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A Termite Bug in Early Miocene Amber of the Dominican Republic (Hemiptera: Termitaphididae)

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ABSTRACT

A new species of the highly specialized hemipteran family of social ectosymbionts, the Termitaphididae, is reported in Miocene amber from the Dominican Republic: *Termitaradus avitinquilinus*, n.sp. It differs from the only other fossil termitaphidid (*Termitaradus protera* Poinar and Doyen), in Miocene Mexican amber, and from modern species by various distinctive features. Two of the three specimens of *T. avitinquilinus* are preserved in a piece of amber with its presumed host, a worker of the basal termite, *Mastotermes electrodominicus* Krishna and Grimaldi. The hypothesis that the family Termitaphididae is ancient and inhabited Pangaea is disputed in favor of a much more recent, Tertiary origin. It is suggested, in fact, that termitaphidids are highly modified Aradidae, possibly derived from Mezirinae.

INTRODUCTION

Highly specialized arthropods that cohabit the nests of eusocial insects, or social ectosymbionts, have evolved repeatedly in virtually every major order of terrestrial arthropods (Wilson, 1971). This attests to the ecological significance of eusocial insects as well as to the overall adaptability of insects in general. Here we report very rare fossils of a group of highly specialized aradoid hemipterans that are obligate inquilines in the nests of termites. Termitaphididae are dorsoventrally compressed, with expanded and flattened lateral laminae, each bearing a series of non-separated lobules and these in turn bearing modified, often clavate, marginal setae (termed *flabella* by many authors). The number of laminae differs between the sexes, with males typically possessing one pair fewer than females, owing to fusion of the meso- and metathoracic laminae. In dorsal aspect these insects super-

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ficially resemble chitons, with the head and other body structures concealed beneath. The dorsal integument is covered with short, papillate or nodulelike setae and a sometimes granular sculpturing arranged in a polygonal pattern. The wings are entirely absent as are the compound eyes and ovipositor.

All of the nine described species of Termitaphididae have been found only in the nests of termites, primarily Rhinotermitidae. The monotypic genus *Termitaphis* (*T. circumvallata* Wasmann, 1902), originally described as a peculiar aphid, lives in the nests of *Amitermes foreli* Wasmann in Colombia (Termitidae: Termitinae). The other eight species of the family are classified in *Termitaradus* and are presently known to live only in the nests of rhinotermitid termites, notably *Coptotermes* (Coptotermitinae), *Heterotermes* (Heterotermitinae), and *Rhinotermes* (Rhinotermitinae) (reviewed in Usinger, 1942). Unfortunately, while termitaphidids are known to live only in termite nests, the exact nature of their association has not been entirely elucidated and it is not known what they feed upon, although it has been hypothesized that they are mycophagous like many aradids. Myers (1924, 1932) provided the most detailed accounts of the family, including interesting natural history observations. In particular, he noted that a termitaphidid moves rapidly when disturbed and would be regularly walked over by the termite hosts as if it were part of the nest wall, at which time it would tightly press itself against and conform to the surface of the wall. Myers (1932) also noted that once a termitaphidid adhered to the substrate, it was challenging to dislodge it without damage.

Typically, highly modified inquilines are rare in the fossil record owing to the peculiarities of their biology, frequently requiring host nests to become interred. Remarkably, four termitaphidid specimens have been recovered in Tertiary amber from the New World: a single individual in Early Miocene amber from Chiapas, Mexico (Poinar and Doyen, 1992), and three individuals in two pieces of contemporaneous amber from the Dominican Republic, newly reported herein. Below is a description of the first termitaphidid species from Early Miocene (Burdigalian) amber of the Dominican Republic. The species has some similarities to the fossil described from Mexican amber (Poinar and Doyen, 1992), but has many features more in line with modern taxa than with the Mexican amber species. Morphological terminology in general follows that of Myers (1924) and Usinger (1942), except that we have more accurately termed the "flabella" as *marginal setae*.

SYSTEMATIC PALEONTOLOGY

Genus *Termitaradus* Myers

Termitaradus avitinquilinus, new species

Termitaradus sp.; Grimaldi and Engel, 2005: 329, fig. 8.76.

Figures 1–3

DIAGNOSIS: The new species is similar to *T. protera* in Mexican amber as both share a greater number of lobules (4) on the terminal abdominal segment than any modern species (2–3 in living species). Unlike *T. protera*, however, the Dominican amber species is more similar in size and proportions to modern species (length 3.57 mm vs. an anomalously large 7.1 mm in *T. protera*), and is not as wide (L/W = 1.59 in T. *avitinquilinus* vs. 1.41 in *T. protera*). In addition, the number of lobules on most of the segmental lobes differs notably from that of *T. protera* (refer to values in description); abdomen dorsally with paramedian, longitudinal ridges, and the marginal setae, like many modern species, are serrate. In lobule number the Dominican species more closely approximates those of modern species, particularly some of the Old World species, but seems to fall into an intermediate position between those taxa and *T. protera*.

