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First Description of Fossil Gardening Ants (Amber Collection Stuttgart and Natural History Museum Basel; Hymenoptera: Formicidae. I: Attini)

By Cesare Baroni Urbani, Basel

With 15 Figures

S u m m a r y

Trachymyrmex primaevus n. sp. is described as the first sure fossil record of gardening ants. More than one dozen workers enclosed in one small piece of Dominican amber evidence a well established population in Hispaniola during Tertiary times.

Since they belong to a subgroup of Attini and from their morphology, a fungus growing behaviour is indicated and a minimum age of this complex ethological-ecological system can be fixed. The age of the Dominican amber is presently considered to be Oligocene or Lower Miocene, a range supported here by new foraminiferal markers. The origin of the fungus growing ants, i. e. of the tribe Attini, must be clearly older since at the time of the Dominican amber, a genus, i. e. a subgroup, already existed. Other genera of Attini must have existed simultaneously and can be expected in additional material of Dominican amber.

Z u s a m m e n f a s s u n g

Trachymyrmex primaevus n. sp., der erste sichere Nachweis fossiler Blattschneiderameisen, wird beschrieben. Über ein Dutzend Arbeiter in einem kleinen Stück Dominikanischen Bernstein belegen die Existenz einer florierenden Population auf Hispaniola während des Tertiärs.

Die Zugehörigkeit zu einer Untergruppe der Attini läßt ebenso wie die Morphologie den Schluß zu, daß es sich um pilzzüchtende Ameisen handelt. Damit ist erstmals die Angabe eines Mindestalters dieses komplizierten ethologisch-ökologischen Systems möglich. Das Alter des Dominikanischen Bernsteins wird derzeit als Oligozän oder Unter-Miozän erachtet. Diese Zeitspanne wird auch durch neue, hier beigefügte Ergebnisse an Foraminiferen bestätigt. Der Ursprung der Blattschneiderameisen, d. h. der Tribus Attini selbst muß deutlich älter sein als der Dominikanische Bernstein, da in diesem ja schon eine Gattung, also eine untergeordnete Gruppe, enthalten ist. Daraus darf man auch schließen, daß gleichzeitig weitere Gattungen der Attini existierten, die im Dominikanischen Bernstein sicher noch zu erwarten sind.

1. Introduction

While SANDERSON and FARR (1960) published a preliminary report on the fossiliferous amber from the Dominican Republic, it was not until 1978 that the first thorough study of the amber itself and its fauna was published. This was done by SCHLEE on the basis of his experience establishing a large scientific collection of amber fossils for the State Museum of Natural History, Stuttgart, Germany (SCHLEE & GLÖCKNER 1978).

It is from this material that the present study dealing with the first fossils of gardening ants is based. The results of other studies have already been published in this journal: Arachnida: Scorpionida and Amblygygi (SCHAWALLER 1979a, b); Insecta: Strepsiptera (KINZELBACH 1979), Diptera — Keroplatidae (SCHMALFUSS 1979). Further papers are in preparation covering different groups such as: Crustacea: Oniscoidea; Arachnida: Pseudoscorpionida and Araneae-Thomisidae; Insecta: Psocoptera and Formicidae, and others. — Apart from this, only one Termite (EMERSON 1971) and one fly and one midge (SCHLÜTER 1976, 1978) have been reported from this amber fauna.

My own experience from a visit to the Dominican Republic and collecting for the Natural History Museum, Basel, Switzerland, Dominican amber pieces containing ants will be published in a series of papers in the near future and will be treated together with the rich material belonging to the Stuttgart Museum.

2. Acknowledgements

Thanks are due to Dr. Dieter Schlee of the Stuttgart Museum for allowing me to study this and other important material, for a careful editing of this paper and for making the photomicrographs.

The drawings illustrating this paper are due to the talent of Armin Coray.

I am grateful to John B. Saunders, Natural History Museum, Basel, for his contribution concerning the age of the amber (cf. chapter 4).

