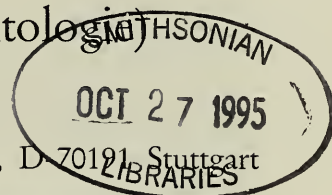# Stuttgarter Beiträge zur Naturkunde

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Invasion and Extinction in the West Indian Ant Fauna revised: the Example of *Pheidole* (Amber Collection Stuttgart: Hymenoptera, Formicidae. VIII: Myrmicinae, partim)

By Cesare Baroni Urbani, Basel

With 12 Figures

Summary

Pheidole primigenia n. sp. is described from Dominican amber. The new species is similar to another Dominican amber species: *Pheidole tethepa* WILSON. This latter species has been re-examined and re-described. The two Dominican *Pheidole* appear to be closely related to each other but show no clear relationships to any Neotropical members of the genus. Their nearest relatives are a few Recent species restricted to the Malayan, Australian and Oceanian regions. This is regarded as an evident new example for the presence of Old World elements in the Dominican amber fauna, a biogeographic aspect which cannot be neglected. A previously established biogeographic analysis of the West Indian ants in which this fact had been omitted (WILSON 1985, 1988) is re-examined and its conclusions are shown to be untenable: Old World ant genera present on Hispaniola show no evidence either of dispersal or of survival capacities greater than Neotropical ones.

The discussion benefits in part from new information on the Dominican amber ant fauna which, to date, is known to comprise the following genera:

Acanthognathus, Acanthostichus, Anochetus, Apterostigma, Aphaenogaster, Azteca, Brachymyrmex, Camponotus, Crematogaster, Cylindromyrmex, Cyphomyrmex, Dendromyrmex, Diplorhoptrum, Discothyrea, Dolichoderus, Erebomyrma, Eurhopalothrix, Gnamptogenys, Hypoponera, Ilemomyrmex, Leptomyrmex, Leptothorax, Linepithema, Myrmelachista, Neivamyrmex, new genus A near *Rogeria,* new genus B of Dolichoderinae, *Octostruma, Oxyidris, Pachycondyla, Paraponera, Pheidole, Platythyrea, Pogonomyrmex, Prenolepis, Prionopelta, Proceratium, Pseudomyrmex, Odontomachus, Solenopsis, Strumigenys, Tapinoma, Trachymyrmex, Wasmannia, Zacryptocerus.*

Zusammenfassung

Pheidole primigenia n. sp. wird aus dem Dominikanischen Bernstein beschrieben. Die neue Art ähnelt *Pheidole tethepa* WILSON, die ebenfalls aus dem Dominikanischen Bernstein bekannt ist, und hier ausführlich erörtert und beschrieben wird. Die beiden Dominikanischen *Pheidole*-Arten sind offenbar nahe miteinander verwandt, sie zeigen aber keine deutlichen Beziehungen zu neotropischen Arten dieser Gattung. Die engste Verwandtschaft besteht vielmehr zu einer kleinen Gruppe von Arten, die heute nur in der malayisch-australisch-ozeanischen Region vorkommt.

Das wird als weiteres wichtiges Beispiel für das Vorkommen altweltlicher Elemente in der Dominikanischen Bernsteinfauna betrachtet. Ihr Anteil ist zwar zahlenmäßig gering, sie sind aber doch biogeographisch bedeutsam.

Es wird ausführlich begründet, warum (z. T. im Licht der neuen Befunde) einige Schlußfolgerungen einer früheren biogeographischen Analyse der westindischen Ameisen (WILSON 1985, 1988) unhaltbar erscheinen: Altweltliche Ameisengattungen von Hispaniola zeigen keineswegs größere Ausbreitungskapazität (dispersal) als größere Überlebensfähigkeit als neotropische.

Außerdem wird eine kritische Liste der bisher im Dominikanischen Bernstein sicher erkannten Ameisengattungen gegeben. Diese Gattungen sind die folgenden:

Acanthognathus, Acanthostichus, Anochetus, Apterostigma, Aphaenogaster, Azteca, Brachymyrmex, Camponotus, Crematogaster, Cylindromyrmex, Cyphomyrmex, Dendromyrmex, Diplorhoptrum, Discothyrea, Dolichoderus, Erebomyrma, Eurhopalothrix, Gnamptogenys, Hypoponera, Ilemomyrmex, Leptomyrmex, Leptothorax, Linepithema, Myrmelachista, Neivamyrmex, new genus A (ähnlich mit *Rogeria*), new genus B (Dolichoderinae), *Octostruma, Oxyidris, Pachycondyla, Paraponera, Pheidole, Platythyrea, Pogonomyrmex, Prenolepis, Prionopelta, Proceratium, Pseudomyrmex, Odontomachus, Solenopsis, Strumigenys, Tapinoma, Trachymyrmex, Wasmannia, Zacryptocerus.*

1. Introduction

One of the purposes of the present paper is to illustrate another case of low evolutionary speed among the Formicidae drawn from the ant genus *Pheidole*. The new fossil species to be described below brings, in addition to affinities with contemporary ones, new evidence for a numerically small but historically important component of the Dominican amber fauna: the presence of Recent Old World affinities. This is a poorly known but unequivocal character of this fauna and it will be discussed at some length in this paper.

The genus *Pheidole* presently contains several hundred species in the tropics and temperate regions of the world but it is very rare in the fossil record. The fact had been already noted by BROWN (1973) who supposed that this genus should have been absent or very rare in the northern hemisphere until the Middle Miocene and that its present great species diversity should have been attained after that time.

1.1. Previous historic, subfossil, and fossil records of *Pheidole*

The known fossil and subfossil records for the genus are the following:

CARPENTER (1930) described a species, *Pheidole tertiaria,* based on two winged gynes from the Florissant shale of Colorado (Miocene), and BROWN (1973) reported the presence of minor workers in Mexican amber probably referable to this genus but without describing them. MACKAY & ELIAS (1992) found abundant remains of *Pheidole* spp. in packrat (*Neotoma*) middens of the Chihuahuan desert ranging in age from > 43,000 to 150 years BP: the sole fully recognizable species, *P. subdentata,* is still frequent in neighbouring areas of the Chihuahuan province. There are, in addition, mentions of other Recent species of *Pheidole* in copal from Zanzibar (WHEELER, 1910) and from Celebes (VIEHMEYER, 1913).

Copal may be reliably dated by the ^{14}C radiocarbon method. There are some age determinations revealing that copal of usual, typical appearance may be very young, only decades or centuries old: 20 to 50 years for East African copal pieces (BURLEIGH & WHALLEY, 1983), less than 250 years for a Colombian copal sample, and younger than 280 years for a Dominican Republic (near Cotui) copal piece (SCHLEE, 1984: 35). This means that copal inclusions are too young to be called fossils and even sub-

fossils: they are simply Recent species from historical times. The same is true for most of the above mentioned Chihuahua desert material since its origin is from the younger end of the time scale mentioned above.

The first record of *Pheidole* from Dominican amber dates from SCHLEE (1980, plate 21). The ant in this picture is not formally identified, although the superb preservation conditions of the specimen and the quality of the picture leave few doubts as to its most probable generic assignment.

WILSON (1985 a) published, under the name *Pheidole tethepa*, the first formal description of a very similar Dominican amber species based on three poorly preserved specimens.

I have studied four better preserved specimens belonging to one or two new Dominican amber species different from, but very close to, *Pheidole tethepa*. These specimens permitted the recognition of characters not properly visible in the *tethepa* type material and, in this paper, I shall describe them and attempt an interpretation of their taxonomic and biogeographic significance.

1.2. Available explanations of the origin of West Indian biotas drawn from the amber fauna

The species described in the present study show obvious Old World affinities, a character conflicting sharply with biogeographic inferences published in a very elegant and original paper on the origin of the West Indian ant fauna (WILSON, 1985 c). In fact, several doubts about the conclusions reached in that analysis have existed ever since its publication. These will be documented in detail in chapter 5 of the present paper; among the most significant ones, here, it may be sufficient to mention that the main conclusions of WILSON (l. c.), i. e. important immigration and insignificant extinction in the West Indian ant fauna since amber times, are the result of erroneous and incomplete data analysed by an inappropriate statistics used to draw conclusions logically extraneous to the initial formulation of the problem (see later, chapter 5). Professor Wilson, during a visit to Basle in 1986, first suggested we publish a joint correction of these points but later considered his recognition of the existence of the Dominican *Leptomyrmex* (published by BARONI URBANI, 1980 and omitted from WILSON's 1985 c analysis) as being sufficient (BARONI URBANI & WILSON, 1987). Recognition of the presence of the Australian genus *Leptomyrmex* in Dominican amber, however, represents only a partial correction of the data from which Professor Wilson drew his conclusions but not of the conclusions themselves. My offer of a second joint manuscript containing most of the corrections appearing now in this paper was first accepted, then delayed for several months and finally declined.

Professor Wilson's later refusal of a joint correction (proposed by him in 1986) was motivated by his understanding (September 1987) that such a correction conflicted with his former analysis and with a forthcoming chapter in a book. Conflict between the two is unavoidable since this book chapter (WILSON, 1988) proposes again the 1985 conclusions without change. Later on, a further establishment of these conclusions had been secured by a recent book dedicated to "the next generation of myrmecologists" (HÖLLDOBLER & WILSON, 1990), where no reference to other papers is made, while dealing with the Dominican amber ant fauna (pages 9—21 and 23—25), apart from those by WILSON himself. Unfortunately the erroneous conclu-

Fig. 1. Specimen Do-3708-a. — A: lateral view. B: dorsal view of the head.

sions in these publications, having a broad biogeographic significance, are referred to without criticism by others.

