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The ant genus *Aphaenogaster* in Dominican and Mexican Amber (Amber Collection Stuttgart: Hymenoptera, Formicidae. IX: Pheidolini)

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With 5 Figures

Summary

Aphaenogaster amphioceanica n. sp. from Dominican amber and *A. praerelicta* n. sp. from Mexican amber are described from a single worker each. The most apparent characters of *amphioceanica* are the antennal hollows marginated laterally by a prominent carina, and the head with a "neck". This same combination of characters is present in *A. feae*, *A. laevior*, and *A. beccarii*, all Indomalayan, and in *A. swammerdami* from Madagascar. One additional case of relationship between the Dominican amber fauna and Recent Indomalayan biota is observed. On the other hand, *A. praerelicta* shows clear affinities with the Recent Hispaniolan *A. relicta*. The main difference between *praerelicta* and all the known American *Aphaenogaster* is the presence of a pair of pronotal spines which is probably apomorphic for *praerelicta*. Two Recent New Guinean species (*A. loriae* and *A. quadrispina*) also have pronotal spines, but these spines are very different in shape from those of *praerelicta*. Considering the numerous differences between *praerelicta* and the Recent New Guinean species, it is likely that this character has been convergently selected at least twice during *Aphaenogaster* evolution.

Zusammenfassung

Zwei neue Arten der Gattung *Aphaenogaster* werden beschrieben: *A. amphioceanica* n. sp. aus Dominikanischem, und *A. praerelicta* n. sp. aus Mexikanischem Bernstein, von denen jeweils 1 Arbeiterin zur Verfügung stand. Die auffälligsten Merkmale von *A. amphioceanica* sind: Vorstehende Carina am Lateralrand der Antennenhöhlungen und das Vorhandensein einer nackenartigen Verlängerung des Kopfes. Dieselbe Merkmalskombination tritt bei den indomalayischen Arten *A. feae*, *A. laevior* und *A. beccarii* sowie bei *A. swammerdami* von Madagaskar auf. Dies ist ein weiterer Fall von Beziehungen zwischen der Fauna des Dominikanischen Bernsteins und der rezenten indomalayischen.

Andererseits zeigt *A. praerelicta* deutliche Ähnlichkeiten mit der rezenten *A. relicta* von Hispaniola. Der Hauptunterschied zwischen *A. praerelicta* und allen bekannten amerikanischen *Aphaenogaster*-Arten ist das Vorkommen von 1 Paar Pronotum-Dornen bei *A. praerelicta*, wahrscheinlich eine Apomorphie dieser Art. Zwei rezente Arten von Neu-Guinea (*A. loriae* und *A. quadrispina*) haben zwar ebenfalls Pronotum-Dornen, aber in deutlich abweichender Form. Wegen der zahlreichen Unterschiede zwischen *A. praerelicta* und den rezenten Arten von Neu-Guinea darf man wohl schließen, daß die Pronotum-Dornen während der *Aphaenogaster*-Evolution mindestens zweimal konvergent entstanden.

1. Introduction

The genus *Aphaenogaster* is distributed world wide except in the Afrotropical and southern Neotropical regions. It also has a rich fossil and subfossil record which can be listed as follows:

Oligocene. – Baltic amber: *A. sommerfeldi* (MAYR, 1868), *A. mersa* and *A. oligocenica* (WHEELER, 1915).
Florissant shales, Colorado: *A. mayri* and *A. donisthorpei* (CARPENTER, 1930).
Oberrhein region, Germany: *A. maculipes* (THÉOBALD, 1937a).
Aix-en-Provence, France: *A. maculata* (THÉOBALD, 1937b).
A. berendti MAYR (1868) from Baltic amber was transferred to the genus *Stenamma* by WHEELER (1915).
Miocene. – Brunn-Vösendorf, Austria: *A. pannonica* (based on wing imprints) (BACHMAYER, 1960).
Chôjabaru, Japan: *A. avita* (based on wing imprints) (FUJIYAMA, 1970).
Radoboj beds, Croatia: *Ponera fuliginosa* HEER (1849) and *Poneropsis livida* HEER (1867) (both based on wing imprints) tentatively transferred to *Aphaenogaster* by MAYR (1867).
Quesnel beds, British Columbia: *A. longaeva* SCUDDER (1877).
Late Quaternary. – Chihuahuan desert of United States and Mexico: *Aphaenogaster huachucana, A. albisetosa* and specimens near *A. texana* (MACKAY, 1992).