3. Material and methods

The material examined consists of a total of 13 entire or nearly entire specimens plus a few fragments embedded in a single piece of Dominican amber (1 cm³) cut and polished for jewellery. During this investigation the stone has been cut into seven pieces in order to allow better observation. All specimens run under the collection number Do-377 of the amber collection of the State Museum of Natural History, Stuttgart (cf. chapter 6.1.). The holotype is the specimen represented in the photograph (Fig. 5) of this paper and is the ant nearest to the groove excavated by the goldsmith into the amber piece (Do-377-K-1).

The drawing showing the full dorsal view of the ant (Fig. 2) published here is a true reconstruction in the sense that every detail has been seen, but in different specimens, some of differing size. The body proportions have been combined into a single ideal specimen.

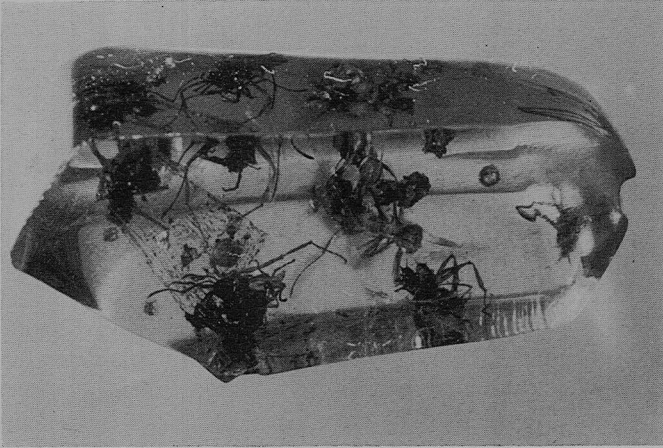


Fig. 1. Dominican amber piece containing the fossil gardening ants. It is the half of the original piece, and contains Nos. Do-377-K-5 to Do-377-K-13, and shows the dense dirty net-like structure (no spider net), in which several of the ants are involved. — This piece has subsequently been cut into 4 pieces in order to separate specimens 5+6; 7+8+9; 10; 11+12+13 for better observation and to enable the photomicrographs (figs. 4 to 13). — Magnification 5 x.

4. The age and origin of the Dominican amber

The amber is mostly found in the dark grey carbonaceous sandstone in the Cordillera Septentrional and, to a minor extent, also in the Cordillera Oriental and on the beaches around Sabana de la Mar, Dominican Republic (Isle of Hispaniola/Greater Antilles).

Since most of the fossiliferous material available in collections has been obtained through amber shops in the Dominican Republic or amber dealers in Europe, the exact provenance of the material is unknown. This is also true for the specimen studied in the present paper.

The age of the Dominican amber is reported to be Oligocene or Lower Miocene (25—35 million years), but such approximate estimations need to be confirmed.

Due to the courtesy of JOHN B. SAUNDERS (Natural History Museum, Basel) who collected and identified foraminiferal samples, I am able to add here some new indication on the age of Dominican amber:

A sample of clayey silt collected at the large amber quarry at Palo Alto near Santiago, Cordillera Septentrional, has produced a planktonic foraminiferal marker whose age range is Lower Oligocene to Middle Miocene with an absolute time span from 38 million years to 15 million years B.P. This is in agreement with earlier estimates of the general age of the amber. However, it could be somewhat older than the matrix, since the amber at the Palo Alto workings is obviously washed in to a marine environment, i. e. it represents a secondary layer.

A second sample, from a small amber working on the road South of Palo Alto, has so far produced a slightly less extended time range due to the presence

of a planktonic foraminiferal marker known only between Middle Oligocene and Middle Miocene.

It is worth adding, perhaps, that the Cordillera Septentrional, particularly the Palo Alto area, represents by far the richest source of fossiliferous amber coming on the market.

Direct determinations of the amber age by the uranium fission track method are now planned with samples collected from different mines.

5. Previous indications of fossils supposed to be *Attini*

FRIČ & BAYER (1901) concluded from a fossil leaf with irregular semi-circular cuts the presence of leaf cutting ants in the Upper Cretaceous from Bohemia. They even give it a generic and specific Latin name, „*Atta praecursor*“. However, cuts of this sort could equally have been produced by a lot of different (and even more probable) beings like Tenthredinid larvae, *Megachile*, etc. — apart from many other unknown Cretaceous creatures. Thus, it is obvious that „*Atta praecursor*“ is, at best, worth remaining in the literature just as an example of fertile imagination.