For these reasons I feel obliged to caution biogeographers against the fallacies implicit in what otherwise, due to the apparent elegance of its reasoning, might eventually become a piece of standard knowledge.

2. Material and methods

Among the material presently available to me, I have been able to examine thirteen samples of Dominican and Mexican amber containing *Pheidole*. All these specimens

Fig. 2.   Specimen Do-4440. — A: lateral view. B: dorsal view of the head.

show a "usual" *Pheidole* habitus and are likely to belong to species groups already known from the Neotropical fauna. Professor Wilson is currently revising the Neo-tropical members of this genus and is planning to describe them. He is of course in the best position to judge their taxonomic status and I shall leave him the difficult task of establishing the most probable relationships of these species. The ants dealt with in this paper exhibit obviously non-Neotropical affinities and, for this reason, they will be discussed separately by me. Four amber samples, all belonging to the collection of the Stuttgart Museum of Natural History (Department of Phylogenetic Research), contained ant specimens relevant in this context. They can be briefly de-scribed as follows:

Do-3708. — A large, light Dominican amber piece containing a homopteron, a micro-hymenopteron, three fragments of flowers and two ants. The preservation conditions of the first ant (Do-3708-a, Fig. 1) are good, though its observation is ren-dered difficult by the presence of numerous air bubbles. The specimen Do-3708-b is represented by a head without antennae articulated to a prothorax without legs belonging to the same species as the Do-3708-a but embedded in a dark-coloured amber layer and further shaded by a diagonal fissure. I shall comment the presence of this fragmentary specimen only here since I have been unable to take any measure-ment on it, or to use it further in the species description.

Do-4440. — A small, yellow Dominican amber sample containing only one ant (Fig. 2) and insect excrement. The ant is intact and well visible due to the reduced number of amber impurities. Because of the body position of the specimen, its study results relatively easy.

Do-4434. — Another small, originally oval, very clear Dominican amber sample containing only an ant (Fig. 3), a psocid, and pollen grains. Three air bubbles (one on the left antennal club, one on the left gena and one on the right side of the propo-deum) prevent a complete view from all sides. Nonetheless the head is clearly visible
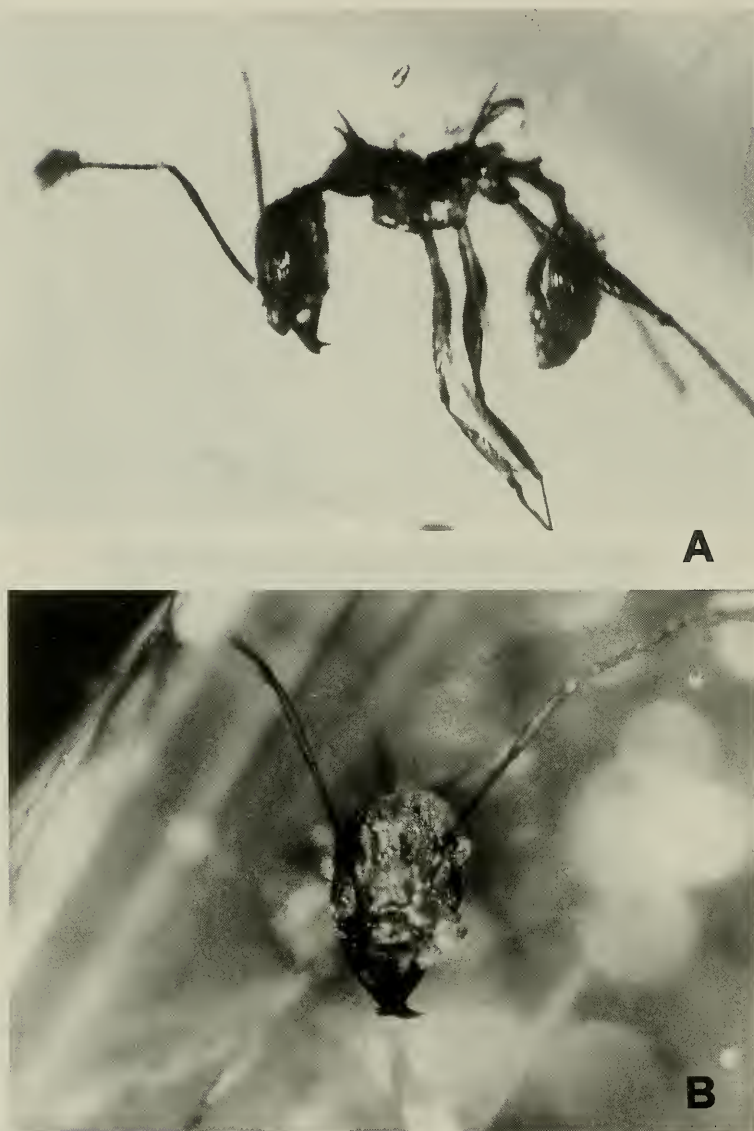
Fig. 3.   Specimen Do-4434. — A: lateral view. B: dorsal view of the head.

in dorsal and right lateral view and the rest of the body can be examined in detail from the left side.

Do-1645-K. – A dark yellow amber piece with green reflexes. It contains several leave and vegetable fragments, a chalcidid wasp, and an ant (Fig. 4). The ant is complete and in good shape. Only part of the left profile is covered by an air bubble. This is the specimen already depicted in a colour plate by Schlee (1980, plate 21). The head in dorsal view reveals some remarkable distortion particularly evident in the asymmetric position of the eyes (see Fig. 4 B). This distortion may not be due to dif-

Fig. 4.   Specimen Do-1645-K. — A: lateral view. B: dorsal view of the head. The asymmetry
          in the position of the eyes visible in B persists after immersion in sucrose solution.

ferences in diffraction of the amber surrounding the specimen since it remains unal-
tered after immersion of the amber sample in 66% sucrose solution.

   Most parts of these ants are well preserved. Hence their morphology may be con-
sidered as reliable except for the antennal scapes. These appear to be laterally com-

pressed in the specimens Do-3708, Do-4434 and Do-4440; the specimen Do-3738-a shows a lateral compression of the left funiculus, too. For this reason the scapes which appeared very thin in dorsal view and too broad in lateral view, in figure 5 (based on specimen Do-4440), have been drawn with a round section as usual for minor workers of Pheidolini and as visible in the amber specimen Do-1645-K. The most probable diameter of the round section at different distances from the articulation with the head has been calculated as the average of the minimum and the maximum width measured at the same distance from the cephalic articulation.

Although this is not suggested by asymmetric deformations of the head of the specimen Do-3708, Do-4440 and Do-3738-a, it is likely that the broad range of head lengths I measured (see later the HL values under the species description and the relative figures) may be equally attributable to some pressure exerted on (some of) the specimens. No other body parts of these ants from the Stuttgart collection differ among the specimens or from plausibly related contemporary ants in a way which might suggest that the morphology described in this paper may have been modified by pressure, heat, or other unknown factors.

DLUSSKY (1986) proposes a method, based on transformation grids, to reconstruct the original shape of deformed specimens in amber. This method has been used also in preparing an illustration for this paper (Fig. 5) but it can account reasonably well only for deformations affecting the symmetry.

In addition to this material I have been able to re-examine the Dominican amber sample from the mine La Toca containing the holotype and paratype of *Pheidole tethepa* WILSON and deposited in the Museum of Comparative Zoology in Cambridge, Massachusetts. This has been partly cut and polished again in order to improve examination of the specimens. The holotype appears distorted as shown in the original figure of WILSON (1985 a, Fig. 4). The head of the paratype specimen is badly damaged and the body is partly covered by air bubbles and amber impurities, although the trunk appears in much better shape than in the holotype and is probably not or only very little deformed. Unfortunately, the position of the specimen does not permit cutting away of the amber inclusions and re-polishing without severe damage to the appendages.

All the amber specimens have been observed, measured and drawn in 66% sucrose solution. All photographs, except Fig. 4 B, have been equally taken in sucrose solution. The ant drawings are a product of the talent and the patience of ARMIN CORAY.

The statistical treatment of the data has been performed using the SAS/STAT package (1989) and the program 4F of the BMDP package, Release 7 (DIXON, 1992).

