New Termitaphididae and Aradidae (Hemiptera) in Mexican and Dominican amber

GEORGE POINAR, JR. & ERNST HEISS

Abstract

A new species of termite bug, Termitaradus dominicanus POINAR, n. sp. (Hemiptera: Termitaphididae) and a new genus and species of flat bug, Brevisensoria incrustata POINAR, n. gen., n. sp. (Hemiptera: Aradidae) are described from Dominican amber. Termitaradus dominicanus POINAR, n. sp. is distinguished from previously described members of the genus by lobules with terminal flagella composed of two to four minute, non-serrate setae, with each setal group embedded in a hardened envelope or deposit. Brevisensoria incrustata POINAR, n. gen., n. sp. can be separated from other members of the Aradidae by the absence of compound eyes, ocelli and wings, modified head fused to the prothorax, unique antennal structure and the dorsal forming a continuous body covering with a peripheral margin bearing lobes. The oval body shape, convex dorsum with incrustations, convex ventrum, absence of lobules and unique structure of the antennae distinguish the new genus from members of the Termitaphididae. In addition, five specimens of Termitaradus protera POINAR & DOYEN in a single piece of Mexican amber that also contains seven worker termites are characterized.

Keywords: Dominican amber, Tertiary termite bugs, Tertiary flat bug, Mexican amber.

Zusammenfassung


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1. Introduction

Termite bugs of the family Termitaphididae (Hemiptera) represent extremely modified hemipterans that occur in termite colonies worldwide. They have lost their eyes and wings and the head, thorax and abdomen are fused into a protective shield covering the shortened legs and antennae. Such structural modifications allow them to survive in the confines of termite nests. The world-wide distribution of extant forms and fossils in Mexican and Dominican amber indicate an ancient origin for this group, certainly extending back at least to the Cretaceous and probably even earlier (POINAR & DOYEN 1992).

Flat bugs of the family Aradidae have oval to ellipsoidal dorsoventrally flattened bodies with porrect heads bearing prominent antennae. They are found under bark or associated with dead wood, presumably obtaining nourishment from wood-rotting fungi. Many species have lost their wings and have a rough surface that blends with the surroundings, thus depending on camouflage rather than
flight to avoid detection. Some 475 species are known from the Neotropics (Kormilev & Froeschner 1987).

The present paper describes a new species of *Termitaradus* and a new genus and species of aradid, both from Dominican amber, and briefly characterizes five new specimens of *Termitaradus protera* Poinar & Doyen, 1992 together with seven worker termites, in Mexican amber (Fig. 1).

**Acknowledgements**

We thank W. Weitschat for the loan of the amber piece with the Mexican termitaradids and Art Boucot and Roberta Poinar for comments on earlier drafts of this manuscript.

**2. Materials and methods**

The Mexican amber piece is elliptical in shape, measuring 38 mm in length, 15 mm in width and 12 mm in depth. The amber originated from the Simojovel area of Chiapas, Mexico. Locations of the Chiapas mines and a synopsis of Mexican amber are presented in Poinar (1992). Amber from this region was produced by *Hymenaea mexicana* (Fabaceae) (Poinar & Brown 2002) and occurs in lignitic beds among sequences of primarily marine calcareous sandstones and silt. The amber is associated with Balumtun Sandstone of the Early Miocene and the La Quinta Formation of the Late Oligocene with radiometric ages from 22.5 to 26 million years (Berggren & Van Couvering 1974). Since the amber is secondarily deposited in these marine formations, it is undoubtedly somewhat older than the above dates. The specimen is in the collection of W. Weitschat Hamburg, Germany.

The amber containing the Dominican specimens originated from mines in the northern mountain range (Cordillera Septentrional) of the Dominican Republic, between the cities of Puerto Plata and Santiago. Amber from this deposit was produced by *Hymenaea protera* Poinar, 1991 (Fabaceae). Dating of Dominican amber is controversial, with the youngest proposed age of 20–15 mya based on foraminifera (Iturralde-Vinent & MacPhee 1996) and the oldest as 45–30 mya based on coccoliths (Čepek in

![Fig. 1. Piece of Mexican amber containing five complete or partial specimens of *Termitaradus protera* Poinar & Doyen (white arrows show four specimens), together with seven complete or partial worker termites (black arrows show two specimens). — Scale: 4.0 mm.](image-url)
Most of the amber is secondarily deposited in turbiditic sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al. 1994), so the amber could be older than the Miocene dates. The Dominican amber specimens are deposited in the Poinar collection maintained at Oregon State University.