BROWN (1973) records the presence of „some-winged myrmicines [which] appear to be attine males resembling those of *Mycetosoritis*“ in the amber of Chiapas (Mexico) which should be contemporary with the Dominican amber. Because these specimens are neither determined more precisely nor described, it is likely that they are poorly preserved or not suitable for a formal description. At the present time we are therefore not allowed to draw any conclusion, except, perhaps, the existence of the subfamily Myrmicinae.

It is remarkable that no attines have been recognized among the rich collection of North American Tertiary ants described by CARPENTER (1930).

6. The first fossil gardening ant (worker caste)

Trachymyrmex primaevus n. sp.

Holotype: Worker in Dominican amber, preserved in the amber collection of the State Museum of Natural History, Stuttgart (Department of phylogenetic research), No. Do-377-K-1.

Paratypes: Workers included in the same piece of amber, Nos. Do-377-K-2 to Do-377-K-9. Same collection as holotype except one part of the amber piece containing the specimens Nos. Do-377-K-7, Do-377-K-8, and D-377-K-9, which has been donated to Natural History Museum, Basel (Department of Entomology) where they have been entered in the collection with the number PE 154. 1—3.

Derivatio nominis: Latin „primaevus“ (= of the first age, of the youth time), referred to the attine evolution.

Diagnosis: A little polymorphic *Trachymyrmex* of small size with particularly slender body and pedicel, with prominent eyes, feebly tuberculate integument and antennal scapes without lobe at the base.

Description (measurements in mm): Total length, mandibles excluded, 3.7—4.4 (holotype 4.1); head length 0.72—1.00 (holotype 0.76); maximum head width, eyes excluded, 0.48 (? in a crushed specimen), otherwise 0.76—0.96 (holotype 0.96); maximum diameter of eyes 0.08—0.09 (holotype 0.10); scape length 1.00—1.04 (holotype 1.00); alitrunk length 1.16—1.52 (holotype 1.04);