3. Description of new Dominican amber *Pheidole*

Three specimens from the Stuttgart Museum appear to represent a new species of *Pheidole* which I regard as distinct from but very close to *Pheidole tethepa* WILSON. Its description and diagnostic characters will be given below. The specimen Do-3708-a differs greatly from the other two in the shape of the head, and it is much more similar to *Pheidole tethepa* WILSON in this regard, but the remaining morphology and particularly the pronotal spines exclude its attribution to the latter species. Given the great amount of (probably artifact) variability in the cephalic proportions of all the specimens examined in this paper, the description of this ant as a separate species on the base of this sole character would be meaningless.
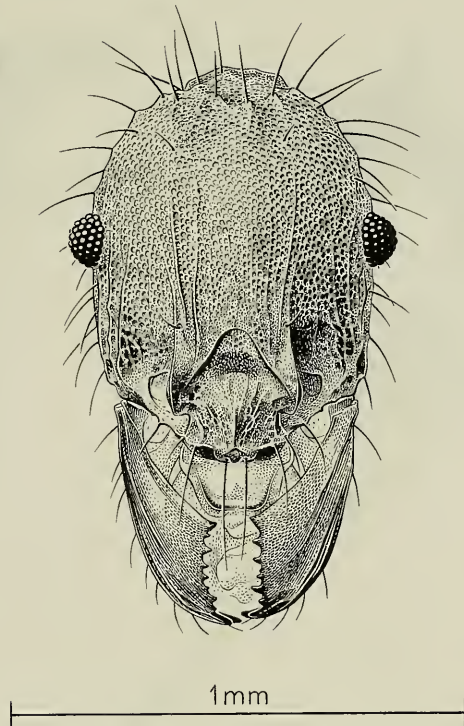
1mm

Fig. 5.   *Pheidole primigenia* n. sp., minor worker, holotype (Do-4440). Head in dorsal view,
very slightly interpreted as described in the methods chapter in order to render it
symmetric; antennae artificially omitted. Drawing by ARMIN CORAY.

Pheidole primigenia n. sp.
Fig. 1–3, 5–7

Holotype: Minor worker in Dominican amber, preserved in the amber collection of the
State Museum of Natural History, Stuttgart (Department of Phylogenetic Research), No.
Do-4440.

Paratypes: Two minor workers in Dominican amber, preserved in the same collection as
the holotype with the numbers Do-4434 and Do-3708-a.

Derivatio nominis: from the Latin *primigenius* (= primitive, ancestral, first of its kind).

Diagnosis. — A Dominican amber *Pheidole* characterized by very long pronotal
spines, unknown in all extant Neotropical species, and much longer than those of the
sole previously known Dominican fossil (*Ph. tethepa* WILSON).

Description (minor worker, measurements in mm).

Total length (mandibles included) 2.88–3.56 (holotype 3.54); head length (without man-
dibles) (HL) 0.64–0.80 (holotype 0.80, paratype Do-4434 0.76); head width (HW) 0.60–0.64
(holotype 0.60); scape length (SL) 0.92–1.12 (holotype 1.12); mandible length (ML)
0.36–0.48 (holotype 0.48); trunk length 1.04–1.08 (holotype 1.08); length of the pronotal
spines 0.23–0.24 (holotype 0.24); length of the propodeal spines 0.36; petiole length
0.20–0.36 (holotype 0.36); postpetiole length 0.20–0.24 (holotype 0.24); Cephalic Index (CI
= 100 x HW/HL) 75.0–100.0 (holotype 75.0); Scape Index (SI = 100 x SL/HW) 143.7–186.7
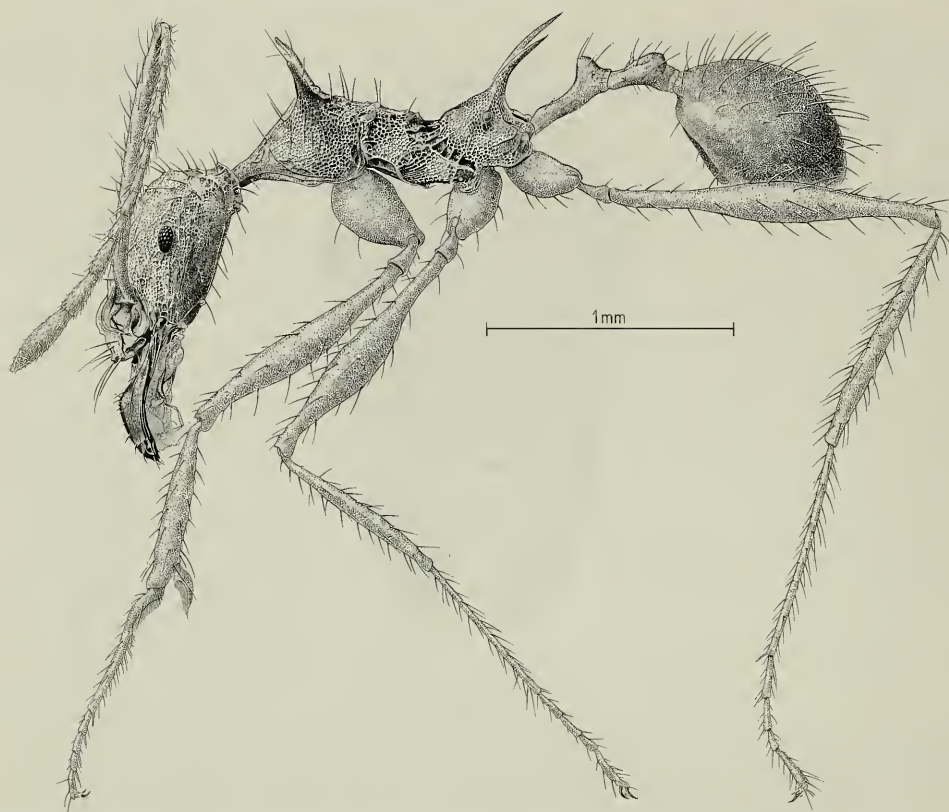(holotype 186.7); Mandibular Index (MI = 100 x ML/HL) 47.4–60.0 (holotype 60.0).

Fig. 6.   *Pheidole primigenia* n. sp., minor worker, holotype (Do-4440), slightly oblique
lateral view. Posterior part of the trunk (partly covered in the holotype), anterior
tibia and basitarsus, posterior coxa and last tarsomere completed from the paratype
Do-4434. Body posture adjusted to enable maximum vision. Drawing by ARMIN
CORAY.

Head moderately elongate, with weakly convex sides and posterior border; ante-
rior clypeal border slightly prominent in the middle and straight; frontal carinae tres-
passing the anterior border of the eyes backwards; postoccipital area bearing a short
"neck" with rounded sides in profile; eyes considerably bulging and behind the
median longitudinal line of the cephalic capsule; mandibles of the usual shape for
minor workers of *Pheidole*, armed with 7−8 larger and 2−3 minute denticles;
palpal formula 2,2 with the apical maxillary joint bearing a pair of long, parallel setae
which, in amber, may appear as an additional joint; antennae with elongated scape
and three-jointed terminal club.

Trunk, dorsally, very thin and elongate forming a pronounced "neck" anteriorly;
the two wider points of the trunk, separate by a marked narrowing of the inter-
pleural distance, are the caudal parts of the pronotum and of the propodeum which
bear each a pair of long, divergent spines; the pronotal spines, in profile, arise at the
top of a marked pronotal declivity and are bent slightly forwards; dorsal profile be-
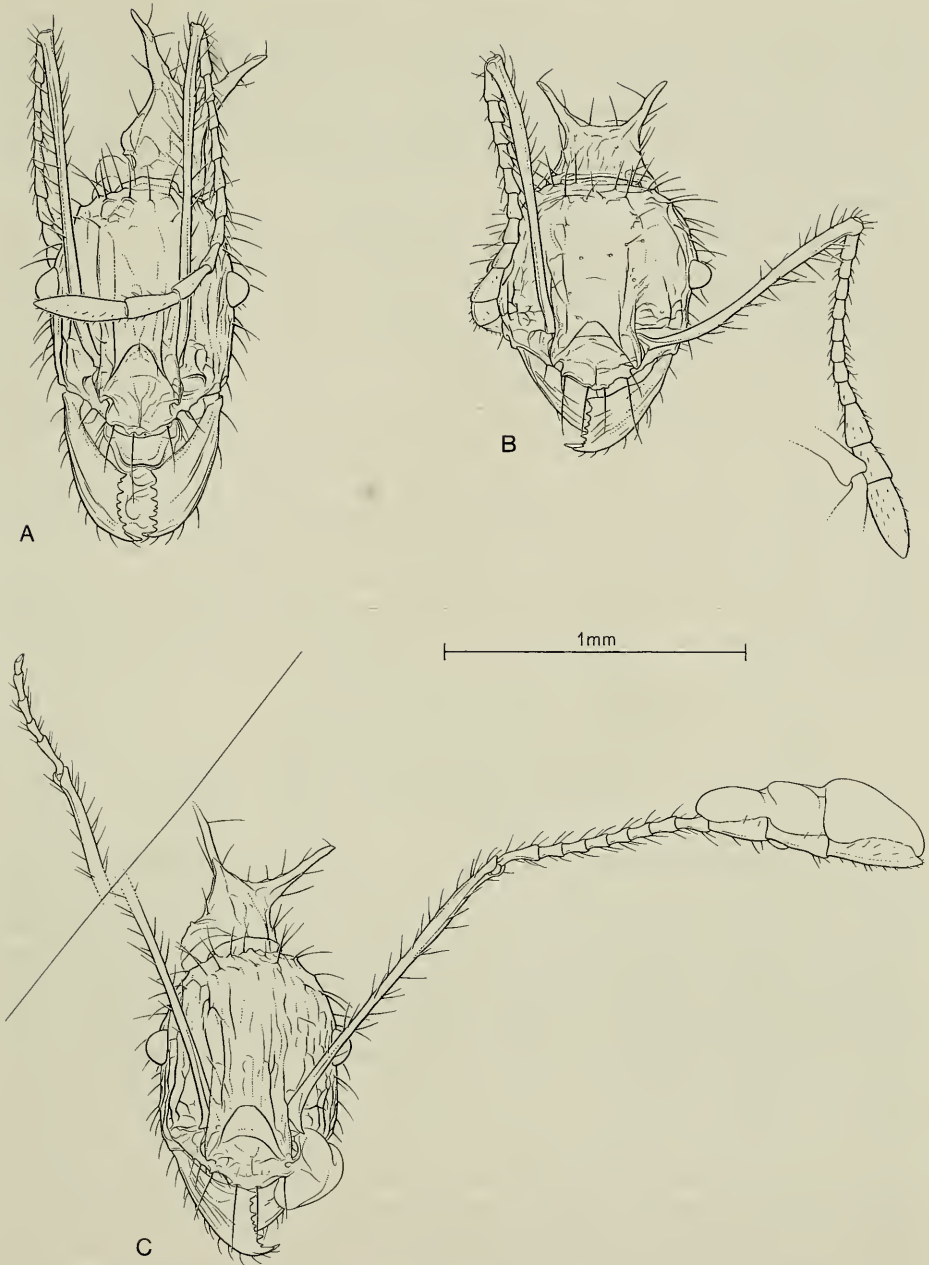tween the two pairs of spines in the form of a saddle; its maximum depth corres-

