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First fossil “true *Macromischa* “ in Amber from the Dominican Republic (Hymenoptera, Formicidae)

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The new species *Leptothorax (Macromischa) praecreolus* is described from Dominican amber of probable Early Miocene age. This species shows apparent affinities with the recent Dominican *L. (M.) creolus*. A cladistic analysis of a selected set of species including the new fossil, all contemporary Hispaniolan *Leptothorax* and one potentially related species from N. Mexico, strongly suggests that *L. praecreolus* should be ancestral to both *L. creolus* and to the Mexican species. If this phylogenetic reconstruction is true, a considerable amount of migration and speciation must be assumed in W. Indian *Leptothorax* since Miocene times.

Keywords: cladistic analyses; Dominican amber; Formicidae; fossil ants; *Leptothorax praecreolus*.

INTRODUCTION

The “subgenus” *Macromischa* of *Leptothorax*, containing 66 named and a few still undescribed recent species, probably constitutes a polyphyletic group but also contains a great proportion of species which show the most bizarre and extraordinary morphologies and colorations known in the ant world fauna (BARONI URBANI, 1978). For this reason *Macromischa* has been considered as a valid genus in most classical myrmecological literature, in spite of strong reasons to presume polyphyly or convergence in its most peculiar characters. In fact only part of the species attributed to it exhibit the metallic colours and complicated integumental sculptures making them so distinctive. The (weak) main diagnostic features supposed to characterize what is still considered the “subgenus *Macromischa*” are an elongate petiolar node coupled with a broad postpetiole and a dorsally non-interrupted trunk. BARONI URBANI (l. c.) also showed that this morphological syndrome holds only for a statistical majority of the species. In addition, some species exhibit a unique enlargement of the middle and hind femora, a probable adaptation to hold prey while stinging which may well have been selected several times.

MAYR (1868) considered *Macromischa* a true genus and described four fossil species from Baltic amber as belonging to it, i. e. *M. beyrichi*, *M. rugosostriata*, *M. petiolata* (senior homonym of *Macromischa petiolata* (FOREL)), and *M. rudis*. MAYR based the generic assignment of these fossil taxa essentially on a general affinity in shape between the fossil and the recent species and on the impossibility to attribute the fossil species to the genus *Myrmica* (the second closest genus in his opinion) because of the lack of tibial spurs on the middle and hind legs.

The first of these amber species (*M. beyrichi*) had been described again later by WHEELER (1910) as *Propodomyrma samlandica* (n. gen., n. sp.), but WHEELER himself, a few years later, (1914) changed his mind and transferred it to *Vollenhovia* (an exclusively Australasian genus in its recent representatives) with the name

of *V. beyrichi* (MAYR). The reasons of this transfer are not specified, if one excludes some complaints about the poor quality of MAYR's description, but the relative text mentions and the figure shows an ant with definitely incrassated femora. In the same paper, the latter three Baltic species described by MAYR are transferred to the genus *Nothomyrmica*, a genus created especially for them since it was evident to WHEELER that "these cannot be included in *Macromischa*". To this new genus WHEELER (l. c.) added a fourth new species (*N. intermedia*) The new genus was compared with the genera *Tetramorium* and *Xiphomyrmex* only, essentially for its lack of tibial spurs, a character equally shared with *Macromischa* and *Leptothorax*. This incongruence did not escape EMERY (1922) who stated that *Nothomyrmica rugosostriata* and *N. petiolata* are *Leptothorax* of the group *rottenbergii* (a species originally described in *Macromischa* by EMERY himself) while the other two species (*intermedia* and *rudis*) are likely to be also *Leptothorax* but with unclear affinities.

Nonetheless, the recent species characterized by this spurious mixture of characters show other peculiarities: they are nearly all Central American, an area from where only 8 additional "non-*Macromischa*" *Leptothorax* species are known (the genus *Leptothorax* is virtually cosmopolitan and comprises a few hundreds of species). Even allowing for some amount of polyphyly, the species actually included in *Macromischa* represent the most impressive case of explosive speciation ever recorded in ants. This is easy to see in the Greater Antilles and particularly on the island of Cuba where the known 33 "*Macromischa*" species represent over 1/4 (26%) of the ant fauna (128 species), and this percent increases to over 1/3 if one excludes the species recorded from Cuba but probably introduced in the island by man (BARONI URBANI, 1978).

But if, on one hand, all the species mentioned until now undoubtedly belong to the genus *Leptothorax*, on the other hand their sharing of one or more peculiar morphological traits, (i. e. parts of a "*Macromischa* syndrome") are likely to be due to polyphyly and the discrepancies in generic or subgeneric attribution of the formerly known fossils appear much more semantic than objective.