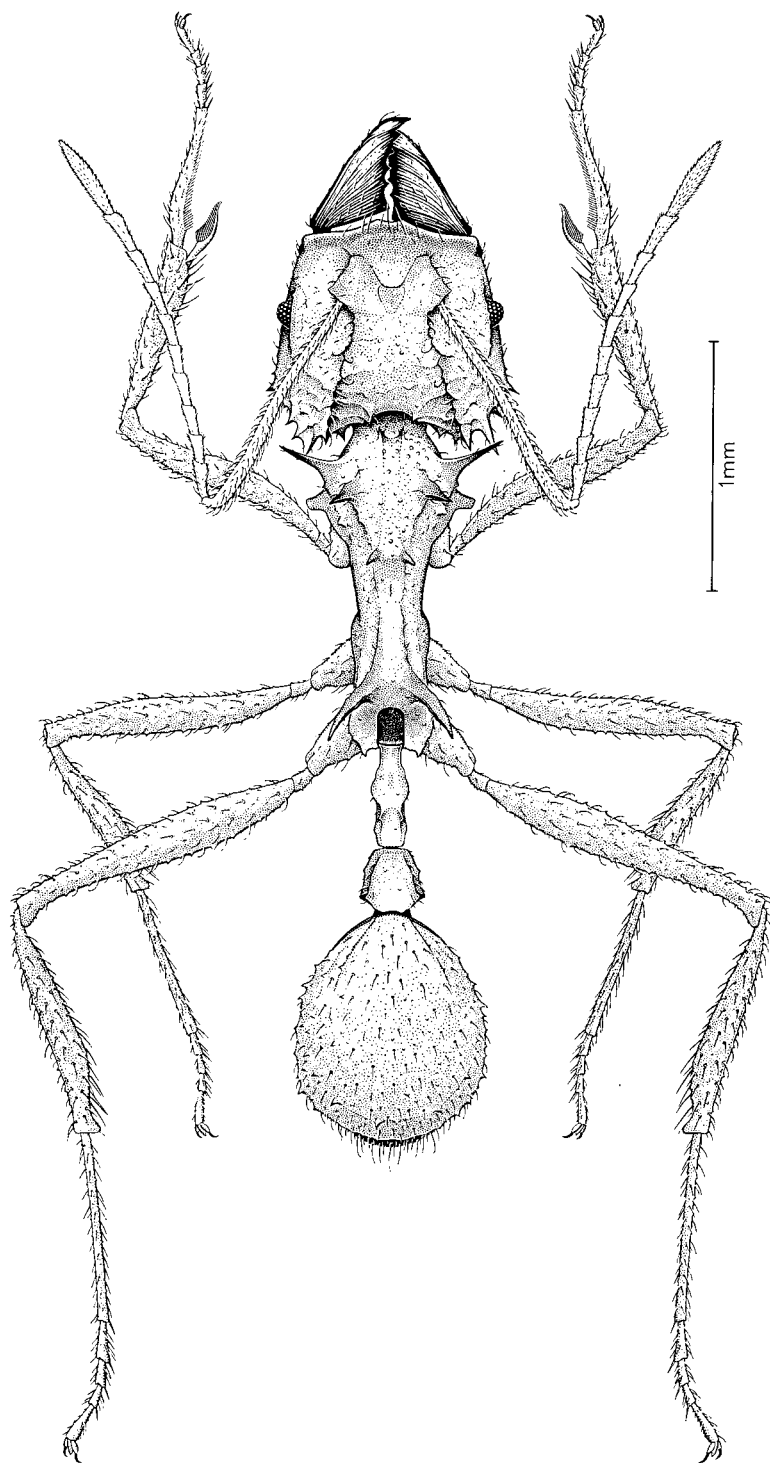
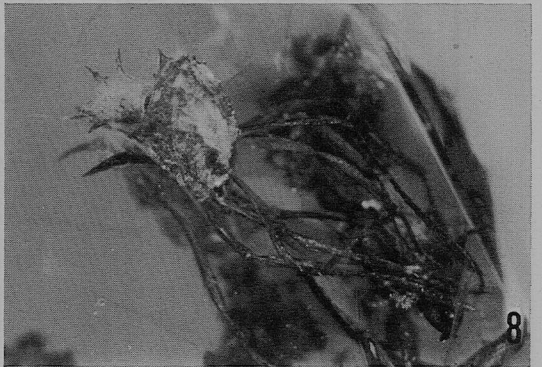
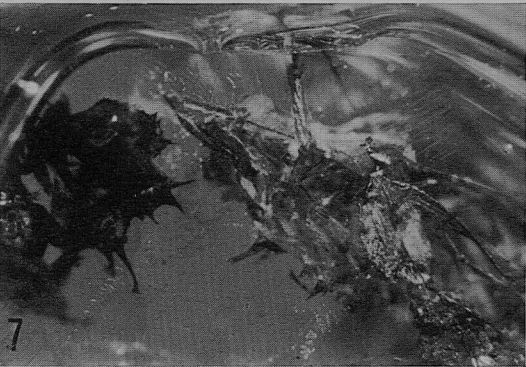
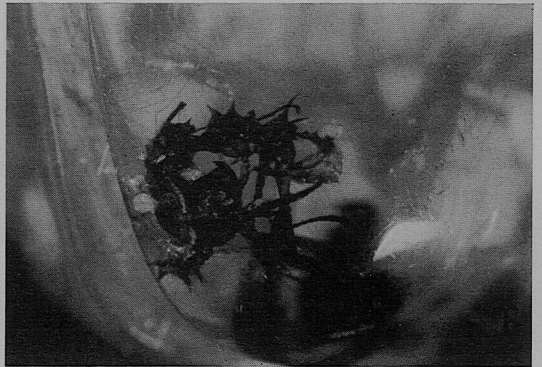
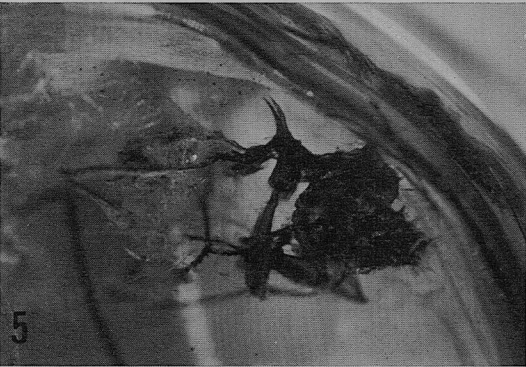
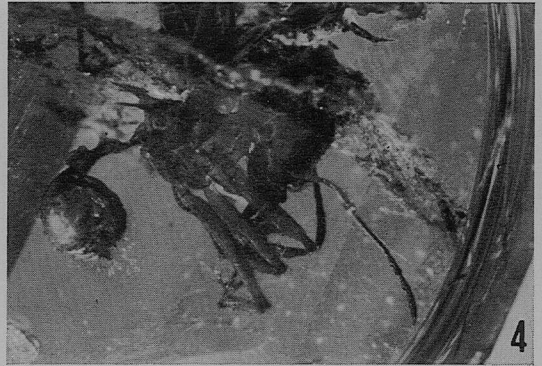
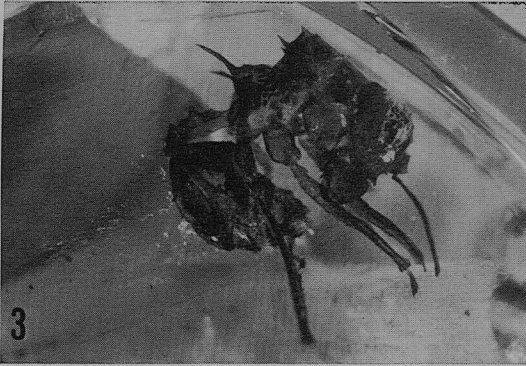
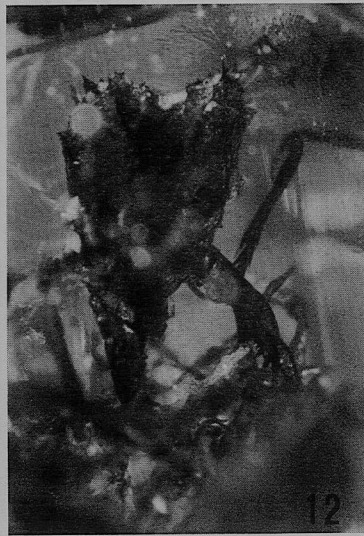