DESCRIPTION: **Female (adult).** Description based largely on holotype female, with ranges and other variation also from paratypes. Total length 3.57 mm; maximal width 2.24 mm. Integument generally reddish brown, although paler on sterna, lobules largely reddish brown although slightly lighter than body of laminae, apices of lobules more weakly sclerotized and paler than remainder; marginal setae typically light reddish brown although some cleared and faint (the latter clearly owing to preservation); ventrally faintly imbricate, without

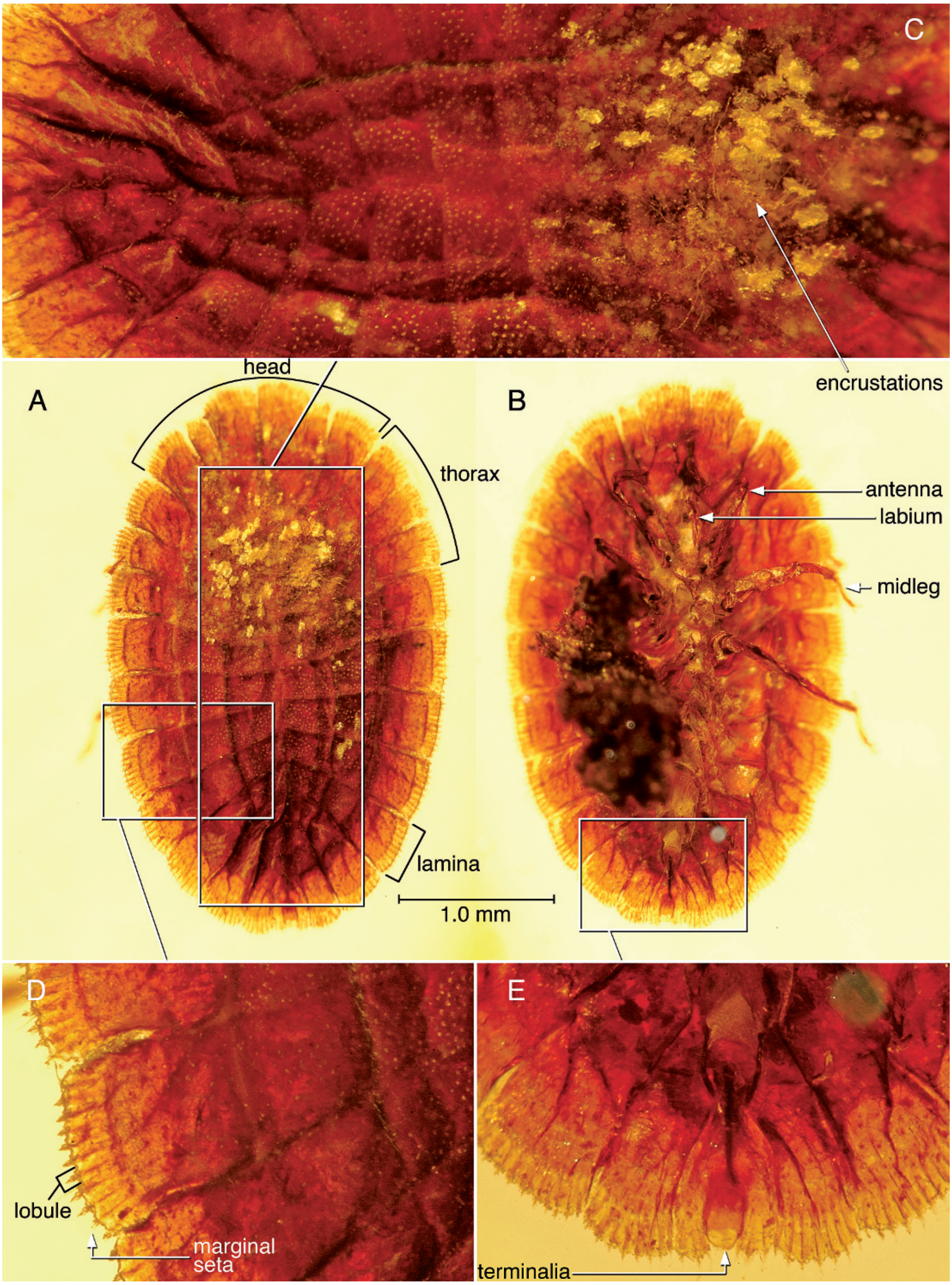

Fig. 1. Photomicrographs of the holotype (AMNH DR 14-425) of *Termitaradus avitinquilinus*, sp. n., in Miocene Dominican amber. **A.** Dorsal habitus; **B.** Ventral habitus. **C.** Detail of dorsum, showing segmentation and fungal encrustation. **D.** Detail of abdominal lamina. **E.** Detail of terminal lamina.