The new fossil species to be described in this paper shows very apparent relationships with recent *Macromischa*, and, in addition, it shares exactly the same geographical origin with one of its most closely related recent relatives.

MATERIAL AND METHODS

The species described in this paper is represented by a single specimen, embedded in a small, rectangular cut piece of Dominican amber purchased in the Dominican Republic as originating from the amber mine "La Toca" by C. BARONI URBANI and belonging to the Natural History Museum of Basel, Switzerland (Collection Number PE 107) (Fig. 1). The amber sample is yellowish in colour and relatively clear. It contains a few additional inclusions that I tentatively identify as part of a dipteran wing, unidentifiable remains of a probable insect cephalic capsule, vegetable tissue and caterpillar's excrements. Part of the integument of the ant, particularly on part of the antennae, trunk, postpetiole, gaster and legs is not clearly visible because these parts are covered by a thin gas layer probably produced by bacterial fermentation and visible as a thin film of differently diffracting substance often assuming shining gold reflexes through its outer amber layer.

Although the preservation condition of this amber piece can be considered as good, some structures are missing: these are all segments of the gaster with exception of the first, the tarsi of the first pair of legs on the right side, and the tarsi of

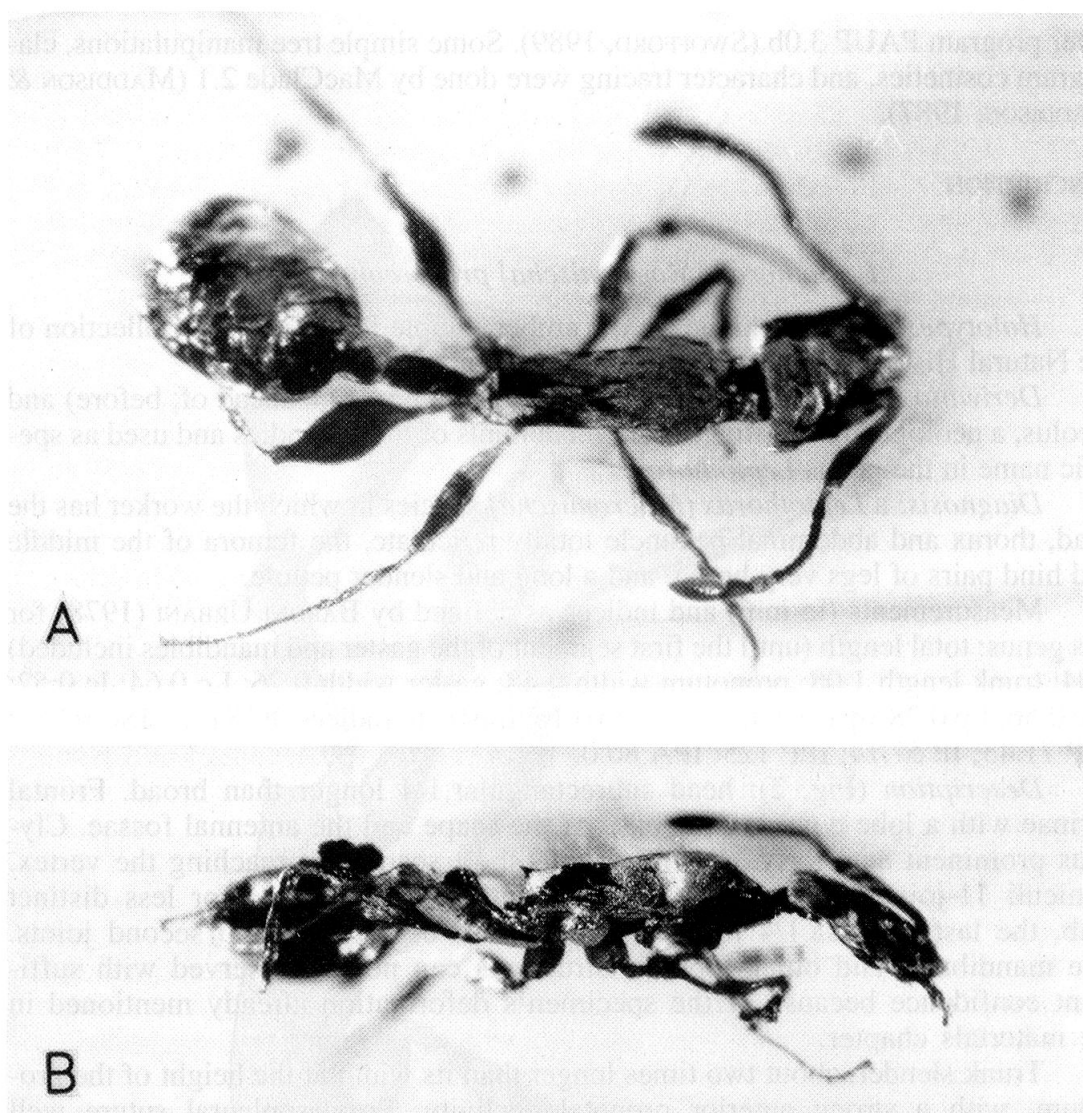


Fig. 1: Micrograph through the amber specimen including the new species with the ant in dorsal (A) and lateral view (B).