Fig. 7. *Pheidole primigenia* n. sp., minor worker, variability in cephalic morphology pro-
bably due to deformation in amber. Only the stronger integument sculpture has been
drawn. The minute reticulate punctuation superimposed to the striation and visible in
Fig. 5 has been artificially omitted from this figure. A) holotype; B) paratype
Do-3708-a; C) paratype Do-4434. Drawings by ARMIN CORAY.

ponds to the propodeal suture; the latter deeply impressed and visible on the pleura; basal and declivitous faces of the propodeum at right angle; propodeal spines much longer than the pronotal spines and directed backwards almost on the same plane as the basal face of the propodeum; petiole elongate, with nearly parallel sides in dorsal view, the node also reduced but angular in profile; postpetiole oval in dorsal view and with a very low, obtuse node in profile. Gaster oval, neither truncated nor broadened anteriorly.

Legs long and slender with slightly broadened femora. A broad, superficial punctate microsculpture is widespread on most head and trunk surfaces but is missing from the gaster and from the appendages which are smooth and shiny; pronotal and propodeal spines also without punctuate sculpture; petiole and postpetiole not entirely smooth but with very reduced punctation. The minute, punctate sculpture of the head and of the trunk is superimposed on a weak, much broader and superficial reticulation. Long, pointed, suberect hairs are frequent on most body surfaces, more frequent on the cephalic capsule and on the gaster; four long hairs on the anterior border of the clypeus. Colour uniformly brown with slightly lighter appendages.

I considered all specimens available for the present study representing the minor worker caste. An explanation for the differences observed in the head measurements might be that the specimens belong to different subcastes as characteristic for contemporary *Pheidole* species. However, this interpretation is rendered less probable by the lack of significant allometric differences in other body parts of the specimens concerned.

<div align="center">

Pheidole sp. ? (prope *primigenia*)
SCHLEE, 1980: 38, pl. 21
Fig. 4

</div>

The belonging of the specimen Do-1645-K to *P. primigenia* is probable but uncertain. This ambiguity is particularly unfortunate since the specimen appears to be much better preserved and better observable than the others described in this paper. Its habitus recapitulates most major features already described for *P. primigenia* from which it differs markedly for the longitudinal striation of the head and (less) of the trunk as visible in Fig. 4. I would be inclined to explain most differences detectable in the cephalic sculpture by means of the better preservation conditions of this specimen as compared with those of the *primigenia* type material. If these sculptural differences could be confirmed by examination of additional material, they would be sufficient to describe a separate species by neontological criteria. One should not forget, however, the possibility that all the specimens described above may belong to a single species and may be separate from each other by some million years age.

The measurements of this critical specimen are as follows:

Total length (mandibles included) 3.32; head length (without mandibles) 0.76; head width 0.60; scape length 0.92; mandible length 0.40; trunk length 1.0; length of the pronotal spines 0.24 ; length of the propodeal spines 0.32; petiole length 0.36; postpetiole length 0.20; Cephalic Index 83.33; Scape Index 153.33; Mandibular Index 52.6.

The recognition of the specimen Do-1645-K, even if it is not formally named in this paper, plays an important role in our understanding of the frequency and of the diversity of this group of *Pheidole* in the Dominican amber fauna. To the best of our knowledge, no related species survive in the contemporary Neotropical fauna.
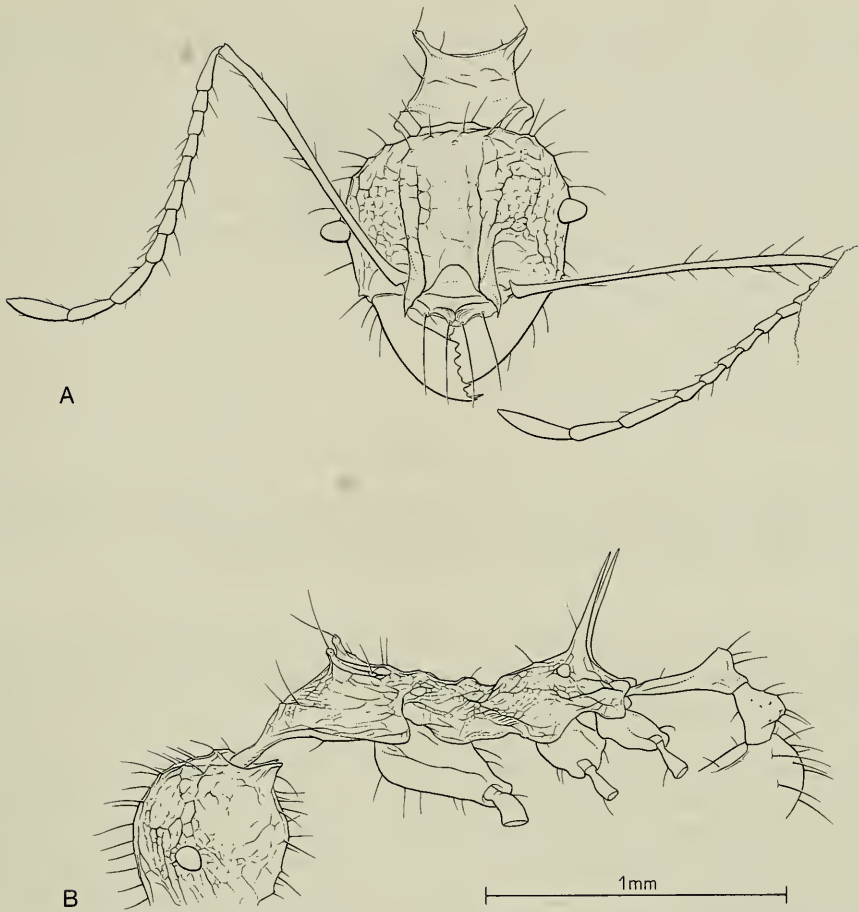
Fig. 8. *Pheidole tethepa* WILSON. Holotype minor worker. A) Head in dorsal view; B) Posterior part of the head, trunk and abdominal peduncle in slightly oblique lateral view. Only the best visible, stronger integument striation has been drawn. The minute reticulate punctuation superimposed to the striation and similar to the one of *P. primigenia* has been artificially omitted from the figure. Drawing by ARMIN CORAY.

4. The systematic position of *Pheidole primigenia* n. sp.

As precise a comparison as possible between the two Dominican fossils *Pheidole tethepa* and *primigenia* is essential for the conclusions to be drawn from the findings presented in this paper. I have been able to re-examine the *tethepa* holotype and paratype. By re-polishing the unique amber piece in which both specimens are embedded and by observing it in the sucrose solution many more details become visible, but some points of doubt remain, particularly because of the remarkable distortions of these ants. In the case of both *Ph. tethepa* specimens, one gets the impression that the main source of deformation should have been a compression of the head along its longitudinal axis. If a sagittal shortening actually affected the specimens in question, its effects on the relative proportions of different parts of the

0.5 mm

Fig. 9.   *Pheidole tethepa* WILSON. Paratype minor worker. Partially oblique view of the pro-
thorax and part of the deformed head showing the prothoracic spines, the micro-
sculpture, and the gular spine. Drawing by ARMIN CORAY.

cephalic capsule and on potentially significant characters like the clypeal morpho-
logy and the frontal carinae raised upwards and projecting over the clypeus cannot
be determined in a reliable way.