Fig. 2. *Trachymyrmex primaevus* n. sp., full dorsal view of the worker. Reconstruction by ARMIN CORAY based on different specimens. Cf. chapter 3.



Trachymyrmex primaevus n. sp., different specimens from the same amber piece:

- Fig. 3. Specimen Do-377-K-10, habitus, lateral view; abdominal segments protruded; magnification 18 x.
 Fig. 4. Specimen Do-377-K-5, habitus, lateral view, abdominal segments introflected; magnification 16 x.
 Fig. 5. Specimen Do-377-K-1 (holotype), lateral view, trunk, dorsal head spines; magnification 16 x.
 Fig. 6. Specimen Do-377-K-3, trunk spines (lateral view), head with mandibles (frontal view) (gaster partly destroyed); magnification 12 x.
 Fig. 7. Specimens Do-377-K-7 (black specimen), alitrunk and head spines, caudal-dorsolateral view, and specimen Do-377-K-8 (whitish specimen) showing ali-



Trachymyrmex primaevus n. sp., different specimens from the same amber piece. Head in frontal view. Mandibles closed (fig. 9 to 11) or open (fig. 12).

Fig. 9. Specimen Do-377-K-2; magnification 20 x.

Fig. 10. Specimen Do-377-K-4; magnification 18 x.

Fig. 11. Same; magnification 40 x.

Fig. 12. Specimen Do-377-K-11; magnification 32 x.

trunk spines (oblique lateral view) and head sculpture (frontal view); magnification 16 x.

Fig. 8. Specimen Do-377-K-9, head and alitrunk spines, frontal view; magnification 18 x.