the third pair of legs on both sides. Part of the body, and particularly the head, appear to have been subject to variable extents of dorsoventral compression, leading to different degrees of deformation of the contours, particularly on the head. For this reason, in this paper, the specimen will be drawn only in full side view and also the discussion/recognition of the most important characters will be largely confined to those visible in profile.

The most probable phyletic relationships between the new species and a selected sample of recent relatives were evaluated by a parsimony analysis. Search of the shortest possible tree was performed by exact exhaustive method and by the Branch-and-Bound algorithm guaranteeing to find all optimal trees. In order to assess a statistical degree of confidence to the results obtained in this way, a bootstrap analysis as described by FELSENSTEIN (1985) was also performed. 1,000 bootstrap replicates were executed. All these methods were implemented by the com-

puter program PAUP 3.0b (SWOFFORD, 1989). Some simple tree manipulations, cladogram cosmetics, and character tracing were done by MacClade 2.1 (MADDISON & MADDISON, 1987).

DESCRIPTION

Leptothorax (Macromischa) praecreolus n. sp.

Holotype: Worker (unique) in the amber sample PE 107 of the Collection of the Natural History Museum of Basle, Switzerland.

Derivatio nominis: From the Latin preposition prae (= ahead of, before) and creolus, a neologism indicating recent inhabitants of the W. Indies and used as specific name in the genus *Leptothorax*.

Diagnosis: a *Leptothorax (Macromischa)* species in which the worker has the head, thorax and abdominal peduncle totally reticulate, the femora of the middle and hind pairs of legs very broad, and a long and slender petiole.

Measurements (in mm) and indices as defined by BARONI URBANI (1978) for this genus: total length (until the first segment of the gaster and mandibles included) 3.04; trunk length 1.08; pronotum width 0.48; gaster width 0.76; Lc 0.64; lc 0.52; Lsc 0.56; Lp 0.28; ap 0.20; Ip 0.16; Lpp 0.16; Ipp 0.20. Indices: IC 81.25; ISC 92.86; IAP 71.43; IP 57.14; IPP 125; IPA 80.0.

Description (Fig. 2): head subrectangular, 1/4 longer than broad. Frontal carinae with a lobe covering the base of the scape and the antennal fossae. Clypeus prominent anteriorly. Antennae with short scape, not reaching the vertex. Funiculi 11-jointed with the last three joints forming a more or less distinct club, the last joint ca. 1/4 longer than the sum of the first and second joints. The mandibular and other cephalic structures can not be observed with sufficient confidence because of the specimen's deformation already mentioned in the materials chapter.

Trunk slender, about two times longer than its width at the height of the pronotum, with a strong anterior pronotal declivity. Promesopleural suture well developed. Propodeum with a pair of thin, short spines diverging backwards; propodeal base forming an angle of about 90° with its dorsum. Femora of the second pair of legs slightly inflated; femora of the hind legs almost two times broader than those of the forelegs. Middle and posterior tibiae without spurs.

Petiole two times longer than broad, its node oval in dorsal view and triangular in profile. Subpetiolar process present. Postpetiole subequal in length and height, its node rounded in dorsal view and oval in profile.

Gaster: first segment oval in profile; in dorsal view the typical "*Leptothorax* shoulders", appear smoothed and less visible.

Sculpture: head capsule, thorax, petiole and postpetiole totally covered by very minute, deep reticulation. The reticulation is slightly wider in the lower pleural regions than in the dorsal parts. Antennae, legs and gaster smooth, completely without sculpture.

Colour dominantly shining dark brown with slightly reddish coxae and antennae.

True erect pilosity very rare and sparse, slightly more frequent on the dorsal parts of the thorax and abdomen, largely constituted by tiny truncated hairs as characteristic for several *Leptothorax* species. Scape and funiculus with relatively hirsute, dense, appressed pubescence.