CARPENTER (1930) regarded the Miocene *A. longaeva* from British Columbia as an ant of unprecised genus.

TAYLOR (1964) went a step further in criticizing the systematic assignment of petrified ants and suggested to emend the generic name *Poneropsis* HEER to include all fossils "apparently belonging to the family Formicidae and . . . otherwise unclassifiable" and characterized by "two closed cubital cells and a single closed discoidal", a combination of characters recurring among several distantly related Formicidae. He transferred *A. fuliginosa* (HEER) to *Poneropsis*.

A large amount of papers have already been published on Dominican amber ants (see e. g. the list in DE ANDRADE, 1994). On the other hand, the only published information on Mexican amber ants comes from BROWN (1973) who listed: males of three or more species of ectatommine Ponerinae, workers probably belonging to *Azteca*, a few workers of the *pyramicus* group of *Dorymyrmex*, *Camponotus*, a few specimens of probably *Lasius*, *Pachycondyla*, males probably of *Mycetosoritis*, two workers resembling *Stenamma*, a probable *Pheidole*, and an almost certain *Crematogaster*, without formally describing any of them.

The contemporary American fauna of *Aphaenogaster* includes 21 species in the Nearctic and 6 species in the Neotropical regions distributed between British Columbia and Nova Scotia in the North to Panama in the South. Only one of them, the Haitian endemic *A. relicta* (WHEELER & MANN, 1914), is known from the Caribic area. The genus *Aphaenogaster*, however, includes about 55 species in the Palearctic region, 4 species in the Afrotropical region (1 in North Sahara and 3 in Madagascar), about 18 species in the Indomalayan region, 4 species in the Oceanian region (all in New Guinea), and 3 species in Australia.

2. Material and methods

Two specimens of *Aphaenogaster* have been examined in two samples of amber from the Dominican Republic and Mexico. The two amber samples are as follows:

Do-4629-B (Fig. 1) from the amber collection of the State Museum of Natural History, Stuttgart (Department of Phylogenetic Research). This piece was selected

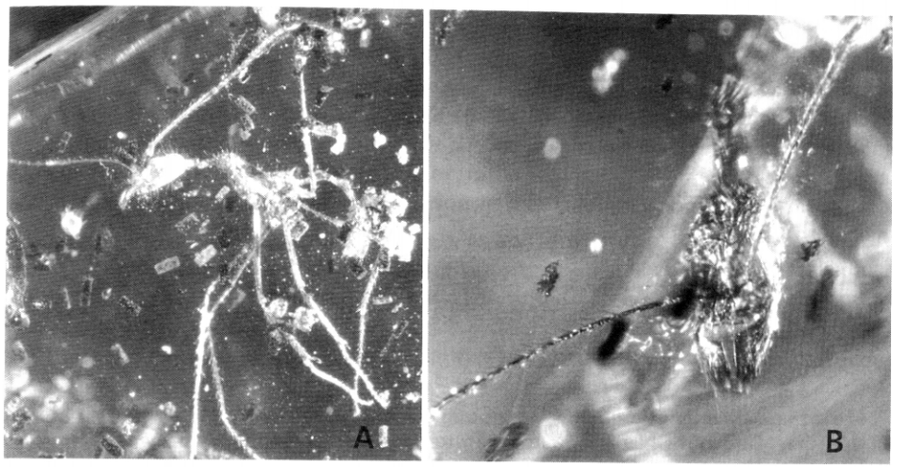

Fig. 1. Specimen Do-4629, habitus, lateral view (A), frontal view of the head (B).