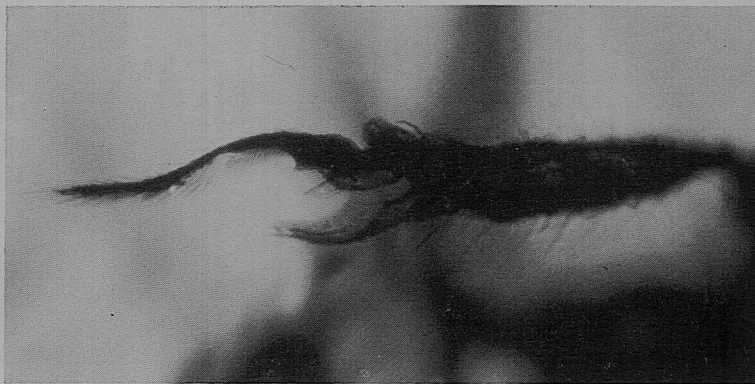


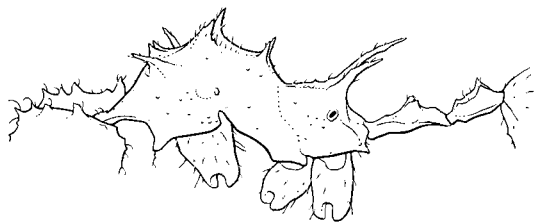
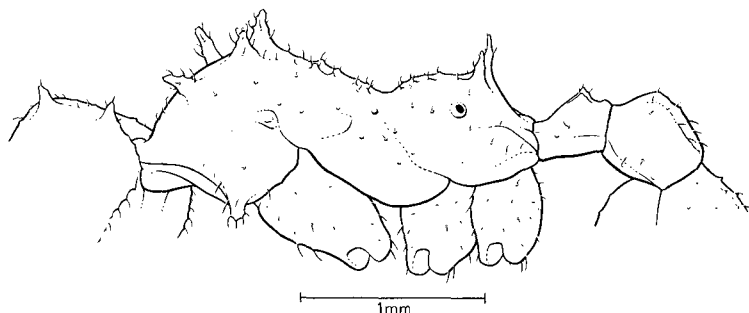
Fig. 13. *Trachymyrmex primaevus* n. sp. Pectinate spur of fore leg. Specimen Do-377-K-12; magnification 100 x.

petiole length 0.44—0.60 (non-measurable in holotype); petiole width 0.10—0.18 (non-measurable in holotype); postpetiole length 0.20—0.36 (non-measurable in holotype); postpetiole width 0.24—0.32 (non-measurable in holotype); hind femur length 0.96—1.56 (holotype 1.28).

Body colour dark brown to black, subopaque with somewhat reddish legs and scapi. Piloosity sparse, mostly erect or suberect, particularly abundant on the head where it is partly represented by curved hairs. Long subdecumbent hairs on the scapi and on the legs. Remaining surfaces covered with fine and sparse pubescence never masking the integument.

Head as shown in figs. 2, 9 to 12. Mandibles heavily longitudinally striate. Distal half of the masticatory border with 3 large teeth, proximal half with 6 small teeth. One row of long, bright bristles (5+1 specimens) inserting in hyaline circular socles by the side of and parallel to the row of the teeth. The 5 bristles are directed transversally to the longitudinal axis of the mandible and surpass the teeth, while the single one, distally separate from the row, does not (not shown in fig. 2). — Cephalic integument finely granulated, opaque. Anterior clypeal border feebly notched. Frontal carinae diverging caudally and reaching the occipital border posteriorly. Posterior third of the cephalic capsule feebly tuberculate or spinose, integument rough. Supraorbital carinae visible for almost one half head length. Occipital corners prominent and dentate. Occipital border feebly emarginate in full-face view. No carinae on vertex. Inferior occipital border marginate and edentate. Eyes comparatively very small and extremely convex, with less than 10 ommatidia across greatest diameter. Scapes of the antennae longer than the head capsule and narrow. All funicular segments decidedly longer than broad.

Alitrunk as in figs. 2, 3 to 8, 14. Integument subopaque and sculpture indistinct. Hairs rare and not arising from prominent tubercles. Pronotum with two dorsal spines and pointed, elongate humeral angles. Lateral teeth low and obtuse, mesial absent. Mesonotum with two pairs of prominent anterior and posterior spines. Propodeal suture obsolete. Propodeal spines elongate, curved and divergent, directed upwards. Legs thin and compressed. Hind femora about as long as the whole alitrunk.