3. Systematic palaeontology

Order Hemiptera
Family Termitaphididae
Genus Termitaradus Meyers

Termitaradus protera Poinar & Doyen, 1992
Figs. 1–2

Five specimens of T. protera occur in a single piece of Mexican amber. Specimen No. 1, a female, is only visible ventrally. It is 6.4 mm in length, 4.6 mm in width, has 14 somatic lobes and exposed antennae, labium and legs (Fig. 2). Specimen No. 2, a female, has only the dorsal side visible. It is 6.5 mm in length, 3.5 mm in width and also has 14 somatic lobes. Specimen No. 3, a female, is 6.0 mm in length and 4.4 mm in width. It is only partially visible dorsally and the number of somatic lobes could not be determined. Specimen No. 4 had only part of the ventrum visible and specimen No. 5 had only the tip of the abdomen preserved. Neither sex nor stage could be determined in the last two specimens.

It was only possible to count the number of lobules on all somatic lobes on one side of specimen No. 1. The head has two lobes, lobe one has 16 lobules and lobe two 6 lobules. The prothorax has a single lobe, which has 12 lobules. The mesothorax has two lobes, the first has 9 lobules and the second 7 lobules. The metathorax has a single lobe with 8 lobules. The abdomen has 8 lobes with the following number of lobules: the first lobe has 12, second lobe 12, third lobe 12, fourth lobe 12, fifth lobe 12, sixth lobe 12, seventh lobe 10 and the eighth (last) lobe 4. The number of lobules on the lobes of this specimen is almost identical to that recorded earlier for T. protera (Poinar & Doyen 1992). A certain degree of variability occurs with the number of lobules on termitaradids, although number of lobules on the terminal (8th) abdominal lobe appears to be stable and is used as a diagnostic character (Usinger 1942; Poinar & Doyen 1992).

Only two of the seven worker termites in the same piece of amber are complete enough to be measured and they are 8.5 mm and 9.3 mm in length, respectively. It is not possible to identify the termites to family since they are workers and diagnostic characters are not visible. The tarsi are four-segmented and the complete number of antennal segments (n = 17) could only be determined on one individual.

Termitaradus dominicanus Poinar, n. sp.
Figs. 3–9, 16A

Holotypus: Female specimen no. HE-4-52 in coll. Poinar. This specimen, which was first reported in Poinar & Poinar (1999), is in an oval piece of clear Dominican amber measuring 13 mm in length, 10 mm in width and 5 mm in depth. 

Derivatio nominis: Named after the Dominican Republic, the country of origin.

Stratum typicum: Dominican amber, Tertiary, Oligocene-Miocene.

Locus typicus: Northern mountain range (Cordillera Septentrional) of the Dominican Republic.

Diagnosis: – A medium-sized termite bug characterized by lobules with terminal flabella composed of two to four minute, non-serrate setae, with each setal group embedded in a hardened envelope or deposit.

Description of holotype. – Length, 6.4 mm; width, 4.3 mm; dorsum dark brown, divided into plates, covered with minute nodular setae ranging from 6–19 μm.
in diameter; ventrum light brown, covered with scattered, elongate setae ranging from 16–55 μm in length; body with 14 contiguous lobes on each side; each lobe with the following number of terminal lobules: head lobules, 12 and 4; prothoracic lobule, 14; mesothoracic lobule, 14; metathoracic lobules, 7, 10; abdominal lobules: first, 14; second, 14; third, 14; fourth, 15; fifth, 15; sixth, 10; seventh, 8; eighth, 4; lobules with terminal flabella composed of 2–4 minute, non-serrate setae; each setal group embedded in hardened envelope or deposit (Figs. 6, 7).

H e a d : Labium four segmented with following lengths: basal segment = 167 μm; second segment = 205 μm; third segment = 179 μm; fourth (terminal) segment = 282 μm; antennae four-segmented; scape shorter than combined lengths of remaining antennomeres; combined lengths of antennomeres 2 and 3 shorter than terminal antennomere.