for the collection by Dr. D. SCHLEE because of some unusual contents, as is indicated in the card index as follows: 6 specimens of woodlice (*Pseudarmadillo cristatus* SCHMALFUSS Paratypes), the unusual ant (! long-stretched shape, but "boiled"=shrivelled), reptile skin (? toe with brush), Scatopsidae (shrivelled), spider (shrivelled), mite, debris, numerous regular ? insect faeces pellets, insect fragments. A yellow piece, 4 × 2 × 1.5 cm, containing the ant to be described here. The ant is complete and appears to have been subject to variable extents of compression, leading to different degrees of deformation on many parts of the body which results in a wrinkled appearance.

A Mexican amber sample (Fig. 2) from the collection of Dr. GEORGE O. POINAR Jr., (Department of Entomological Sciences, University of California, Berkeley, U. S. A.). A yellow amber piece containing, in addition to the ant to be described here, three flies, two springtails, a small wasp, a badly preserved insect, and a few pollen grains. The state of preservation of the ant can be considered as good, though

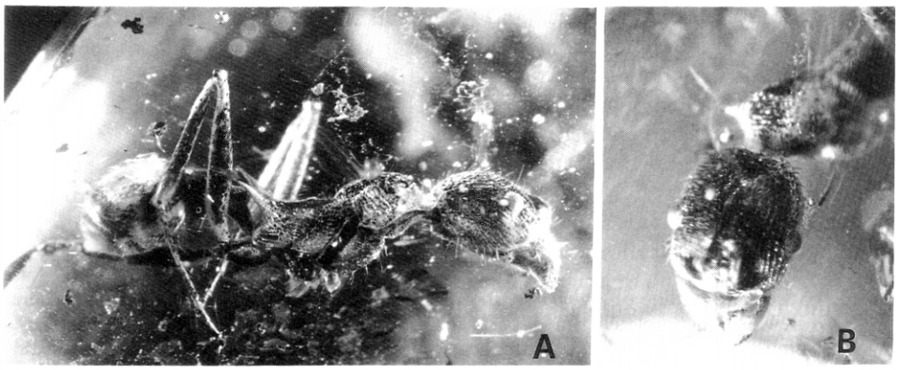

Fig. 2. Mexican specimen, habitus, lateral view (A), frontal view of the head (B).

in *feae*, and 0.10 mm in *curta*; propodeal dorsum in side view sloping up in *amphioceanica* vs. straight in *feae*, and convex in *curta*; body with moderately abundant pilosity in *amphioceanica* vs. body with sparse pilosity in both *feae* and *curta*; size 5.4 mm in *amphioceanica* vs. size 5.5–6.5 mm in *feae*, and 6–9 mm in *curta*; SI 272 in *amphioceanica* vs. SI 204–206 in *feae*, and 196 in *curta*. In addition, *amphioceanica* and *curta* share the four long setae on the anterior border of the clypeus but *feae* possesses six.

Aphaenogaster praerelicta n. sp.
Fig. 2, 4

Holotype: Worker (unique) in an amber sample from the collection of Dr. GEORGE O. POINAR Jr., Department of Entomological Sciences, University of California, Berkeley, U. S. A.

Derivatio nominis: from the Latin *prae* (= ahead of, before) and *relicta* (= a specific name used for an endemic *Aphaenogaster* from Haiti).

Diagnosis. – An *Aphaenogaster* characterized, in the worker, by a pair of short pronotal spines, propodeal spines as long as the basal face of the propodeum, and head without "neck".

Worker (Fig. 4): Measurements (in mm) and indices: Total Length 6.28; HL 1.40; HW 1.16; EL 0.28; EW 0.20; WL 2.08; Petiole maximum length (side view) 0.52; PNW (dorsal view) 0.28; Postpetiole maximum length (side view) 0.40; PPW (dorsal view) 0.48; ML 0.70; CI 82.8; MI 50.0; OI 20.0.

