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The Identity of the Dominican *Paraponera* (Amber Collection Stuttgart: Hymenoptera, Formicidae. V: Ponerinae, partim)

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With 3 Figures

Summary

Paraponera dieteri n. sp. is described from Dominican amber estimated to be 15 to 45 million years old. The genus *Paraponera* was considered monotypic until now and its sole previously known species (*P. clavata*) is not uncommon over large areas of Central and South America, but appears to be absent on all Caribic Islands.

The good preservation of the fossil allows an exhaustive comparison between the two species which differ essentially in allometric and sculptural details. This suggests a low evolutionary rate for *Paraponera* even considering the most conservative age estimates for Dominican amber.

Zusammenfassung

Eine neue Ameisen-Art aus Dominikanischem Bernstein, *Paraponera dieteri* n. sp., wird beschrieben. Die Schätzungen für das Alter des Bernsteins liegen zwischen 15 und 45 Mio. Jahren. Die Gattung *Paraponera* wurde bis jetzt für monotypisch gehalten. Ihre einzige bislang bekannte Art, *Paraponera clavata*, ist in weiten Gebieten Mittel- und Südamerikas nicht selten. Sie scheint jedoch auf den Karibischen Inseln durchweg zu fehlen.

Die gute Erhaltung des Fossils erlaubt einen eingehenden Vergleich zwischen den beiden Arten; sie unterscheiden sich im wesentlichen in Details der Maßverhältnisse und der Skulptur. Dies legt eine nur geringe Entwicklungsgeschwindigkeit der Gattung *Paraponera* nahe, selbst wenn man die geringsten Altersschätzungen für den Dominikanischen Bernstein zugrunde legt.

1. Introduction

The monotypic ant genus *Paraponera* is quite regularly distributed in Central and Southern America: from Nicaragua in the North, and south to Bolivia, Paraguay, and to the states of Amazonas, Mato Grosso and São Paulo in Brazil. Its sole species, *P. clavata* (FABRICIUS), is not uncommon within this range and is famed both for being one of the largest known ants and for the severity of its sting (WEBER, 1937).

These attributes make it well known to the natives. As a consequence, this is one of the few ant species distinguished by several Indian, Spanish and Portuguese local names in different parts of its range. The most frequently cited of these names is probably the Venezuelan "hormiga veinte-cuatro" (twenty-four ant), implying that its sting can kill a man in 24 hours. In Brazil the Portuguese name is "formigão" or "formigão-preto" (big black ant), but the ant is commonly referred to by the Indian-derived names "tocandira", "tocandera" or "tocanquibira", from the Tupi-Guarani "tuca-ndy", meaning the one wounding deeply (SILVEIRA BUENO, 1987). Some Indian tribes used to induce workers of this species to sting boys as a test of courage during ceremonies of initiation to adulthood (SANTOS, 1985). VON IHERING (1928) associates both the name "tocandira" and its use for initiation rituals to the comparably giant ponerine genus *Dinoponera;* the discrepancy can be accounted for if one assumes that the Indians did not discriminate between the two (as VON IHERING also probably failed to do) and recognized and used both genera according to their local availability. The venom of *Paraponera* is proteinaceous and contains a haemolytic component: the symptoms associated with a *Paraponera* sting include burning, several hours of fever, trembling, perspiring, strong pains (sometimes recurring after a few hours), local paralysis, and occasionally large blistering (summarized from HERMANN & BLUM, 1966).

In addition to the giant size and vicious sting, *Paraponera* is a very distinctive ant genus exhibiting a considerable number of clear apomorphies, like the V-shaped antennal scrobes, the strongly constricted postpetiole, the spinose hypopygium, the male abdominal sternite VIII with long anterior apodemes, paired with remarkable probably plesiomorphic traits such as the spinose coxae, toothed tarsal claws and a developed anal lobe on the hind wings. EMERY (1901), in his classification of the Ponerinae, stressed the importance of these characters and placed *Paraponera* in a monotypic tribe, the Paraponerini, close to the Ectatommini. BROWN (1958) synonymised the former with the latter and transferred *Paraponera* to the Ectatommini. Both opinions being based on a different appreciation of the same facts, the "right" classification must await a detailed tribal analysis of the whole subfamily Ponerinae.