T h o r a x : Legs short, robust, length of forefemur, 886 μm; length of foretibia, 714 μm; length of foretarsomeres: 1 = 84 μm; 2 = 252 μm; protibial combs conspicuous, 50 μm in length, 92 μm in width (Fig. 8); five to seven thick spines varying from 75–85 μm in length adjacent to tibial comb on foretibia and on remaining tibial apexes; claws simple, paired, with broad base, from 90–120 μm in length; pulvilli capitate, ranging from 68–72 μm in length (Fig. 9); metathoracic scent glands and groves distinct (Fig. 5).

A b d o m e n : Slightly convex; light brown; with eight visible segments; anal opening between the terminal (8th) body lobes; possible genital opening on proximal portion of 8th abdominal sternite.

S y s t e m a t i c  p o s i t i o n . – The present species can easily be separated from the two previous Dominican amber Termitaradus species. Termitaradus avitinaulinus Grimaldi & Engel, 2008 has serrate marginal setae.
terminating the lobules (each flabellum is composed of a single serrated seta), lacks capitate pulvilli and protibial combs, is smaller (3.6 mm in length vs. 6.4 mm for *T. dominicanus* Poinar, n. sp.) (no measurements or figures were given for the two designated paratypes of *T. avitinauilinus*, both of which are deposited in a private collection). In addition, *T. avitinauilinus* was described as having three head lobes (instead of two as in *T. dominicanus* Poinar, n. sp.) and the basal labial segment is longer than the remaining segments (apical segment longest and basal one shortest in *T. dominicanus* Poinar, n. sp.).

The Dominican amber *T. mitnicki* Engel, 2009 lacks dorsal nodule-like setae but possesses a network of raised, thick carinae, has only 13 body lobes, a three-segmented labium and a single serrate marginal seta terminating each lobule, all of which distinguish it from *T. dominicanus* Poinar, n. sp. The lobules with terminal flabellae are composed of 2–4 minute, non-serrate setae with each setal
group embedded in a hardened envelope or deposit separate *T. dominicanus* POINAR, n. sp. from all other extant and fossil species of *Termitaradus*.

**Discussion.** – One of the most important diagnostic characters of *T. dominicanus* POINAR, n. sp. is the structure of the flabellae. There seems to be some ambiguity regarding terms describing characters in this family. Originally the marginal body sections were termed lobes and each lobe contained a number of lobules. Each lobule was terminated by a flabellum, which varied from circular to elongate. More recent terms used for somatic lobes are marginal laminae and lateral lamellae (SCHUH & SLATER 1995). However MYERS (1924) used “marginal lamina” as a collective term for all of the lobes on the body. The term “marginal setae” has also been used to replace the term “flabellae” regarding the structures terminating the lobules (SCHUH & SLATER 1995). However, this is not satisfactory since there is considerable variation regarding the structure of the flabellae and not all are in the form of setae. The flabellae may be clavate, as in the extant *T. guianae* (SCHUH & SLATER 1995), circular to oblong as in the Mexican amber *T. protera* (POINAR & DOYEN 1992), subtriangular to lanceolate as in the Dominican amber *T. avitinquilinus* GRIMALDI & ENGEL, 2008 or compound, where each flabellum is represented by two to four setae as in the present *T. dominicanus* POINAR, n. sp. In the present work, the term flabellum has been retained, while recognizing that in some species, the flabellum are modified into setae or setal-like structures.

There is only one lobe associated with the mesothorax and two with the metathorax in *T. dominicanus* POINAR, n. sp. However the 5th body lobe is normally small and the suture separating it from the 6th is short, making it difficult to determine if it belongs to the mesothorax or
metathorax. Normally, it is considered part of the mesothorax or is combined with the adjoining lobes (Poinar & Doyen 1992).

The protibial combs are well developed in *T. dominicanus* Poinar, n. sp. and their setae are very fine. These have been referred to as grooming combs (Schuh & Slater 1995). Protibial combs also occur on *T. trinidadensis* Morrison, 1923, *T. guiana*e Morrison, 1923 and *T. protera*, but they are composed of fewer, thicker setae (Morrison 1923; Poinar & Doyen 1992). These combs are not to be confused with the stout setae that occur at the apex of the tibia.

The structure of the pulvilli appears to vary between species. In *T. avitinaulinus* and *T. mitnicki*, the pulvilli are slender and straplike. However, in some species, such as the Indian *T. annandalei* Silvestri, 1921, the pulvilli are capitate with a swollen apex, as in *T. dominicanus* Poinar, n. sp. (Fig. 9).