Description. – Head broad posteriorly, with a feeble occipital concavity and without "neck"; gula with two obtuse teeth. Eyes exceeding by 0.05 mm the margins of the head in full face view. Frontal carinae protruding and parallel. Frontal area deeply impressed. Antennal hollows small. Clypeus with a feeble median sulcus reaching the anterior border, slightly concave. Mandibular blades with an apical tooth 0.09 mm long, and a subapical tooth 1/3 shorter than the apical followed by 4–5 denticles.

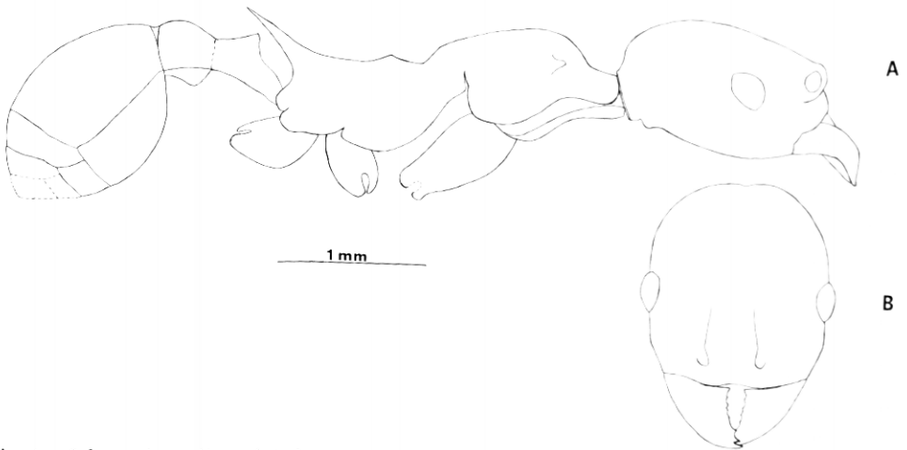

Fig. 4. Schematic outline of *Aphaenogaster praerelicta* n. sp. Worker, holotype. Lateral view (A), incompletely drawn parts correspond to poorly visible body parts. Appendages ommitted. Full frontal view of the head (B).

Trunk robust. Pronotum convex in side view; its humeral angles bearing an obtuse, antero-lateral spine 0.16 mm long. Mesonotum as high as the pronotum anteriorly; its posterior third declivous. Promesonotal suture strongly impressed on the sides and faint on the dorsum. Anterior third of the propodeal dorsum slightly convex, the rest straight. Propodeal spines 0.60 mm long, as long as the basal face of the pronotum, directed slightly upwards and diverging backwards. Propodeal suture completely impressed. Legs stout.

Petiolar node with a subtriangular apex in profile. Postpetiole rounded in side view; its ventral face with an anterior, rounded process.

Gaster nearly round in dorsal view.

Sculpture: head with deep longitudinal rugulation frequently anastomising before the eyes and superimposed with strong, deep minute reticulation and feeble punctures. Mandibles with coarse longitudinal striae. Trunk with the same sculpture as the head; the rugulae on the anterior third of the pronotum and the propleurae transverse; weak and longitudinal on the higher pleural regions. Lower pleural regions reticulate only. Coxae, femora, tibiae, petiole, and postpetiole reticulo-punctate, the reticulation smaller and shallower than that of the head and trunk. Tarsi and distal half of the propodeal spines densely punctate. First gastric tergite covered by strong and deep minute reticulation, effaced and only superficially reticulo-punctate on the rest of the gaster.

Pilosity: body with abundant, long, thick, obtuse hairs disposed as follows: erect on the head, dorsum, pronotum, mesonotum, ventral face of the femora; suberect on the sides of the head and on the gaster; and appressed on the mandibles and on the dorsal face of the femora, tibiae and tarsi. Ventral face of the head and coxae with obtuse hairs slightly longer and finer than those on the dorsum, more abundant on the ventral face of the head than on the coxae. Antero-median border of the clypeus with 4 setae 0.24–0.28 mm long. Masticatory border of the mandibles with a row of 8–9 thick, obtuse hairs. Propodeal dorsum, petiole and postpetiole with the same hairs as the pronotum but rarer, on the propodeum also shorter. Meso- and metapleurae without hairs.