Fig. 14 + 15. Outline of the alitrunk and peduncle of different *Trachymyrmex* species.Fig. 14. *T. primaevus* n. sp. from the Dominican amber.Fig. 15. *T. jamaicensis* ANDRÉ, the presently living species in the island of Hispaniola

Petiole and postpetiole as shown in figs. 2, 4—8, with very few and inconspicuous erect hairs. Petiole pedunculate and elongate, comparatively very narrow and slightly enlarged at the node. Node low with two tubercles on the dorsal surface. Postpetiole flattened and about one half wider than petiole, with a deep dorsal excision separating two small tubercles. Gaster opaque with minute piligerous tubercles.

7. Relationships and discussion

7.1. Morphological relationships

On morphology there is no doubt about the attribution of the new fossil species to the genus *Trachymyrmex*. The diagnostic characters (11-jointed antennae, tuberculate dorsal hairs and long antennal scrobes) are well visible in the fossil.

There are very evident characters which justify the erection of a new species, *T. primaevus*. These are the thin abdominal peduncle and the eyes prominent

on the sides of the head: important characters, which do not match any known living species.

But the definite relationships to the known recent species are not clear at present. For comparison, fig. 15 shows the profile of *T. jamaicensis*, the species living today on the island of Hispaniola.

However, more prominent eyes are known in *Mycetophylax* and the peduncle of the *Myrmicocrypta* species is much more slender than in *Trachymyrmex*. Because both these genera are actually regarded as the most primitive living Attines (KUSNEZOV 1963) and no recent *Trachymyrmex* approaches these two character states, it is easy to deduce that they represent a plesiomorphism of *T. primaevus*.

7.2. Behavioural and ecological remarks

The genus *Trachymyrmex* is one of the 9 or 12 (according to the classification accepted) genera belonging to the tribe Attini. This taxon comprises all the known fungus growing ants (some 200 described species).

The new fossil, *T. primaevus*, fits so well the generic diagnosis of *Trachymyrmex*, and its somatic characters (head shape, tuberculate integument, etc.) are so typical for what one would expect from a fungus-growing ant and are different from other ants, that it is legitimate to suppose that it had a fungus-growing behaviour.

This follows also from the fact that the fossil is a true *Trachymyrmex* and from the supposition that *Trachymyrmex* should rather be near the terminal branch of attine evolution (KUSNEZOV 1963) than near the stem group of Attini. However, as long as no true phylogenetic argumentation exists on the genus level of Attinae, this sort of indirect conclusion remains tentative. Therefore, the direct morphological evidence from the well preserved amber fossil is most decisive.

The fungus growing habit of the gardening ants is an external symbiosis based on complex ethological and ecological factors.

The ants cut with their large and strong mandibles parts of leaves and petals and transport them between the mandibles into their nests which enclose special chambers for the fungus cultivations. The ants do not eat the leaves but use them as medium for cultivating fungus colonies, the fungus being the main or exclusive food. Neither the cutting of the leaves nor the growing of the fungus is accidental. The ants select the material on the basis of its physical and chemical properties and they developed special secreta and special behaviours. (Without the specialized treatment, the fungus grows so slowly that it is overgrown by other microorganisms.) The ants clean the leaf pieces from undesired microorganisms, cut them in small pieces, cover them with saliva and a drop of fresh faeces (with its amino acids, enzymes, etc., originating in part from well growing parts of the fungus cultivation), they then add the correct fungus, transport it to suitable places and rid the cultivation of rival fungus species and of exhausted substratum. The ants eat only special parts of the fungus and are able to let the cultivation continue for an indefinite period.

7.3. Geographical conclusions and some phylogenetic considerations

The present distribution of recent Attini ranges from 40° Lat. N (i. e. approximately the line San Francisco-Washington) up to 40° Lat. S (i. e. approximately Santiago de Chile-Buenos Aires). The distribution of the genus *Trachymyrmex* — with about 40 species, the largest attine genus — coincides almost exactly with the distribution of the whole tribe Attini.