WILSON (1985) describes the presence of an unidentified fossil *Paraponera* in Dominican amber. The single specimen on which the record is based is a badly damaged worker allowing drawing only of one fore tarsal claw and of part of the last gastral somite. If, on these characters, the generic assignment of the specimen in question may be assumed as a reasonable certainty, very little can be inferred about its relationships with the sole extant *Paraponera* species. WILSON, however, underlined the interest of his finding as being twofold: his record represented the largest fossil ant in absolute and another significant document of the dramatic faunal changes in the Caribic since amber times.

The amber collection of the Stuttgart Museum contains one virtually intact worker of *Paraponera* in Dominican amber. It will be described in this paper as the second species in the genus and as an example of presumably low evolutionary speed among ants.

2. Material and methods

The single *Paraponera* worker was embedded in an elongate piece of amber (4.7 x 2.0 cm), brown with green reflections. The amber contains some minor and three major bubbles, one of which renders ventral examination of the ant petiolar area difficult. The ant is obliquely included at about two thirds of the length of the amber specimen with the appendages folded close to the body (Fig. 1). Two major fissures in amber prevent viewing from the right side. In order to improve the examination of the specimen, the amber on the left side of the ant has been cut and polished parallel to its sagittal plane in order to enable lateral vision. The piece had probably originally been polished so as to respect its natural shape as much as possible. As a consequence of this, the ant is completely embedded with its dorsal side only a few mm under the amber surface. This surface, however, is affected by at least three major convexities, one parallel and two transverse to the ant body. Each of these curves on the surface produces a lens-effect making examination of otherwise perfectly preserved parts difficult and creates remarkable distortions on other, well visible parts. Further grin-

Fig. 1. Detail of the amber sample Do-4112 photographed after immersion in 66% sucrose solution to show the good preservation conditions of the ant specimen and the disappearance of deformations resulting from convexities on the amber surface.

ding and polishing of the amber dorsal to the ant was excluded so as to avoid the risk of irreparable damage to the specimen. All previously mentioned visual difficulties, however, have been overcome by observing the amber specimen in a 66% sucrose solution which has a refraction index of 1.558, i. e. very similar to that of amber (WEAST, 1982). A rough appreciation of the good examination conditions attained in this way can be gained by observing the lack of asymmetries in the photograph of Fig. 1, taken after immersion in the sucrose solution.

The amber sample contains only one additional animal inclusion, a small proctotrupid wasp slightly over the *Paraponera* intermandibular space.

The drawing of the fossil presented in this paper is by ARMIN CORAY. Although on one hand, all parts drawn are visible in the amber specimen, on the other, the actual execution of the drawing needed some extrapolation and reconstruction work, the main steps of which will be explained below. The following text is essentially an English rewording of Mr. CORAY's reconstruction protocol:

The specimen is well visible in dorsal view (curved polished amber surface) and on its left side (flat polished surface). The reconstruction was executed basically from the dorsal view, though the lateral view has been necessary on occasion to examine some body parts further or to resolve some details. Just to make an example, the V-shaped antennal scrobes are nearly indistinguishable in dorsal view (covered by the antennal scapes) but very evident in lateral view. The ant has been drawn in an artificial "anatomical" posture in order to represent graphically as much information as possible. Since the legs of the amber specimen are folded close to the body, the relative length of their different parts has been largely extrapolated from measurements on specimens of the Recent species *P. clavata*.

The different body parts have been directly observed in the amber specimen or reconstructed for the drawing as follows:

Head (incl. mandibles and antennae), thorax and abdomen drawn exactly as observed in part with the help of immersion in the sucrose solution.

First pair of legs. (Coxa) and trochanter barely visible in amber, largely inspired from Recent specimens. Femur visible in amber but inspired from Recent specimens for the orientation in the drawing. Tibia (and tarsus) partly deformed or covered by impurities in amber, drawn from the fossil with some details added from fresh material.