Colour: brown with lighter legs and posterior borders of the tergites.

As I already mentioned in the methods chapter, the antennae of this specimen are missing. In spite of the importance of this character in identifying myrmicine genera, I am still confident in the attribution of this specimen to the genus *Aphaenogaster* not only for its general habitus, but also for the following combination of characters: large size, head longer than broad, moderately abundant thick, obtuse hairs, mandibles triangular and not massive, metasternal process absent, promesonotal suture strongly impressed laterally, and propodeal suture impressed.

Relationships. – As already mentioned in the diagnosis, the unique character combination of this species is a pair of short spines on the humeral angles, the head without "neck", and long propodeal spines. *A. relicta* and its subspecies *epinotalis*, both described from Haiti, and some North American species (*A. albisetosa, A. cockerelli, A. macrospina, A. tennesseensis*) share with *praerelicta* the last two characters. Of these five Recent species, the Haitian *relicta relicta* and *relicta epinotalis* appear to be closer to *praerelicta* for their long propodeal spines and similarities in the integumental sculpture. Both these Recent taxa can be separated from *praerelicta* for the following important differences: pronotum with spines in *praerelicta* vs. pronotum without spines in *relicta* and *epinotalis;* frontal carinae with parallel sides in *praere-*

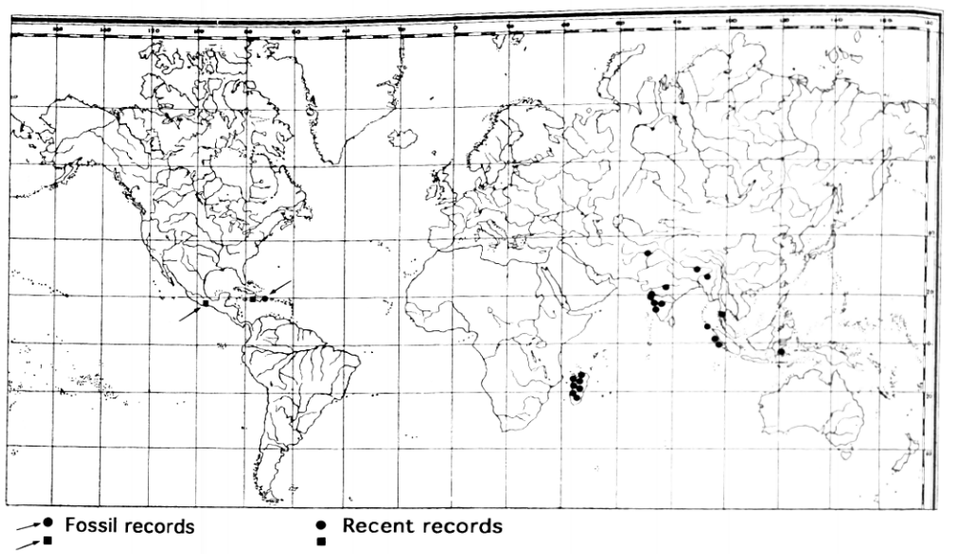

Fig. 5. Distribution of the closest extant *Aphaenogaster* species to the fossil species *amphioceanica* (dots) and *praerelicta* (squares).

licta vs. frontal carinae with rounded lobes in *relicta* and *epinotalis*; propodeal dorsum convex only anteriorly in *praerelicta* vs. propodeal dorsum convex on the whole surface in *relicta* and medially impressed in *epinotalis*; lower pleurae reticulate in *praerelicta* vs. coarsely reticulate-rugulose in *relicta* and *epinotalis*. In addition, *praerelicta* and *epinotalis* share straight propodeal spines which are curved downwards in *relicta*.