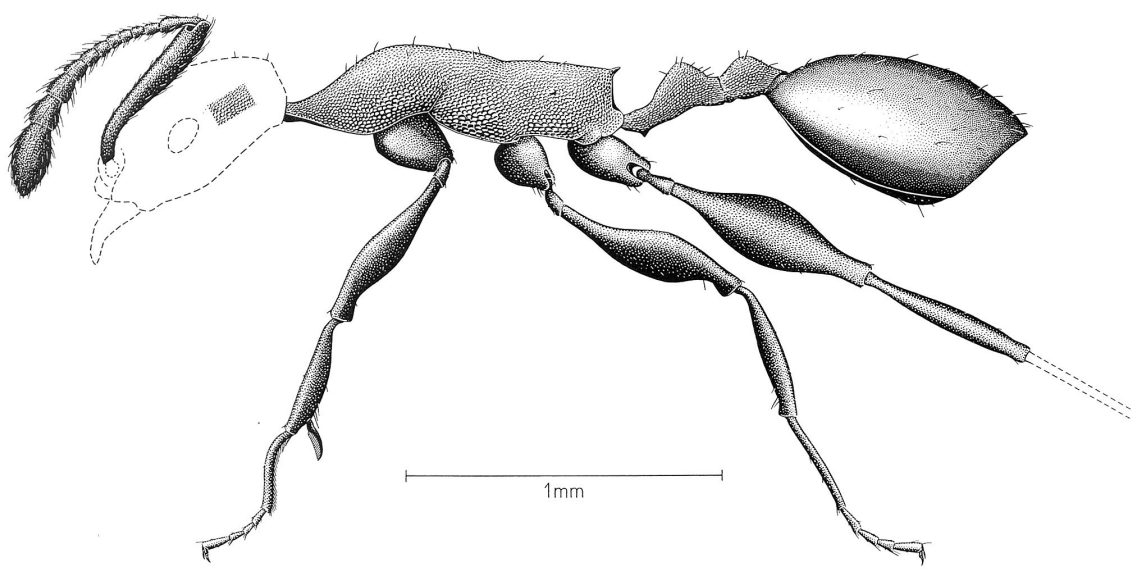


Fig. 2: *Leptothorax praeterosus* n. sp., worker, partly reconstructed lateral view. Drawing by A. Coray. Incompletely resolved or incompletely drawn parts correspond to poorly visible body parts in the unique amber specimen.

DISCUSSION

I regard the species described in this paper as the first “true *Macromischa*” since other fossils previously attributed to this subgenus and already discussed in the introduction are likely to be better considered as *Leptothorax* s. l. In the introduction I insisted, however, on the fact that the subgenus *Macromischa* is probably a polyphyletic group artificially including different very bizarre or extraordinary morphological syndromes. One of the traits common to all these species is that all of them stem from the W. Indies or from other regions nearby. In this perspective, talking of a “true” *Macromischa* makes very little sense if not for the fact that the fossil I describe in this paper shows some traits of the *Macromischa* morphological syndromes, as many “true” ones and in contrast with the previous doubtful fossils from the Baltic, it also comes from the W. Indies.

Of the three diagnostic characters generally reported as typical for *Macromischa*, *L. praecreolus* clearly shows two, i. e. the continuous dorsal profile and the elongated petiole, while the third one (broad postpetiole) is much less distinctive and may be comparable to an average *Leptothorax* species.

For its general habitus, size, morphology, and particularly for the short propodeal spines and the narrow postpetiole, this species closely resembles the sympatric and allochronic recent species *L. creolus* BARONI URBANI. *L. creolus* is described from a single specimen from Bani (Dominican Republic) and BARONI URBANI (1978) regarded it as the unique representative of one of the 12 species groups he recognized within *Macromischa*.

The new fossil species and the recent one clearly differ at least in the following characters:

- Sculpture of the head, thorax, and abdominal peduncle, reticulate in *L. praecreolus*, as opposed to *L. creolus*, who's head is longitudinally striated, with the exception of a superficial reticulation on the sides of the head. The thorax is reticulate, with the exception of the neck, the propodeal spines, and the posterior pleural sides; and the lateral parts of the abdominal peduncle are without sculpture.

- Femora of the middle and hind legs remarkably thickened in *L. praecreolus* as opposed to slightly thickened in *L. creolus*.

- Petiole with a long and slender peduncle in *L. praecreolus* as opposed to short and thick in *L. creolus*.

Another important character, the pilosity under the head, present only in *creolus* among the recent species, cannot be observed with confidence in the fossil.

L. praecreolus, hence, appears to show one typical *Macromischa* character (the enlarged middle and hind femora) which is absent or reduced in the taxon which is likely to represent its closest recent relative. This morphology had been explained by BARONI URBANI (1978) as an adaptation to hold prey while stinging. If this is true and *creolus* and *praecreolus* are really sister species, this difference can be interpreted only as (A) a case of paraphyletic character evolution, or (B) secondary loss in *creolus* of a poorly rentable plesiomorphy.

