	2	2	2	2	2	2	2	1	1	1
Papyrius	?	2	2	2	2	2	2	2	2	2	2	2	1	1	1
Philidris	?	2	2	2	2	2	2	2	2	2	2	2	1	1	1
Tapinoma	1	2	2	2	2	2	2	2	2	2	2	2	2	1	1
Technomyrmex	1	2	2	2	2	1&2	1&2	2	2	2	2	2	1&2	2	2
Turneria	?	2	2	2	2	2	2	2	2	2	2	2	1	1	1