For the purpose of the comparison between *Pheidole primigenia* and *tethepa* the
drawings of the latter species given here in Figs. 8—9 should account for most of the
significant characters. The integumental sculpture of *tethepa* has not been completely
represented in the figures because it is not properly visible in the original specimens.
A minute punctation very similar to the one described and drawn for *primigenia* is
present at least on parts of the integument of the *tethepa* holotype but, due to the dif-
ficulties in observation, only the sculpture visible on the prothoracic region of the
paratype has been reproduced in Fig. 9. A slightly different appreciation of the
broader reticulation superimposed to the microsculpture of both species may equally
result from their different preservation conditions. My subjective guess is that the
integumental structure of the two species is at least very similar. The following
measurements (in mm) and indices may complete the redescription of *tethepa* (H =
holotype, P = paratype):

Total length (mandibles included) 3.2 (P)—3.24 (H); head length (without mandibles) 0.64
(H); head width 0.72 (H); scape length 0.96 (H and P); mandible length 0.40 (H); trunk length
1.00 (P)—1.20 (H); length of the pronotal spines 0.12 (H); length of the propodeal spines 0.36
(P)—0.40 (H); petiole length 0.32 (H and P); postpetiole length 0.24 (H and P); Cephalic
Index 112.5 (H); Scape Index 133.3 (H); Mandibular Index 62.5 (H).

Comparing the descriptions and the figures of the two species it appears that *Phei-
dole primigenia* differs from *tethepa* essentially in the length of the pronotal spines
(twice as long in the former as in the latter). Another character potentially of great
importance is the presence of two large gular spines visible in both *tethepa* specimens
(Fig. 8, 9) and absent or very rounded in *primigenia*. Since the head of the *tethepa*
type material has been deformed to a great extent I prefer to be cautious about the
value of this difference which, if confirmed, would separate the two species by a dif-

ferent order of magnitude. For the same reasons (probable artifacts due to the sagittal compression of the head) I would not attribute much value to the perpendicular frontal laminae of *tethepa*. Due to the close similarity of the two species in many details, I consider the cephalic morphology of the better preserved and better observable *primigenia* to be actually shared by the two species in spite of some doubts and contrasts appearing in the drawings. The eyes of *primigenia* are remarkably protruding from the sides of the head, though to a lesser extent than in *tethepa*, but they are asymmetrically deformed in the latter species and I am inclined to attribute at least part of their conical appearance in *tethepa* to the same sagittal compression of the head already mentioned. The specific distinction but close relationships between *Pheidole primigenia* and *tethepa*, hence, can be regarded as reasonably reliable.

WILSON (1985 a) described *tethepa* in *Pheidole* as a tentative generic assignment; he suspected that it might be invalidated by the presence of exophthalmic eyes and proportionately large mandibles. The ocular morphology has already been discussed above. In addition to probable deformations in amber (demonstrated by the asymmetric appearance of *tethepa*) the eyes of *primigenia* do not differ in a significant way from those of some members of the Malayan-Notogean subgenus *Pheidolacanthinus* (see Fig. 10, 11) where they are also more protruding than in other species of *Pheidole*. The Mandibular Index is 47—60 in *primigenia* and 62 in *tethepa*, much higher than in most *Pheidole* species where the MI is around 35—40, but — in a non-random sample of species measured for this study — it appears to be 54 (i. e. within the range of *primigenia*) for the Indomalayan *Pheidole dugasi* FOREL. Hence, the placement of both species, *tethepa* and *primigenia*, in *Pheidole* appears to be the sole possible solution.

In revising the Indomalayan genus *Acanthomyrmex*, MOFFETT (1986) suggested that *Pheidole tethepa* may represent the sister taxon of that genus. This hypothesis is based on similarities in the cephalic morphology between *Acanthomyrmex* and the *tethepa* holotype; I have already shown that these characters are with great probability due to strong deformation of the latter. They can only be interpreted as artifacts if the close relationship between *primigenia* and *tethepa* is to be maintained.

Within the genus *Pheidole*, the presence of pronotal spines in both species discussed here immediately calls to mind the Australian-Malayan subgenus *Pheidolacanthinus*. This had already been noted by WILSON (1985 a) who referred correctly to the striking differences between *tethepa* and all Neotropical *Pheidole* and the similarity of thoracic structures between *tethepa* and *Pheidolacanthinus*. However, he concluded that "the pronotal spines were almost certainly derived independently from the Old World *P. quadrispina* group" (lapsus calami for *Pheidole quadrispinosa* (SMITH) from New Guinea).

The subgenus *Pheidolacanthinus* itself is a taxon of unclear significance. EMERY (1922) suggested that it should represent an artificial set of species grouped together on the base of a simple adaptational character (the presence of pronotal spines). He justified his point of view by stressing the great morphological differences between some members of this subgenus and by suggesting a similarity between two Malayan *Pheidolacanthinus* (*lokitae* and *quadrensis*) and the Indian *Pheidole* (s. str.) *sulcaticeps* greater than the one existing between the former two Malayan species and other members of the subgenus *Pheidolacanthinus*. Similar apparent affinities can be supposed between *P. (Pheidolacanthinus) sexspinosa* and *singularis* and the Australian *P.* (s. str.) *variabilis* MAYR.

The adaptational hypothesis to explain the presence of pronotal spines is more than plausible, but the supposed phylogenetic relatedness between *lokitae* and *quadrensis* and *sulcaticeps* and the one between *sexspinosa*, *singularis* and *variabilis* are not certain.

The following two arguments can be considered in favour of the homoplastic origin of the pronotal spines:

1. Pronotal spines are known only for the subgenus *Pheidolacanthinus* but other species of *Pheidole* (e. g. *P. sulcaticeps* from India and *P. variabilis* from Australia) possess humeral angles more or less toothed. As a matter of fact, to EMERY's examples of similarity in pronotal structure one should add at least *Pheidole caldwelli* MANN from Viti Levu.

EMERY's argument, however, is not conclusive in this context. The hypothetical demonstration, for example, of a relationship between *P.* (s. str.) *sulcaticeps* and *P. (Pheidolacanthinus) quadrensis* greater than the one between the latter species and *P. (Pheidolacanthinus) cervicornis*, would imply the synonymy of the two subgenera *Pheidole* s. str. and *Pheidolacanthinus* as they are currently defined (and this was EMERY's aim), but this will not automatically indicate that all these species (i. e. including *sulcaticeps*) belong to different clades. More or less angulate pronotal spines are known from a much wider array of species in *Pheidole*. Such a structure is present also in a major worker of an undescribed *Pheidole* species from Mexican amber sent to Professor WILSON for study.

2. One Australian species, *P. (Pheidolacanthinus) mjoebergi* FOREL, shows pronotal spines only in the major workers and not in the minor ones (FOREL, 1915) and another (*Pheidole aristotelis* FOREL from Sarawak) has pronotal spines in the minor workers only while the major ones have a weakly angulate pronotum.

The uneven caste distribution of this character and the undoubted great morphological differences among some *Pheidolacanthinus* species may be explained by the antiquity of their differentiation. The solution to this problem would be possible only by means of a phylogenetic analysis of the whole genus *Pheidole*, a task far beyond the scope of this paper. One should remember, in addition, that there are other non-related *Pheidole* species with mesonotal instead of pronotal spines (e. g. *P. annemariae* FOREL from Madagascar) but I don't think that the presence of the former morphology can be seriously used to demonstrate the polyphyly of the latter. None of these arguments appears to be completely cogent.

On the other hand, there are two arguments which can be interpreted as favouring the monophyly hypothesis:

1. The pronotal spines are a rare character in ants and unique for *Pheidolacanthinus* among the plethora of *Pheidole* species.

2. All the 25 extant species sharing this trait have a circumscribed geographical distribution (Fig. 12). Even *P. sulcaticeps*, *P. variabilis*, and *P. caldwelli* hypothetically linking some *Pheidolacanthinus* to other *Pheidole* clades are restricted to neighbouring areas in the Indomalayan and Notogean regions.

If, on the one hand, it is conceivable that the pronotal spines may have been selected more than once in a convergent way, it is less persuasive that this character originated more than once or survived more than once within the same geographic area only.

Whatever the most probable phylogeny (and hence the taxonomic status) of the "subgenus *Pheidolacanthinus*" could be, from a purely morphological point of view,
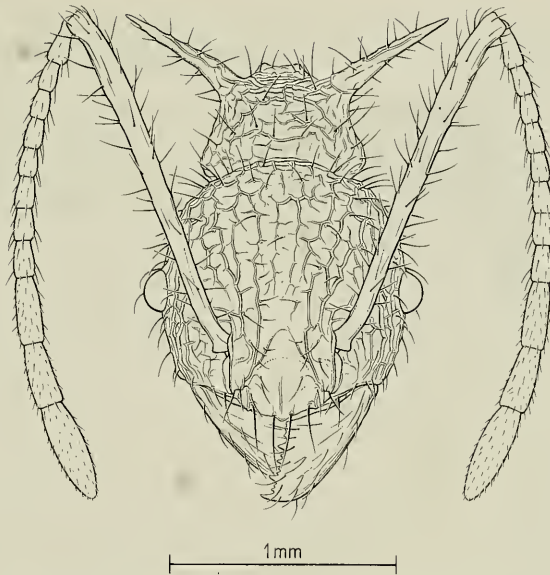
Fig. 10.   *Pheidole lokitae* FOREL. Syntype minor worker from Sumatra. Head in dorsal view; integument microsculpture artificially omitted. Drawing by ARMIN CORAY.

I am unable to see sufficiently relevant differences among its species to justify their attribution to different, recognized or recognizable non-related clades.

Since no sure indications for polyphyly are available at the present state of knowledge, the monophyly hypothesis should still be preferred in terms of parsimony.