The proportions of the labial segments also vary to some degree within the genus. While three segments have been described for several species, including the Dominican amber *T. mitnicki*, *T. dominicanus* Poinar, n. sp. and *T. panamensis* Myers, 1924 clearly have four-segmented beaks. In all species, the terminal segment is the largest.

The curious specimen of *Termitaphis circumvallata*, which was recovered from termite (Amitermes forelli Wasmann, 1902) nests in Colombia, South America, has traditionally been included in the family Termitaphididae (Usinger 1936; Schuh & Slater 1995). It is characterized as having an egg-shaped body with the lateral margins curved upward and almost meeting dorsally. The dorsum is divided into lobes which bear lobules along their margins. Each lobe bears a terminal, marginal seta (Wasmann 1902; Usinger 1942). This condition where flabellae are represented as single setae is found in the African *Termitaradus subafra* (Silvester 1911) and the Dominican fossil, *T. airtinquilinus*. Myers (1932) noted that when specimens of *Termitaradus jamaicensis* were turned on their backs, they “arched the side-plates in the form of a half cylinder” to right themselves. We suspect that *T. circumvallata* was killed on its back (probably in a cyanide jar) attempting to right itself. The normal body configuration of *T. circumvallata* was probably flat with downturned sides. The upturned lateral margins represent a death response when it died on its back. If upturned body margins were the natural position of *T. circumvallata*, the legs and undersides would be exposed to termite attack. Further study of the specimen is necessary to determine if it is indeed a species of *Termitaradus* that died in an unnatural position. Morrison (1923) was also suspicious of the description of *T. circumvallata* and considered the specimen almost identical to his *Termitaradus guiana*e Morrison, 1923.
**Tab. 1.** Comparison of *Termitaradus* (Termitaphididae) and *Brevisensoria* POINAR, n. gen (Aradidae).

<table>
<thead>
<tr>
<th>Character</th>
<th><em>Termitaradus</em></th>
<th><em>Brevisensoria</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Lobules</td>
<td>present</td>
<td>absent</td>
</tr>
<tr>
<td>Margins of lobes</td>
<td>with lobules</td>
<td>with setae</td>
</tr>
<tr>
<td>Abdominal lobe 8</td>
<td>with two to four flabellae</td>
<td>with six setae</td>
</tr>
<tr>
<td>Antennae</td>
<td>geniculate</td>
<td>not geniculate</td>
</tr>
<tr>
<td>Scape insertions</td>
<td>under head margin</td>
<td>at head margin</td>
</tr>
<tr>
<td>Body contour</td>
<td>flat-slightly contour</td>
<td>dome-shaped</td>
</tr>
<tr>
<td>Dorsum</td>
<td>minute papillae-like setae incrustations or network of raised, thick carinae</td>
<td>incrustations</td>
</tr>
<tr>
<td>Ventrum</td>
<td>convex-rounded</td>
<td>concave</td>
</tr>
<tr>
<td>Leg size</td>
<td>small in relation to body</td>
<td>large in relation to body</td>
</tr>
<tr>
<td>Head dorsum</td>
<td>without umbo</td>
<td>with bilobed incrusted umbo</td>
</tr>
</tbody>
</table>

**Fig. 10.** *Brevisensoria incrustata* POINAR, n. gen, n. sp.; dorsal view; in Dominican amber. Arrow shows bilobed incrusted umbo on dorsum of head. – Scale: 370 μm.

**Fig. 11.** *Brevisensoria incrustata* POINAR, n. gen, n. sp.; ventral surface; in Dominican amber. Note protruding antennae. – Scale: 290 μm.
Fig. 12. *Brevisensoria incrustata* POINAR, n. gen, n. sp.; partial reconstructed drawing of ventral surface; in Dominican amber. – Scale: 430 μm.

Fig. 13. *Brevisensoria incrustata* POINAR, n. gen, n. sp.; detail of dorsum of head; in Dominican amber. – Scale: 133 μm.

Fig. 14. *Brevisensoria incrustata* POINAR, n. gen, n. sp.; anterior view; in Dominican amber. – Scale: 155 μm.

Head: Small, dorsally bearing single large bilobed incrusted umbo; clypeus short, cylindrical, not prominent; labium four-segmented, arising shortly behind head apex; (thirteen); lobe 4 nine; lobe 5 six; lobe 6 six; lobe 7 seven; lobe 8 eight; lobe 9 nine; lobe 10 eight; lobe 11 seven; lobe 12 six; lobe 13 six; lobe 14 six.
Fig. 15. *Brevisensoria incrustata* POINAR, n. gen, n. sp.; marginal setae on two abdominal lobes; in Dominican amber. – Scale: 72 μm.