Second pair of legs. Coxa and trochanter visible but impossible to focus the microscope on these parts properly; preliminary sketch from the fossil and final drowing adjusted to the proportions of Recent specimens. Femur and tibia completely visible either in lateral or ventral view, only details taken from Recent specimens. Tarsi well visible in 3/4 to dorsal view; Recent specimens used only to reconstruct the full dorsal view.

Third pair of legs. Coxa and trochanter visible in the fossil; Recent specimens used as comparison with parts of the fossil difficult to view adequately. Femur and tibia well recognisable, particularly in lateral view, though partly covered by femur II and tibia II; tibia fully visible in full dorsal view; the half-median view of the drawing is inspired from Recent specimens after transformation of the contours drawn from the fossil. Tarsi visible only in perspective, particularly the first tarsomere; the relative proportions of the tarsomeres are derived from Recent specimens.

Sculpture. The ant body is partly covered by a thin spotty gaseous film of irregular size and distribution. This does not affect the major body sculpture (i. e. the striae), but sometimes makes appreciation of the underlining microsculpture difficult. For some body parts (petiole, postpetiole, scape, legs) the structure visible on gas-free parts has been arbitrarily extended to the whole sclerite.

Pilosity. The body pilosity has been drawn exclusively from the fossil; the one on the legs and the legs' spinulae have been largely but not exclusively reproduced from Recent specimens.

3. Description of the new species *Paraponera dieteri* n. sp.

Fig. 2

Holotype: Worker (unique) in Dominican amber bearing the number Do-4112 in the collection of the State Museum of Natural History, Stuttgart (Department of Phylogenetic Research). Fifth median left tarsomere missing, abdominal tip morphology confused by contact with the amber surface, otherwise complete.

Derivatio nominis: The species is named after DIETER SCHLEE who built up the Dominican amber collection of the Stuttgart Museum with great investment of time and energy, an investment without which this and many other contributions to the study of amber would not have been possible.

Diagnosis. – A (relatively) very small *Paraponera* characterised essentially by a narrow head and dominant longitudinal rugosity, particularly before and on the infraspinal area of the pronotum.

Description. – Worker. Head longer than broad, sub rectangular. Anterior clypeal border slightly lobate, with two small denticles at the edges of the lobe. Occipital border straight. Frontal laminae feebly sinuous, continuing posteriorly into deep, V-shaped antennal scrobes. Mandibles robust, armed with 10–11 small, irregular denticles. Eyes at the middle of the sides of the head, slightly protruding from from the cephalic capsule in dorsal view. Antennae with straight scapes trespassing backwards the occipital border of about their maximum width. Second antennomere (first funicular joint) much shorter than all the others. Antennomeres 3–11 continuously decreasing in size from the base to the apex. Last antennomere (12) only slightly longer than the preceding one.

Trunk relatively short and narrow, with parallel sides broadening inconspicuously at the height of the humeral angles. Humeral spines short and expanding laterally on the same plane as the pronotal surface. Propodeum unarmed, with the superior face passing by means of a broad curve into the descending one. Petiole sessile, with an abrupt anterior face and a superiorly flat node. Ventral petiolar spiniform process covered by the femur in lateral view but partly visible in ventral and oblique views. Postpetiole broadly campaniform, twice as broad as the petiole and articulated over its whole width with the first gastral segment. Dorsal stridulatory organ very well visible. Gaster narrow, slightly broader than the postpetiole.

Colour uniformly black.

Sculpture composed essentially of heavy, irregular rugae longitudinally arranged over most of the body. Head longitudinally rugose over most of its surface, the rugae interrupted only by weak anastomoses; clypeal and frontal areas only finely longitudinally striate; external face of the mandibles longitudinally striate. Trunk equally longitudinally rugose; the rugae partly effaced on the dorsum, running parallel on the sides and joining medially on the propodeal declivity where they are transverse. Posterior face of the petiole irregularly longitudinally rugose. Postpetiole with weak reticulate impressions. Gaster proper smooth and shining. Appendages punctate.