The same reasoning can be extended from the contemporary members of *Pheidolacanthinus* to the Dominican fossils *Pheidole primigenia* and *tethepa* (see the figures 6 and 11): assuming their monophyly is still much simpler and convincing than assuming a non character-supported homoplastic origin of the pronotal spines. On the contrary, a relationship between the Dominican fossils and some contemporary species is additionally suggested by the eyes, protruding from the sides of the head more than in other *Pheidole*. I consider the Malayan and Sumatran contemporary *Pheidole lokitae* represented here in Figs. 10 and 11 as the most closely related species to both fossils, *primigenia* and *tethepa*.

I believe, in addition, that many of the arguments about the true or presumed polyphyly of the subgenus *Pheidolacanthinus* are irrelevant to the relationships between the Dominican fossils and the extant Old World species. The ambiguity stems from an incorrect way of posing the problem. I have already said that since there is no known character supporting the hypothesis of an independent origin for the pronotal spines in the amber fossils and in some of the Old World species mentioned above, then regarding this character as homologous appears to be the easiest solution. The correct question to be posed is whether this character is shared among the taxa discussed in this paper by symplesiomorphy or by synapomorphy. This cannot be decided in a satisfactory way on the currently available information; the acceptance of the one or of the other alternative is destined to affect the retention or the rejection of *Pheidolacanthinus* as a valid subgenus. I shall show in the next chapter
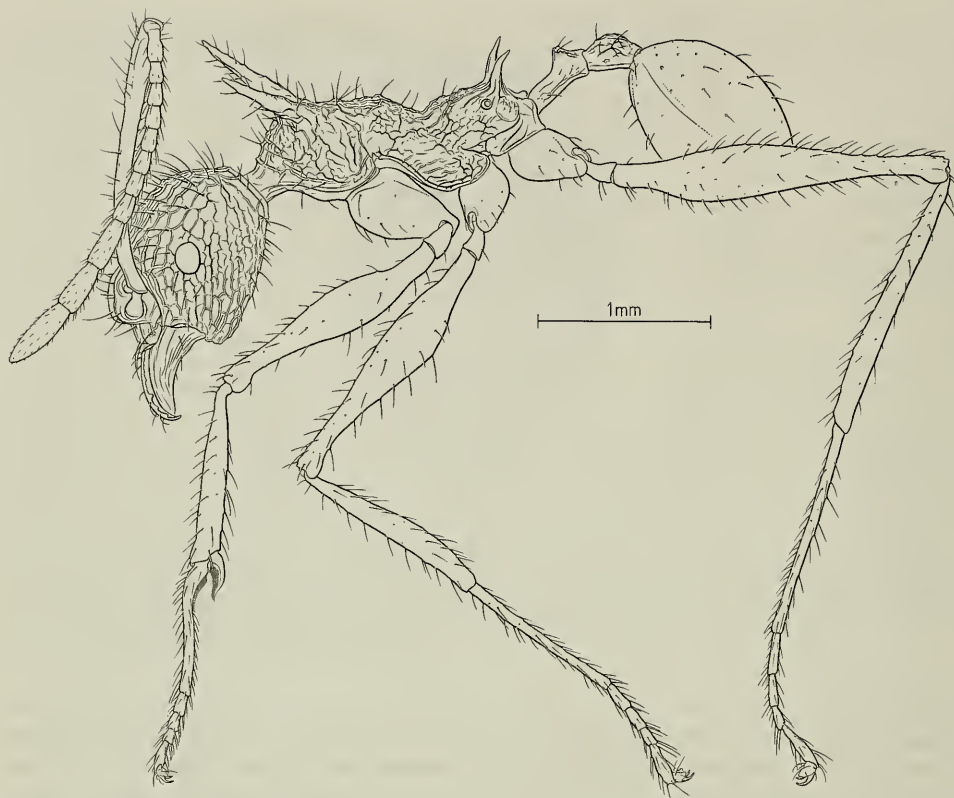
Fig. 11.   *Pheidole lokitae* FOREL. Syntype minor worker from Sumatra, slightly oblique lateral view; integument microsculpture artificially omitted. Body posture uniformed to the one of Fig. 6. Drawing by ARMIN CORAY.

that an incapacity to answer this question, on the other hand, affects the biogeographic meaning of the Dominican fossils only to a minor extent.

5. Biogeographic significance of the Dominican fossils: local extinction and trifling invasion

The Dominican amber fauna is often superficially reputed to have exclusively Neotropical affinities as one would expect a priori by judging from its geographical location only. BARONI URBANI (1980) described the first Dominican fossil member of the Australian genus *Leptomyrmex*, but this record has been doubted by WILSON (1985 b and 1985 c) who excluded it from his biogeographic analysis of Dominican amber ants (1985 c, 1988). In this 1985 analysis the Dominican amber ants are compared essentially with the Recent Neotropical fauna.

Later, however, WILSON recognized the presence of *Leptomyrmex* in Dominican amber (BARONI URBANI & WILSON 1987) but without changing his explanation as to the origin of the West Indian ant fauna. I have already written in the introduction that — in addition to the unexpected relationships between the Dominican amber and the Recent Australian faunas which are completely omitted from WILSON's ana-

lysis — there are also other, simple and impartial reasons which force me to consider Professor Wilson's explanation of the origin of the West Indian fauna as substantially wrong.

The analysis of WILSON (1985 c) attempted a statistical demonstration that Old World genera of ants present in the Recent Hispaniolan fauna are more numerous (expressed as "have reached the Antilles more often and became extinct less frequently") "and hence show evidence of greater colonizing ability" than they are in the fossil fauna (i. e. the presence of Old World ant genera in the Caribic area is greater today than it was in amber times and this should be explained by dispersal).

Some scientists, probably best represented by MAYR (1946) and DARLINGTON (1957), suppose that species and higher taxa originated in a geographically limited "center of origin" from which they spread in space through time. Members of this school refer explicitly in their work to the writings of DARWIN. Others scientists, best personified by CROIZAT et al. (1974), assume an earlier cosmopolitanism of the ancient floras and faunas followed by speciation through morphological specialization and area restriction. These scientists do not recognize a single historical leader, but, to my knowledge, the first to formulate clearly principles similar to those supported by the second school was TROUESSART who stated (1890, page 312): "la faune actuelle n'est . . . qu'un reste très incomplet d'une faune antérieure plus riche et plus généralement répandue".

It is clear if there could be shown that the cosmopolitanism in the present Caribic fauna exceeds that in the amber fauna — as it is asserted by WILSON (1985 c, 1988) — this could be a strong argument in favour of the first school of thought. On the contrary, presence of faunal elements in the Central American amber fauna now restricted to the Old World — like *Leptomyrmex* or the *Pheidole* discussed in this paper — can be an evidence for a former greater cosmopolitanism of the ant fauna and, hence, a proof in favour of the second biogeographic school.

The original analysis from which the conclusions of WILSON (1985 c, 1988) had been drawn contains several factual, methodological and logical sources of error. These sources of error can be grouped in the following five categories affecting 1) the data, 2) the definition of the variables, 3) the choice of the statistical test, 4) the statistical constraints, and, 5) the hypothesis tested. I shall explain each of them in the following five paragraphs:

1. The data. — The units of count on which the analysis is based are "ant genera and well-marked subgenera". It may prove difficult to find two taxonomists agreeing entirely on the same list of genera, but consideration of "well-marked" subgenera adds to the list a major component of subjectivity. It appears that consideration of these subgenera does not change anything significant either with respect to the distribution patterns of the Hispaniolan ants or to the major conclusions to be drawn about them besides than lengthening the list of taxa. Under paragraph 3 I shall show the necessity for greater sample sizes enabling the statistical treatment of the data and the failure to attain an acceptable size in the analysis by WILSON (1985 c). The list of taxa, in itself, is either very subjective or erroneous in some respects. Additional changes are necessary today because of taxonomic information published after 1985; new ant genera have been equally recorded in amber after 1985 and some are still unpublished. I shall give an updated list of the Hispaniolan ant genera in which all differences with WILSON's list are individually justified in parentheses after each generic name. Excluding three genera probably introduced on Hispaniola by man

and already listed as such by WILSON, the following are the fossil and extant Hispaniolan genera of ants known to date (changes or additions to WILSON's list are preceded by an asterisk):

Acanthognathus (reported in amber by BARONI URBANI & DE ANDRADE, 1994), *Acanthostichus* (present in amber only, DE ANDRADE, in preparation), *Acropyga, Anochetus, *Apterostigma* (present in amber only, DE ANDRADE, in preparation), *Aphaenogaster, Azteca, *Brachymyrmex* (present also in amber, BARONI URBANI unpublished), *Camponotus, Crematogaster, Cylindromyrmex, Cyphomyrmex, *Dendromyrmex* (present in amber only, DE ANDRADE, in preparation), *Diplorhoptrum¹, *Discothyrea* (present in amber only, P. S. WARD personal communication), *Dolichoderus* (= *Monacis* = *Hypoclinea*, synonymies by SHATTUCK, 1992), *Ephebomyrmex, Erebomyrma, *Eurhopalothrix* (present also in amber, P. S. WARD personal communication), *Gnamptogenys, Hypoponera, Ilemomyrmex, *Leptomyrmex* (reported in Dominican amber by BARONI URBANI, 1980), *Leptogenys, Leptothorax* (= *Nesomyrmex* = *Macromischa*, synonymies by BOLTON, 1982), *Linepithema* (= *Iridomyrmex*, synonymy by SHATTUCK, 1992), *Monomorium, Mycocepurus, Myrmelachista, Neivamyrmex*, new genus A near *Rogeria* (cited as such by WILSON, not seen by me; BARONI URBANI & DE ANDRADE, 1994, report a poorly preserved specimen similar to *Rogeria* which has been omitted from the list to avoid possible redundancy), *new genus B of Dolichoderinae (present in amber only, DE ANDRADE, in preparation), *Octostruma, Oxyidris, Pachycondyla, Paraponera, Pheidole, Platythyrea, *Pogonomyrmex* (present in amber only, P. S. WARD personal communication), *Prenolepis* (given as extinct on Hispaniola by WILSON, it is actually represented on the island by the Antillean endemic *P. gibberosa* ROGER recorded from Haiti by AGUAYO, 1932, and reported also by KEMPF, 1972), *Prionopelta, *Proceratium* (present in amber only; LATTKE, 1990), *Pseudomyrmex, Odontomachus, Solenopsis* (= *Euophthalma*,