In order to test both the most probable phyletic reconstruction of the relationship between *L. praecreolus* and *L. creolus* and the most parsimonious character evolution on this reconstruction, I attempted a cladistic analysis of all known Hispaniolan *Leptothorax* and of the Mexican *L. ocarinae* BARONI URBANI which is somewhat similar to *L. creolus* and may be closer than the latter to *praecreolus* in petiolar shape. Since the internal phylogeny of the genus *Leptothorax* is far from being known, I selected a not too distantly related extrageneric representative for the out-

Table 1. Presence (1) or absence (0) of 23 potential synapomorphic characters among the known contemporary Hispaniolan species of *Leptothorax*, the fossil *L. praecreolus*, the potentially related Mexican *L. ocarinae*, and *Myrmica scabrinodis*. The latter has been included into the data matrix for the purpose of outgroup comparison. See text for further explanations.

SPECIES	CHARACTERS																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>L. creolus</i>	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1
<i>L. flavidulus</i>	0	1	0	0	0	0	0	1	0	1	1	1	1	1	0	1	1	0	1	0	1	1	0
<i>L. hispaniolae</i>	1	0	1	1	1	1	1	0	1	0	0	1	1	1	1	2	0	1	1	0	1	0	1
<i>L. pastinifer</i>	0	1	0	0	1	1	1	1	0	1	1	1	1	1	1	2	1	1	1	1	1	1	1
<i>L. sallei</i>	1	0	1	1	1	1	1	0	1	0	0	1	1	1	1	2	0	1	1	1	0	0	1
<i>L. praecreolus</i>	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0	0	1	0	1	0
<i>L. ocarinae</i>	1	1	0	1	1	1	0	0	1	1	0	0	0	0	1	1	0	0	1	1	1	1	1
<i>M. scabrinodis</i>	1	0	0	0	1	1	1	1	1	0	0	1	0	1	0	0	1	1	0	1	0	0	0

group comparison: *Myrmica scabrinodis* NYLANDER, assumed to represent a non-specialized typical myrmicine.

The cladistic analysis has been performed exclusively on cladistically informative characters and I made no attempts to include autapomorphies in the data matrix. The following 23 characters have been retained as satisfying this requisite and of probable phylogenetic significance:

- 1- Head striated (1) or not (0)
- 2- Head reticulated (1) or not (0)
- 3- Head abundantly covered with many hairs (1) or with a few only (0)
- 4- Hairs of the dorsal surface of the head longer than the maximum diameter of the eyes (1) or shorter (0)
- 5- Head length ≤ 0.64 mm (0) or ≥ 0.75 mm (1)
- 6- Head width ≤ 0.52 mm (0) or ≥ 0.62 mm (1)
- 7- Antennal scape trespassing the occipital border (1) or not reaching it (0)
- 8- Trunk straight in profile (0) or convex (1)
- 9- Trunk striated (1) or not (0)
- 10- Trunk reticulated (1) or not (0)
- 11- Posterior lower pleural side of the trunk, propodeal spines and peduncle of the petiole sculptured (1) or smooth (0)
- 12- Propodeal spines much longer than their distance at the base (1) or shorter (0)
- 13- Propodeal spines longer than or subequal to their distance at the tips (1) or much shorter (0)
- 14- Propodeal spines more than twice as long as the subspinal area (1) or shorter than the subspinal area (0)
- 15- Femora of the middle and hind legs incrassated (1) or not (0)
- 16- Pedunculum of the petiole short (0), normal (1) or long (2)
- 17- IAP ≤ 60.0 (0) or IAP ≥ 63.88 (1)

- 18- Node of the petiole with a differentiated anterior face (1) or not (0)
 19- Postpetiole broadly ariculated to the gaster on all its width (1) or not (0)
 20- Postpetiole sculptured (1) or not (0)
 21- Gaster with (1) or without (0) the typical *Leptothorax* shoulders
 22- Body hairs truncated (1) or not (0)
 23- Body bicolor (1) or unicolor (0)

The distribution of these characters and of their states among the species considered for comparison is given in Table 1. For the cladistic analysis evolution from one character state to another has been supposed to be unordered, although, *a posteriori*, assuming ordered character evolution proved to produce a cladogram with exactly the same topology and only one extra step.

The data matrix of Table 1, in fact, allows the construction of only one most parsimonious cladogram of length 43 (Fig. 3). As a result, the *Leptothorax* species considered for the analysis fall into two distinct clades: one comprising the Hispaniolan endemic *L. hispaniolae* and *L. sallei*, and another including all other species considered, including the Mexican endemic *L. ocarinae*. *L. praecreolus*, hence, is likely to be the sister group of both *creolus* and *ocarinae*, two species which BARONI URBANI (1978) considers as representing two separate, monotypic species groups within *Leptothorax*.