The Attini extend only a little more to the south with the genus *Acromyrmex* and on the west coast of California a little more to the north with the genus *Cyphomyrmex*. But the highest latitudinal record still belongs to *Trachymyrmex* with one record at 40°50' Lat. N (WEBER 1970).

Most attine genera are absent from several Caribbean islands. The Recent fauna of Hispaniola includes only *Cyphomyrmex*, *Mycocepurus* and *Trachymyrmex*, while e. g. the large gardening ants (*Atta*) are entirely absent (CHERRETT 1968, WEBER 1972).

Until now — i. e. without a fossil proof — it was impossible to give any indication, how long the Attini have existed on the Greater Antilles. The special reasons for this are the attines' active flying during the nuptial period (MOSER 1967) combined with strong active and passive dispersal (see WEBER 1972 for a review).

Accidental landing of some winged females on the island of Soldado Rock (at 9.5 km from Trinidad and 12.5 km from the Venezuela mainland) are recorded, although no attines are living on the island (CHERRETT 1969). On the other hand there is evidence that some Caribbean islands like Curaçao and Guadelupe have been invaded only during the last few decades by the attine *Acromyrmex octospinosus* which has now become established. — From all this information one can deduce that the attines have had several opportunities to colonize Hispaniola and probably did so, but, perhaps, were usually unable to establish settlements because of saturation of the insular biotas. Recent establishment in the Caribbean area may have been favoured by the action of man on natural environments.

The fossil record available now — more than one dozen workers in one small Dominican amber block — clearly indicates a well established attine population in Hispaniola during early or middle Tertiary times.

Since the fossils belong to *Trachymyrmex*, i. e. a subgroup of Attini (and not to the stem group of Attini), it is clear that also other attine genera must have existed simultaneously. Thus, we have a chance to find them in additional fossil material, but at present we cannot say which genera. If we had a „Hennigian“ phylogenetic analysis and diagram (synapomorphy scheme) already available we would be able to deduce those genera.

In addition, there are some other questions which could be solved by means of a Hennigian synapomorphy scheme. They are especially concerned with the distributionary history. The fossil, *T. primaevus* n. sp., is apparently absent from the recent record of the genus, while other species exist, even in the Antilles. Did the genus *Trachymyrmex* come once or several times independently to Hispaniola? Some examples for such considerations may be added.

(1) If *T. primaevus* could be recognized as sister species (or stem group member) of all the recent Antillean *Trachymyrmex* species we were allowed to assume a unique arrival.

(2) If *T. primaevus* could be recognized as sister species of other *Trachymyrmex* species, say, South American ones (and the Caribbean species excluded from this phylogenetic unit), an independent multiple arrival of *Trachymyrmex* would be probable.

(3) If *T. primaevus* could be recognized as stem group member of a phylogenetic unit comprising species other than the Caribbean ones, the primary direction of dispersal would be indicated to be from the Caribbean islands to the continent, and the recent Antillean *Trachymyrmex* species must have arrived by a secondary immigration.

(4) If *T. primaevus* would be sister species (or stem group member) of a group comprising some of the Caribbean *Trachymyrmex* species and some of the continental species (and the rest of the Caribbean species excluded) this would also indicate a multiple arrival of *Trachymyrmex* on the Caribbean islands.

Until now there exist only less precise proposals concerning phylogeny and distributionary history. KUSNEZOV (1963) proposed an arbitrary dendrogram showing *Trachymyrmex* near to the end of the phylogenetic branching of attine evolution, and WEBER (1972) supposed — without fossil evidence — that the attines probably originated in the moist lowland tropics of northern South America where the climate has been warm and stable since the Tertiary period. The discovery of *T. primaevus* helps in setting this origin as clearly before Miocene at least, since some major splitting into the present recognized genera was apparently accomplished. Increasingly detailed knowledge may be expected from future phylogenetic analyses and from fossils belonging to additional parts of the attine phylogenetic diagram.

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Author's address:

Dr. C. Baroni Urbani, Naturhistorisches Museum, Augustinergasse 2, CH-4001 Basel, Switzerland.