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¹ This genus is listed as a well-defined subgenus of *Solenopsis* by WILSON (1985 c). Formerly regarded a synonym of *Solenopsis*, it was raised to generic status by BARONI URBANI (1968), an opinion shared by many but not by BROWN (1973), who did not justify his point of view, and by BOLTON (1987), who recognized the consistency of the genitalic characters particular to *Diplorhoptrum* but doubted their generic value. His point of view has been followed by CASEVITZ-WEULERSSE (1990). Since no intermediate forms are known between the two genera, and the male genitalia of *Diplorhoptrum* are highly distinctive and unique among all Formicidae in many important structural details (see the description by BARONI URBANI, 1968), then accepting the synonymy of the two genera would require some objective evidence, evidence which has not yet been produced. A more crucial criticism of the splitting of the two genera was formulated in a personal communication by PHILIP S. WARD: the separation of *Diplorhoptrum* from *Solenopsis* on the basis of genitalic morphology would make *Solenopsis* paraphyletic. I am forced to agree with this view if morphological characters only are considered. In addition to the morphological differences, however, there is good presumptive evidence that the two genera also differ (a) karyologically, and (b) biochemically. Species of *Diplorhoptrum* are reported to have a diploid chromosome number $2n = 22$ and species of *Solenopsis* $2n = 32$ (see e. g. the review by CROZIER, 1975). The venom produced by the poison glands of *Diplorhoptrum* contains 2-alkyl-6-methylpiperidines only as *trans*-isomers and *N*-methylpiperidines; the latter compounds are unknown from *Solenopsis* and 2-alkyl-6-methylpiperidines are present in *Solenopsis* in both *cis*- and *trans*- forms . For the time being I regard the diploid chromosome number $2n = 32$ as a plausible synapomorphy of *Solenopsis*. The diploid number $2n = 22$ of *Diplorhoptrum* should be considered the plesiomorphic condition since it is shared by *Diplorhoptrum* and by the related genus *Monomorium*. The capacity of synthesising 2-alkyl-6-methylpiperidines appears to be a strong synapomorphy of *Diplorhoptrum* + *Solenopsis*. I am inclined to consider the presence of the *cis*-isomere in *Solenopsis* the apomorphic condition since the *trans*-isomere is shared by both, *Diplorhoptrum* and *Solenopsis* and the related genus *Monomorium* produces different alkaloidal venoms. On the contrary, the unique presence of *N*-methylpiperidines in *Diplorhoptrum* should be regarded as an additional synapomorphic character for this genus (information on the chemicals compiled essentially from ATTYGALLE & MORGAN, 1984).

synonymy by ETTERSHANK, 1966), *Strumigenys*, (= *Smithistruma*, synonymy by BARONI URBANI & DE ANDRADE, 1994), *Tapinoma*, *Trachymyrmex*, *Wasmannia* (present also in amber, DE ANDRADE, in preparation), *Zacryptocerus* (= *Paracryptocerus* = *Hypocrypto-cerus*, synonymies by KEMPF, 1973).

This list is likely to experience further changes in the future for purely taxonomic reasons. At least the following genera may prove to be junior synonyms of others: *Erebomyrma* = *Oligomyrmex*, *Ephebomyrmex* = *Pogonomyrmex*, and *Zacrypto-cerus* = *Cephalotes*. In case of demonstration of one or more of these synonymies, *Oligomyrmex* would then represent one additional extinct genus distributed in the Old World, the suppression of *Ephebomyrmex* would render *Pogonomyrmex* present in the Recent and fossil fauna, and merging *Zacryptocerus* into *Cephalotes* would change nothing for the purpose of the present analysis.

2. The definition of the variables. – The statistical analysis is based on the presence/absence among Hispaniolan ant genera and subgenera of the following four traits: (a) Flightless queen, (b) Large individuals or colonies, (c) High specialization as predators or social parasites or in nest site, and, (d) Also found in living Old World fauna. Only traits (c) and (d) are found to differ among living and fossil genera in a statistically significant way. The paper does not indicate which genera are attributed to which variable. Variables (a) and (d) are objective ones and there should be no disagreement on their individual generic attribution. On the contrary, under the extant Dominican genera with large colonies (trait b) I would consider at least *Solenopsis* and *Crematogaster*. WILSON considers this trait to be present in 4.5% out of 22 genera (i. e. in only one genus) and I am unable to decide in an objective way which one I should remove from the list and why. Variable (c) is even more hetero-geneous and difficult to assess; it groups genera highly specialized either as preda-tors, or as social parasites, or in nest site. One could argue again about the most proper attribution of genera like *Pheidole* comprising perfectly omnivorous species, others restricted to seed predation and others feeding on termites only, or genera like *Crematogaster* embracing "normal" terricolous species together with others con-structing only carton nests on trees and others living in hollow rhizomes of epi-phytes. Possession or not of these traits appears to be particularly difficult to extend to the fossils. But the trait I had the greatest difficulty in assessing is the social parasi-tism. Although eleven Hispaniolan ant genera contain a numerically insignificant fraction of social parasitic species world-wide (none of which is known to me from Hispaniola) I have up to recently inquired which Hispaniolan ant genus can be con-sidered under any circumstances as being socially parasitic as a whole. It was only recently that I allayed my doubts while discovering that such genus appears to be unknown to WILSON as well: no one of the 34 Hispaniolan "genera and well marked subgenera" on which WILSON's analysis is based neither a single Hispaniolan species is cited as being exclusively or prevailingly parasitic in the list of parasitic ants of the world published by HÖLLDOBLER & WILSON (1990). Trait (c), hence, has been ex-cluded from the statistical analysis. Discharging variables (a) and (b) because no stati-stical difference had been demonstrated for them and variable (c), too vaguely defined, the re-analysis presented in this paper will be focused on trait (d) which is objectively definable and of the highest biogeographic interest.

3. The choice of the statistical test. – The choice of the *G*-statistics of independence is not appropriate for a sample of the size of the Dominican amber ant genera and subgenera included in WILSON's analysis (*n* = 34). SOKAL & ROHLF

(1969, page 598) state that "when no computer is accessible the chi-square or G-tests can be used to yield approximate probabilities when sample sizes are so large as to make desk calculator operation impractical. When n is smaller. . . the approximations are not so good". Other statisticians (e. g. Koch & Bhapkar, 1982) are more tolerant about the sample size which is judged appropriate when it includes individual counts $m_{ij} \geq 5$. Wilson's analysis is based on the following quantities, given as percentages in his paper and translated into integers by me: 0%, 4.5%, 4.5%, 68% of 22 (= 0, 1, 1, 15 genera per category) and 8.3%, 25%, 33.3%, 33.3% of 12 (= 1, 3, 4, 4 genera per category). In the literature, one often finds the suggestion as how to deal with small numbers ($n < 200$) by applying Yate's correction, though its use is not recommended by Grizzle (1967), yet this appears unimportant in this context since no mention to the use of correcting factors is made in the paper.

4. The statistical constraints. − Wilson (l. c.) admits that "some genera and subgenera possess more than one trait, and many possess none; hence the percentages do not sum to 100". This violates the basic assumption of independence necessary to any test of contingency. Practically, the data did not conform to the algebraic symmetry of the G table which imposes $(a + c) + (b + d) = (a + b) + (c + d) = a + b + c + d = n$, where $a, b, c, d, \ldots$ are the cells in a contingency table and n is the total number of observations.

A formally correct and updated contingency table for the Hispaniolan ant genera is presented here in Table 1.

Combining the resulting individual 2×2 tables by Mantel-Haenszel statistics gives a non-significant global result with $p = 0.277$. This result may be explained, in part, by the small figures relative to the variable apterous vs. winged gyne (recorded in 0, 0, 1 and 1 cases respectively). Association between the variables extinction and

Tab. 1.   Distribution of three potentially significant traits considered by Wilson (1985 c) among the ant genera known from Hispaniola.