Dominican amber is generally assumed to be Lower Miocene in age (BARONI URBANI & SAUNDERS, 1982, based on stratigraphic dating of the embedding layer

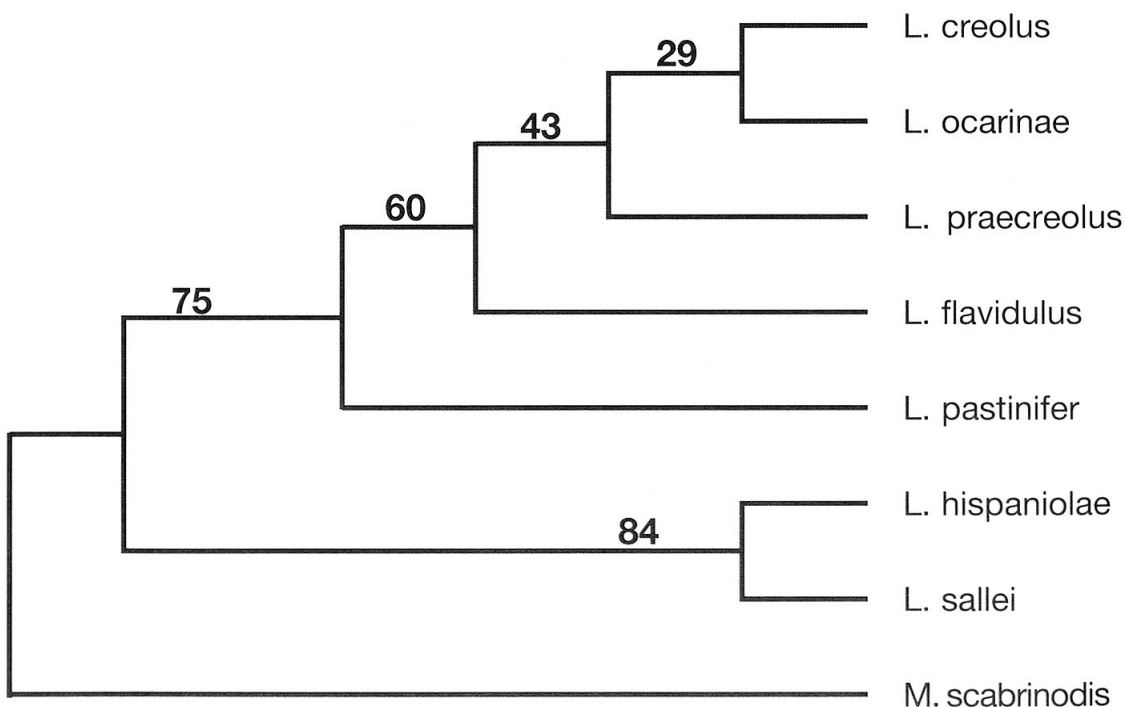


Fig. 3: Unique most parsimonious cladogram of the Recent species of *Leptothorax* recorded from Hispaniola, of the fossil *L. praecreolus* from Hispaniolan amber and of the Mexican *L. ocarinae*. *Myrmica scabrinodis* has been added to the analysis for the outgroup comparison. The figures below each dichotomy represent the percent of cladograms in which the dichotomy has been found among 1,000 bootstrap replicates. For further explanations see text.