Fig. 16. A. *Termitaradus dominicanus* POINAR, n. sp.; lateral view; in Dominican amber. – Scale: 1.06 mm. B. *Brevisensoria incrustata* POINAR, n. gen, n. sp.; lateral view; in Dominican amber. – Scale: 380 μm.

labium surpassing base of head, reaching fore coxae; prothoracic sulcus for reception of tip of labium; lengths of labial segments: basal segment, 103 μm; second segment, 64 μm; third segment, 115 μm; fourth (terminal) segment, 167 μm; antennae four-segmented, not geniculate, positioned forward beyond head body lobes; scape thick, narrowed slightly at base; scape shorter than combined lengths of pedicel and basiflagellum; pedicel attaches subapically to scape; combined lengths of pedicel and basiflagellum longer than either distiflagellum or scape; sulci adjacent to clypeus under first head lobe for reception of scape; additional sulci under second head lobe for reception of remaining antennal segments; lengths of antennomeres: 1 = 154 (141) μm; 2 = 115 (103) μm; 3 = 103 (115) μm; 4 = 205 (210) μm.

Thorax: Wider than long; legs long in proportion to body; when extended, hind legs could reach 8th sternite; trochanters free; lengths: forefemur = 385 μm; foretibia = 308 μm; mesofemur = 385 (397) μm; mesotibia = 346 μm; metafemur = 385 μm; metatibia = 346 μm; protibial comb composed of closely set fine setae; 5–7 large protruding spines at base of all tibiae; tarsi two-segmented, with basitarsus about one third length of distitarsus; claws simple, paired, with linear pulvilli.

Abdomen: Slightly concave; light brown; with eight visible segments; anal opening between the terminal (8th) body lobes; possible genital opening between 7th and 8th abdominal sternites.
Systematic position. – It is difficult to determine the subfamily status of Brevisensoria, however since the metathoracic gland has an associated scent gland channel, it is tentatively assigned to the Mezirinae. While the presence of metapleural scent glands has been used to establish the adult status of bugs in general (Schuh & Slater 1995), this is not the case with some aradids. For instance the L5 nymph of Brachyrhynchus membranaceus (Fabricius, 1798) possesses metapleural scent glands (Fig. 17), thus it is not known whether the apterous B. incrustata Poinar, n. gen, n. sp. is a small adult or a nymph.

While there are no extant or extinct known aradids with a body form similar to Brevisensoria, some extant apterous aradids have an incrustate body surface, show fusion of the body segments and possess body lobes (Schuh & Slater 1995). Nymphs of the mezirine species, Dysodiis lunatus (Fabricius, 1798), have a series of rounded lobes on each side of the body (Fig. 18). The L2 nymph of Brachyrhynchus membranaceus has nearly contiguous body lobes with those of the abdomen bearing short marginal setae (Fig. 19), which is similar to the condition in Brevisensoria.

Up to the discovery of Brevisensoria, all aradids had compound eyes (even though some are reduced) and the head and antennae were clearly exposed (Schuh & Slater 1995). Lacking eyes, Brevisensoria narrows the characters that separate aradids from termitaradids and raises the question of whether the Termitaphididae warrant family status or if they are just a highly autapomorphic clade within the Aradidae. For the present, however, we feel that there are enough significant differences between
Brevisensoria and members of the genus Termitaradus to retain the family status of Termitaphididae (Tab. 1).

Discussion. – The habits of Brevisensoria are unknown and there are no other fossils in the amber. The absence of eyes indicates a confined habitat, but the incrustate dorsum suggests that camouflage was essential for survival. The downturned lateral margins and dorsal shield show that Brevisensoria lived in a habitat where a defensive posture was important. It may have inhabited termite, bird or mammal nests, similar to some aradids (Myers 1924; Kormilev 1967; Usinger 1936).

4. References


Addresses of the authors:

Dr. GEORGE POINAR, Jr., Department of Zoology, Oregon State University, Corvallis, OR 97331, U.S.A.

E-mail: poinarg@science.oregonstate.edu

Dr. ERNST HEISS, Josef-Schrafft-Strasse 2a, 6020 Innsbruck, Austria

E-mail: aradus36@gmail.com

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