Ant genera	Status	Gyne	Old World	Count
Neivamyrmex	extinct	apterous	absent	1
Leptomyrmex ([1])	extinct	apterous	present	1
Acanthognathus, Acanthostichus, Apterostigma, Azteca, Cylindromyrmex, Dendromyrmex, Erebomyrma, Ilemomyrmex, new genus A, new genus B, Octostruma, Oxyidris, Paraponera, Pogonomyrmex	extinct	winged	absent	14
Discothyrea, Dolichoderus, Prionopelta, Proceratium	extinct	winged	present	4
none	extant	apterous	absent	0
none	extant	apterous	present	0
Brachymyrmex, Cyphomyrmex, Ephebomyrmex, Linepithema([2]), Mycocepurus, Myrmelachista, Pseudomyrmex, Trachymyrmex, Wasmannia ([2]), Zacryptocerus	extant	winged	absent	10
Acropyga, Anochetus, Aphaenogaster, Camponotus, Crematogaster, Diplorhoptrum, Eurhopalothrix, Gnamptogenys, Hypoponera, Leptogenys, Leptothorax, Monomorium, Pachycondyla, Platythyrea, Prenolepis, Odontomachus, Solenopsis, Strumigenys, Tapinoma	extant	winged	present	20

([1]) Shattuck (1992) reports the presence of winged gynes in some undescribed species, but these species show a very different habitus from "usual" Leptomyrmex as the one described from amber.
([2]) Old World records due to human introduction not considered.

presence in the Old World is high ($X^2 = 10.16$ with $p = 0.0014$). Due to the small figures involved, individual 2 × 2 tables for each pair of variables have been analysed by means of the FISHER's exact probability test (two-tailed). Excluding from the calculations the absence of female wings which is known in two genera only, there is only one statistically significant difference between the number of extant ant genera present in the Old World (20 = 40%) and those extinct (4 = 8%). The difference between these two quantities is highly significant with $p = 0.0031$. This result confirms one of those obtained by WILSON (1985 c).

5. The hypothesis tested. The result confirmed here under 4. indicates, however, that genera now extinct on Hispaniola are statistically less represented in the Old World than those still alive on the island. The biogeographical meaning of this result is not very clear: the only significance one can extrapolate from it is that ant genera which have undergone extinction on Hispaniola since amber times had narrower distributions than those still present on the island today. WILSON's extrapolation that dispersal took place only or mainly after amber times is illegitimate. The reason for this is that the statistics compared extinct versus non-extinct genera, i. e. the second category contains extant and fossil genera together and, as such, it comprises genera which may have undergone dispersal before, during, or after amber times.

To test the hypothesis that dispersal was posterior to amber times or that it increased in time, one should compare the presence/absence of the two following categories in the Hispaniolan ant genera present in the Old World: fossil only and extant only, as arranged here in Table 2.

Tab. 2. Presence or absence of Hispaniolan ants in the Old World tabulated to test dispersal among fossil and extant genera.

Ant genera	Status on Hispaniola			Status in the Old World	Count
	fossil only	fossil and extant	extant only		
Discothyrea, Dolichoderus, Leptomyrmex, Prionopelta, Proceratium	●			present	5
Acanthognathus, Acanthostichus, Apterostigma, Azteca, Cylindromyrmex, Dendromyrmex, Erebomyrma, Ilemomyrmex, new genus A, new genus B, Neivamyrmex, Octostruma, Oxyidris, Paraponera, Pogonomyrmex	●			absent	15
Acropyga, , Leptogenys, Monomorium			●	present	3
Ephebomyrmex, Mycocepurus			●	absent	2
Anochetus, Aphaenogaster, Camponotus, Crematogaster, Diplorhoptrum, Eurhopalothrix, Gnamptogenys, Hypoponera, Leptothorax, Pachycondyla, Pheidole, Platythyrea, Prenolepis, Odontomachus, Solenopsis, Strumigenys, Tapinoma		●		present	17
Brachymyrmex, Cyphomyrmex, Linepithema[1], Myrmelachista, Pseudomyrmex, Trachymyrmex, Wasmannia[1], Zacryptocerus		●		absent	8

[1] Old World records due to human introduction not considered.

In fact, only extinct genera allow an inference about ancient (i. e. before present) dispersal. Similarly, only the genera which colonised Hispaniola after amber times should be considered for younger (i. e. after amber times) dispersal. The table shows that five Hispaniolan extinct ant genera reached the Old World, versus only three extant genera with a comparable distribution. This contrasts with WILSON's conclusions and with conventional biogeographic expectation. According to the "centre of origin" hypothesis, older distributions of taxa (like those of the extinct amber genera) should be narrower than those of the extant ones. This hypothesis, however, assumes taxa of comparable rank (i. e. genera) and comparable evolutionary speeds (a factor virtually unknown among ants).

The different frequencies in Table 2 appear to be statistically significant (MANTEL-HAENSZEL Chi-Square = 8.654 with p = 0.003, FISHER's exact probability = 7.25×10^{-3}). Excluding from the analysis 25 genera reported from both, the contemporary and the amber fauna of Hispaniola and allowing no inference about their presumed time of dispersal, shows that 5 (= 20%) of the remaining ant genera reached the Old World and have undergone extinction on Hispaniola versus 3 (= 12%) genera which presumably colonized Hispaniola after amber times and show a similar distribution pattern. This difference is too small and is not confirmed statistically (two tailed FISHER's exact probability = 0.281). This result, however, could be modified (i. e. the difference could become statistically significant) by demonstrating the probable synonymy between *Erebomyrma* and *Oligomyrmex* previously mentioned.

We are forced to conclude that the study of the Hispaniolan ant genera, fossil and Recent, does not endorse any of the two major biogeographical schools mentioned above: there is no evidence for dispersal since amber times and a modest numerical indication of an opposite phenomenon (i. e. broader geographic distributions among extinct rather than among extant genera) cannot be demonstrated statistically.

The Australian genus *Leptomyrmex*, until recently, appeared to represent the sole typical Recent Old World element within the Dominican amber fauna as a whole. This record, therefore, had been regarded either as wrong or as exceptional. More recently, GRIMALDI (1991), described two mycetobiine woodgnats from Dominican amber belonging to Old World tropical genera and KRISHNA & GRIMALDI (1991) reported the first *Mastotermes* from Dominican amber. This genus of termites comprises only one Recent species in northern Australia but was already known through several fossils from different Eocene — Miocene deposits in Europe and from Mexican amber (probably Early Miocene). The distribution pattern of *Mastotermes* is not too different from the one of the ant tribe Leptomyrmecini which are recorded from the contemporary Australian-Oceanian fauna, and, as a fossil, from Dominican and Sicilian amber (probably Miocene).

In this paper I present evidence for even closer (species-group level) affinities between the Dominican and the contemporary Old World fauna. As a matter of fact, DE ANDRADE (1994) was the first to report the existence of Old World relationships at species-group level in the Dominican amber ant fauna. She described a new species of amber *Anochetus*, a genus of ants represented in Dominican amber by different species, some with Neotropical and one with New Caledonian and Oceanian affinities, as is the case for the *Pheidole* discussed in this paper. In another paper by DE ANDRADE (1995) a comparable species level Old World relationship is reported for a Dominican amber *Aphaenogaster*. These three examples of species-group Old World affinities in the genera *Anochetus*, *Aphaenogaster* and *Pheidole*, together with the

Fig. 12. Geographic distribution of the amber fossils discussed in this paper (indicated by an arrow) compared with the one of their most related contemporary species of *Pheidole* subg. *Pheidolacanthinus* (dotted area).

case of the genus *Leptomyrmex*, may suggest that the geographic distribution of ants narrowed in time contrarily to the expectations of the "center of origin" hypothesis and according to the thinking exemplified here by CROIZAT et al. (1974). Or, at least, species-group level extinction in the Hispaniolan ant fauna was greater than genus-level extinction since amber times.

The close relationship between Dominican amber and the Recent Notogean fauna at species-group level implies that the ants experienced an evolutionary speed even lower than the one we were already forced to assume by the simple presence of non-related congeners as was the case for *Leptomyrmex*. It is worth recalling here that *Pheidole tethepa* has been described from amber from La Toca which, with an esti-mated age of 15−45 million years (ČEPEK in SCHLEE, 1990: 53) or 30−40 million years (POINAR, 1992), is among the oldest deposits reported from the Dominican Republic.

However, suggestive the fact that these contemporary Old World elements survive today essentially in the Malayan, Australian and Oceanian realms (see Fig. 12), it is impossible to hypothesize previous privileged continental connections between these regions and the Caribic area.

The sole explanation reasonably applicable to these coincident Dominican and Notogean distributions is that already invoked for *Leptomyrmex* and *Mastotermes*, i. e. a former cosmopolitanism of these clades which survived today only or mainly in the refuge of the Notogea, as is the case for many other animal and plant relics. The broad Oceanian extension of "*Pheidolacanthinus*" visible in Fig. 12 is due essen-tially to the records of *Pheidole sexspinosa* EMERY, a New Guinean species which must have colonized several Polynesian islands in much more recent times.

An alternative explanation to the Old World affinities of the amber ant fauna would be considering the previously mentioned contemporary Notogean records as due to immigration from the New World instead of being due to area restriction since amber times. However, we have no evidence supporting this hypothetical mi-gratory route from the probable relationships of the extant Notogean ant fauna.

The major changes affecting the world ant fauna since Dominican amber times, hence, seem not to concern the faunal composition in a remarkable way but are cha-racterized essentially by dramatic contractions or extensions of the distribution areas. The Dominican amber is offering an increasing number of examples of former broader distribution of clades surviving only in relic areas today.

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