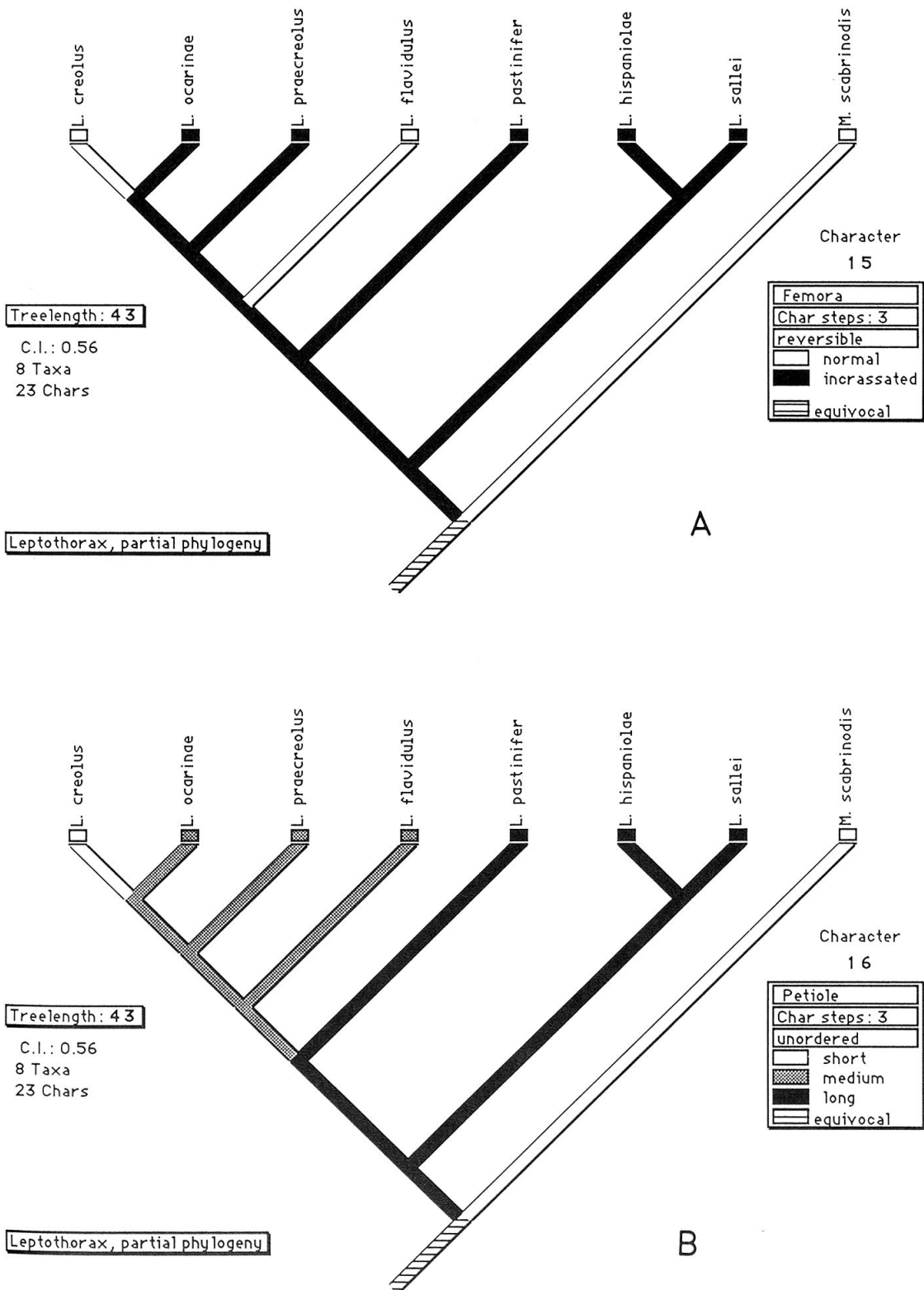


Fig. 4: Most parsimonious evolution of two characters of the “Macromischa syndrome” among the species considered in this paper. Both the increased femora (A) and the elongated petiole (B) appear to be plesiomorphic traits within *Leptothorax*: their absence in a number of species, hence, should be due to secondary loss.

through benthic foraminifera from the mine of Palo Alto), though there is general agreement on the fact that there must be a huge variation from mine to mine (see e. g. SCHLEE, 1984). Successive age determinations by Nuclear Magnetic Resonance (LAMBERT *et al.*, 1985) referred at least one amber mine (La Toca, the one where *L. praecreolus* should have been collected) to the Eocene, though these results are questioned by KRISHNA & GRIMALDI (1991).

Assuming the phylogenetic reconstruction I present here as true may imply a large amount of speciation and/or radiation among Caribbean *Leptothorax* since Miocene times if *L. praecreolus* is to be considered the taxon ancestral to both *L. creolus* and *L. ocarinae*. Although the ancestral position of *L. praecreolus* remains speculative at the present state of knowledge, this hypothesis appears to be consistent with the available information. This, in fact, can be tested by considering plesiomorphic all *praecreolus* character states in PAUP (or by applying it the instruction “Make Ancestor” in MacClade): both these manipulations imply no increase in the length of the tree of Fig. 3. The geographic range of *L. praecreolus* being unknown, one should assume either speciation of *creolus* and *ocarinae* on a restricted area and successive migration of the latter, or speciation in a large Central American area followed by drastic contraction of the distribution of the recent species.

The phylogenetic results attained here permit two additional speculations concerning the evolution of the two traits of the “*Macromischa* syndrome” recognizable in *L. praecreolus* (Fig. 4). The short petiole of the recent Dominican *creolus* appears to be due to secondary loss of an old leptothoracine character. In a similar manner, the presence of “normal” legs for these ants appears to be a homoplasically shared convergence.