Pilosity. Most of the body covered by long, suberect, pointed hairs, thicker and shorter on the legs, on the scapes, and much shorter on the genae and the mandibles. Funiculi mostly covered by minute pubescence.

Measurements (in mm) and indices, compared with 7 workers of *P. clavata* from different localities in Brazil, French Guyana, Peru, and Costa Rica selected as representing the size variation among the material available for the present study. Measurements reported by WILSON (1985) for the amber specimen examined by him are given in parenthesis after those referring to the *P. dieteri* holotype.

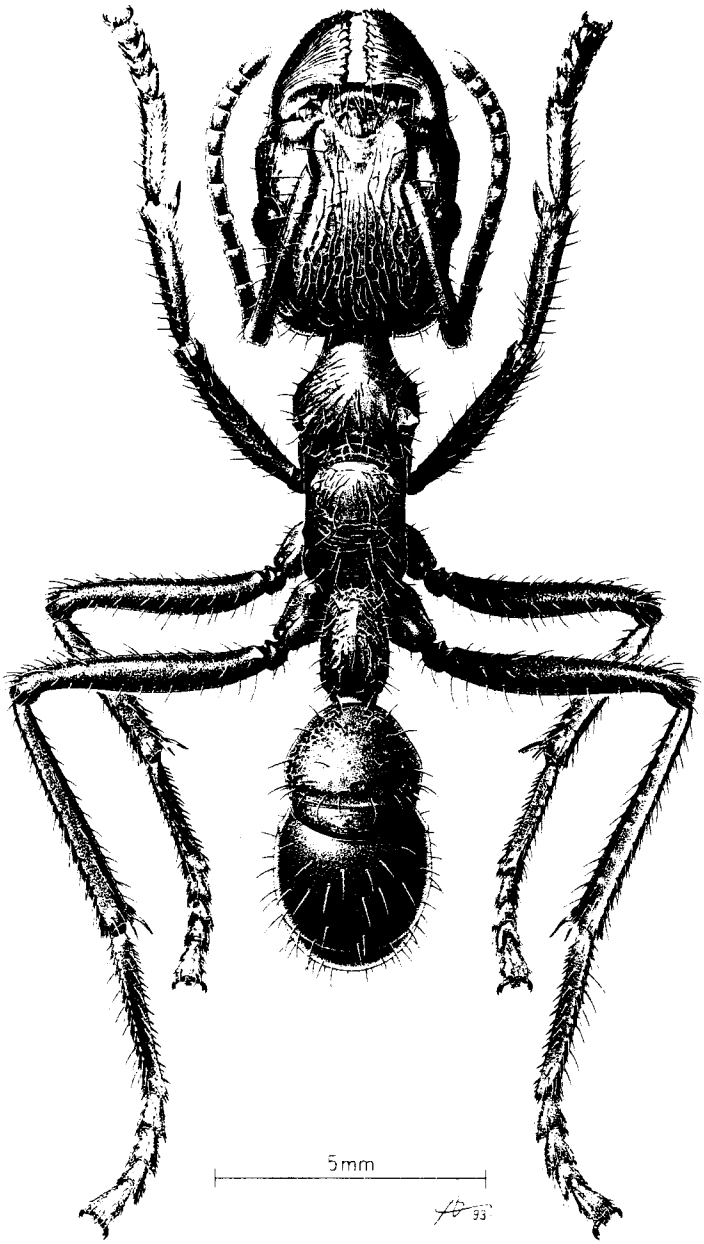

Fig. 2. *Paraponera dieteri* n. sp., worker, holotype. Drawing by ARMIN CORAY. Body posture artificially modified to allow maximum drawing of visible information. Imperfectly visible parts of the legs have been drawn by partial inference from *P. clavata* and reconstructed. Further explanations in text.