A. praerelicta differs from all known American species of *Aphaenogaster* by the presence of pronotal spines. *A. loriae* and *A. quadrispina* from New Guinea are the only Recent species exhibiting this character world-wide. Both New Guinean species differ from *praerelicta* by their head with a "neck", longer pronotal spines, more slender body, larger size, and faint sculpture. Because of these numerous differences, I consider the pronotal spines in the fossil and the two New Guinean species as convergent. Circumstantial evidence for this conclusion comes also from the fact that *A. sagei* Forel from Himalaya has an anteriorly angulate pronotum, in spite of being morphologically very different from the other species discussed here. *Aphaenogaster praerelicta* is likely to represent a clade ancestral to the extant *relicta* from Hispaniola and indicates, as such, close relationships between the Mexican amber and the Recent Hispaniolan faunas.

4. Discussion

The Dominican *Aphaenogaster amphioceanica* shows a combination of rare characters to which I am inclined to attribute phylogenetic value. The most important of these is probably the presence of marginated antennal hollows to be found today only in some species of Madagascar, Hindustan, India, Burma, Sumatra, Celebes and in an undescribed species collected by Baroni Urbani in S. Bhutan. I have previ-

ously (de Andrade, 1994) described a fossil *Anochetus* similar to *cato* from the Oceanian region. Baroni Urbani (1995) reports two Dominican *Pheidole* close to the Malayan *P. lokitae*. One of the two species described in this paper (*Aphaenogaster amphioceanica*) represents another example of faunal relationships between the Dominican amber and the Old World tropics, a distribution pattern recently reviewed by Baroni Urbani (1995). On the other hand, I do not claim close relationships between *praerelicta* and the Old World species, since it is likely that all these species share the presence of pronotal spines by symplesiomorphy because of their numerous differences in sculpture and head morphology. The distribution of the fossil species and their closer extant relatives is given in Fig. 5.

Two Recent *Aphaenogaster* species are known from Mexico (*ensifera* and *mexicana*) and one from the Caribbean islands (*A. relicta*) from Haiti. *A. praerelicta*, described in this paper from Mexican amber is very close to *relicta*, which because of its unique morphology had already been considered as an ancient insular relic by Wheeler & Mann (1914). *A. praerelicta*, however, differs from all known American species of *Aphaenogaster* by the presence of pronotal spines, a character which I regard as autapomorphic. The pronotal spines of the New Guinean *loriae* and *quadrispina* are likely to be convergent because of their important structural differences.

According to Poinar (1992) the age of the Mexican amber ranges between 22.5 to 26 Ma (Early Miocene-Late Oligocene), the age of Dominican amber between 15–40 Ma (Middle Miocene to the Oligocene-Eocene boundary) depending on the mine (Čepek in Schlee, 1990 and Poinar, 1992), and the Baltic amber (with three fossil *Aphaenogaster* species) between 35–50 Ma (Early Eocene-Early Oligocene). The age of all the other petrified fossil *Aphaenogaster* is Oligocene. We are forced to hypothesize, hence, that the migration/dispersal of the genus *Aphaenogaster* took place before that time, i. e. at least 40 Ma ago.

Ward (1992) observed a reduction in species number of Hispaniolan ants since amber times in the ant genus *Pseudomyrmex*. A similar phenomenon has been reported later by Baroni Urbani & de Andrade (1994) for the tribe Dacetini and by de Andrade (1994) for the subtribe Odontomachiti. Similarly, the genus *Paraponera* is known in Dominican amber but is absent in the Recent contemporary Antillean fauna (Baroni Urbani, 1994). All these phenomenona have been explained by intervening or changing insularity factors on Hispaniola. Although this explanation can account reasonably well for the extinction of *A. amphioceanica* from the contemporary Dominican fauna it explains less well the contrary phenomenon reported here for *A. relicta* and *praerelicta*, i. e. survival of the first on Hispaniola and extinction of the second on the Central American mainland.

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