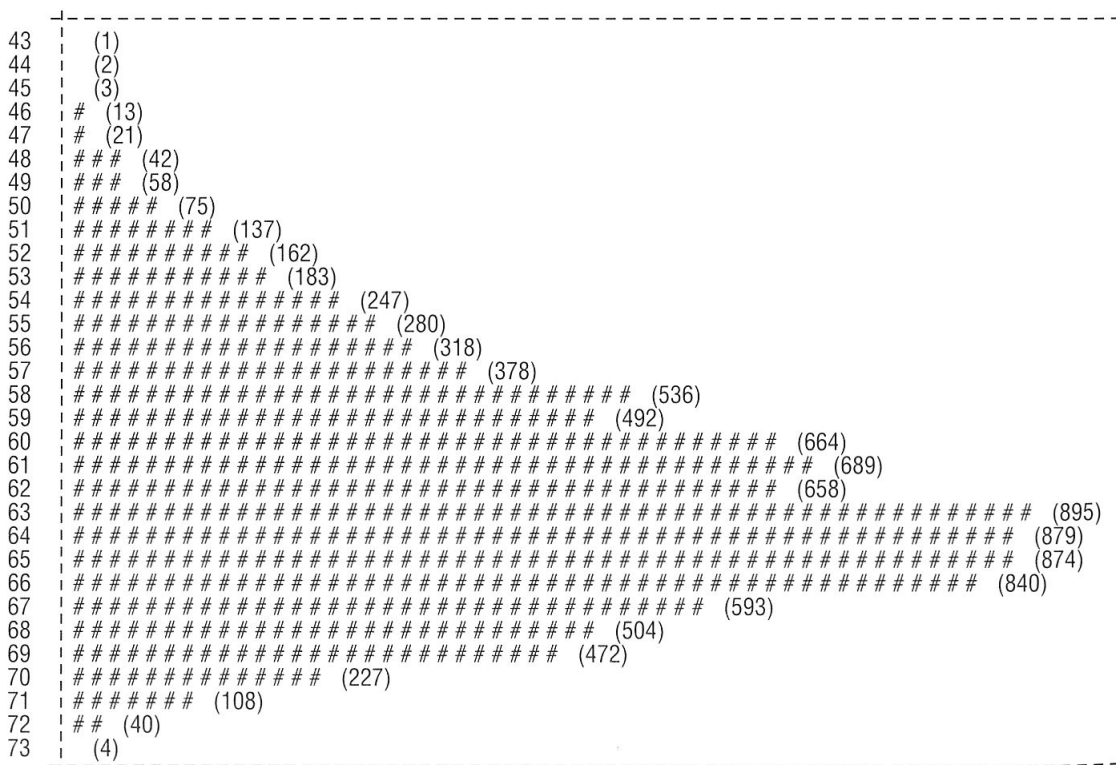


Fig. 5: Frequency distribution of the total number of optimal and suboptimal trees of length variable between 43 and 73.

The results of the bootstrap analysis of the same data matrix from which the most parsimonious cladogram has been drawn entirely confirmed this tree topology but with frequencies of the individual dichotomies far below the usual statistical levels (Fig. 3). Both dichotomies involving the three species on which I focussed my attention (*creolus*, *ocarinae*, *praecreolus*) appear in the bootstrap tree as minority compatible groups only.

Particular care should be used when parsimony is employed as the sole decision criterion: Fig. 5 gives the frequency distribution of length of 10,395 cladograms which could be constructed on these same data and which have not been retained only since they are less parsimonious.

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I would like to express my warmest thanks to CESARE BARONI URBANI for calling my attention on this problem and for the continuous encouragements, suggestions and help through all the stages of the taxonomic and cladistic analysis. I am grateful to KEVIN PRIER for his patient and much needed improvements of the English.

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(received March 4, 1992; accepted September 22, 1992)

JEANNERET, P. Approche biogéographique de la distribution des tordeuses phyllophages des vergers de pommiers non traités (région lémanique): diversité et espèces. *Bull. Soc. Ent. Suisse* 65 (1-2): 155-164.

L'auteur nous a communiqué que le tab. 3 de son article comportait des erreurs. Il devrait donc être modifié comme suit:

Tab. 3. Indices de régression (R^2) et signification (test F) liant les indices au nombre d'arbres (N) et au degré d'isolement (I) de chaque parcelle (calculés pour 11 vergers de pommiers non traités de la région de Nyon-La Côte).

	SHANNON N	SIMPSON N	Dominance N		SHANNON I	SIMPSON I	Dominance I
R^2	0,32	0,18	0,35		0,42	0,62	0,56
F	1,92	0,88	2,18		6,52	14,93	11,42
Sign.	$P>0,05$	$P>0,1$	$P>0,05$		$P<0,05$	$P<0,005$	$P<0,001$