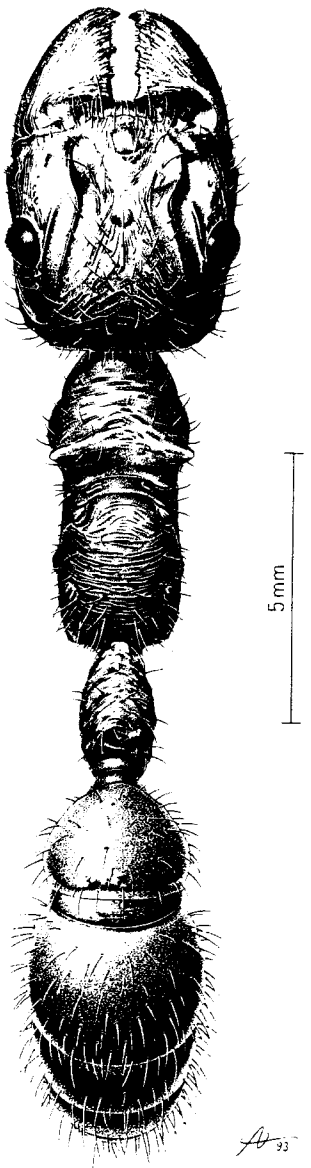

Fig. 3. *Paraponera clavata* (FABRICIUS), small worker from St. Jean de Maroni (French Guyana). Drawing by ARMIN CORAY. This specimen is similar in size to the fossil *P. dieteri* and the different body parts have been drawn in comparable orientation (i. e. petiole articulated upwards and partly folded over the propodeal declivity) in order to facilitate the comparison. Appendages artificially omitted.

	dieteri	*clavata*
Total length (mandibles excluded)	19.8	22.7– 25.1
Head length (HL)	4.5 (4.4)	4.3– 4.9
Head maximum width (eyes excluded) (HW)	3.6	4.0– 4.9
Scape length (SL)	3.6 (3.6)	4.3– 4.8
Trunk length	5.1 (5.4)	5.5– 6.1
Pronotum maximum width (spines excluded)	2.4	2.6– 3.0
Petiole maximum width	1.3	1.3– 1.6
Postpetiole length (PPL)	1.9	2.1– 2.6
Postpetiole maximum width (PPW)	2.5	2.5– 3.2
Gaster maximum width (GW)	3.0	3.3– 3.9
Cephalic Index (HWx100/HL)	80.0	90.7–100.0
Scape Index (SLx100/HW)	100.0	97.9–115.4
Postpetiole Index (PPWx100/PPL)	131.6	120.1–128.1
Gastral index (PPWx100/GW)	83.3	78.8– 84.2

Discussion. – WILSON (1985) correctly noticed the small size of the Dominican amber *Paraponera* available to him, a size at or slightly below the lower limit known from extant specimens. His specimen, in addition, appeared to lack a subpetiolar process, a character often considered of generic significance for *Paraponera*, but he doubted the validity of this trait and preferred not to propose a new specific name for the fossil on the base of this sole piece of evidence. The specimen which allowed the present study confirms the dwarfism of the Dominican *Paraponera*, and, by showing a postpetiolar process, the interpretation that WILSON gave of his specimen. The present amber sample, however, by its much better preservation conditions, allows the identification of a certain number of characters which I consider of specific value. Fig. 3 shows, for the sake of comparison, a small worker of *P. clavata* from St. Jean de Maroni (French Guyana) among the most comparable ones to the fossil for its small size. Besides the general small mass and considerable reduction of the pronotal spines, *P. dieteri* can be considered specifically distinct from *clavata* at least because of its proportionally much narrower head (CI = 80, vs. CI > 90 in *clavata*), for the longitudinal rugulation of the body (present to some extent also in *clavata* but never in front of and between the pronotal spines where it is markedly transversal or, rarely, absent), and for the reticulation of the postpetiole (consistently smooth in all specimens of *clavata* I have been able to see).

Considering the allopatry of *P. dieteri* and *clavata* (no *Paraponera* are known from the contemporary Antillean fauna), the magnitude of the time gap between the two species (a minimum of 15 million years according to the current estimates of Dominican amber age given by POINAR, 1992), the various selection factors certainly involved in geographic separation between *dieteri* and *clavata* and in extinction of the first vs. survival of the second, the response of Latin American *Paraponera* populations to all these pressures could be properly defined as the tiniest imaginable.

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