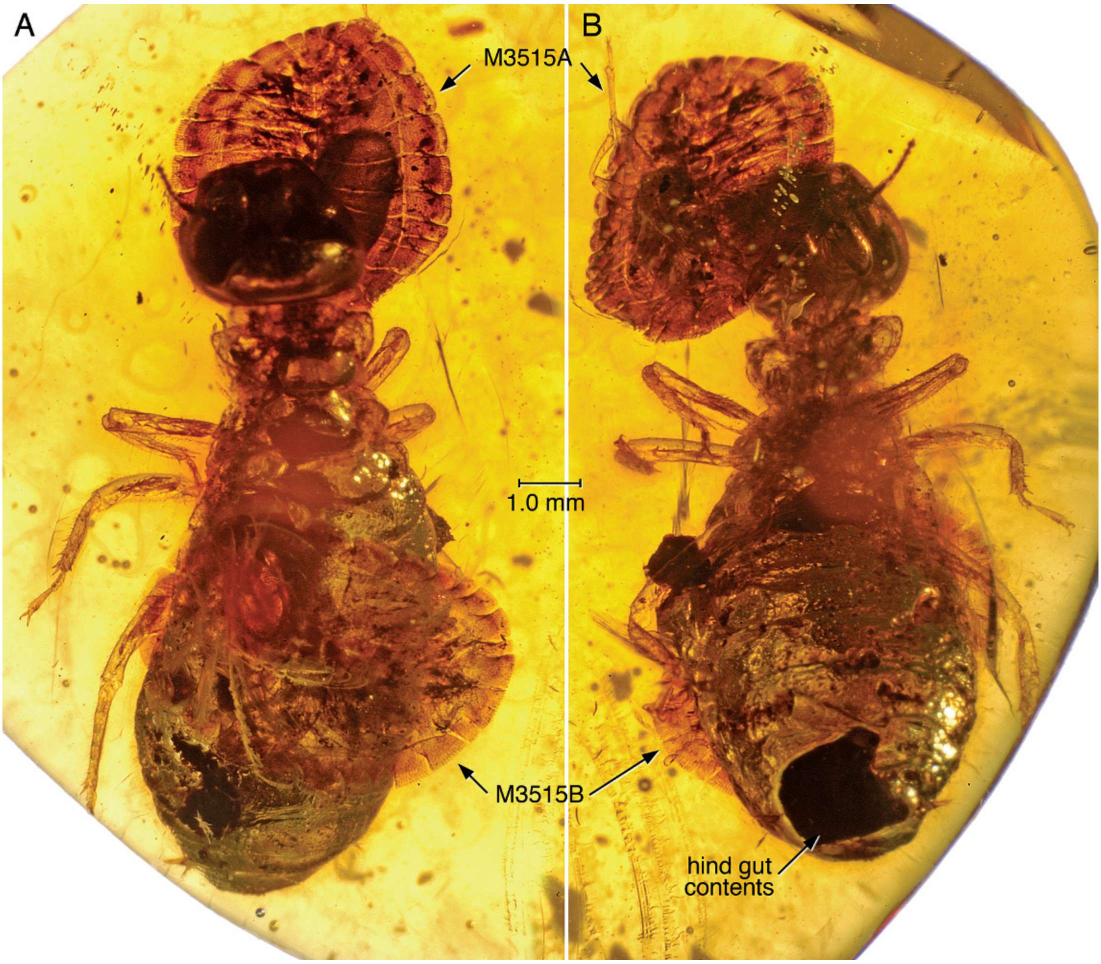

Fig. 2. *Termitaradus avitinquilinus* paratypes (M3515A, B) preserved with a worker of *Mastotermes electrodominicus*. **A.** Dorsal view of termite. **B.** Ventral view.

punctures; dorsally faintly imbricate without punctures, minutely and weakly granulose on body (cf. fig. 5C), with scattered, sparsely serrate setae except on laminae and on head, more sparse on pro- and meso-thoracic segments, such setae with golden coloration. Encrustations of fungi on thoracic nota (fig. 1C). Antenna four-segmented, geniculate; first article elongate, length approximately equal to that of distal three segments combined; second and third cylindrical but short, combined length about as long as apicalmost article; apicalmost article slightly swollen, elongate, approximately one-half the length of first article (cf. fig. 4C). Basal antennomere with subapical patch of granules (sensilla? glandular pores?), apical antennomere with finely textured subapical patch (sensilla?). Granular patches similar to that on apex basal antennomere also occur along most of the length of each tibia (fig. 3). Labium four-segmented (cf. fig. 4C), basalmost segment slightly longer than others. Coiled stylets visible beneath cleared cuticle of clypeus in paratype M3515A (fig. 3).

Legs with stout femora, greatest widths of femora 3–4× that of tibiae; tarsi dimerous, basal tarsomere one-half the size of apical one; claws large, without subapical teeth; pulvilli present, slender, and straplike, lengths approximately equal to that of claws (cf. fig. 5A). Foretibia with longitudinal row of

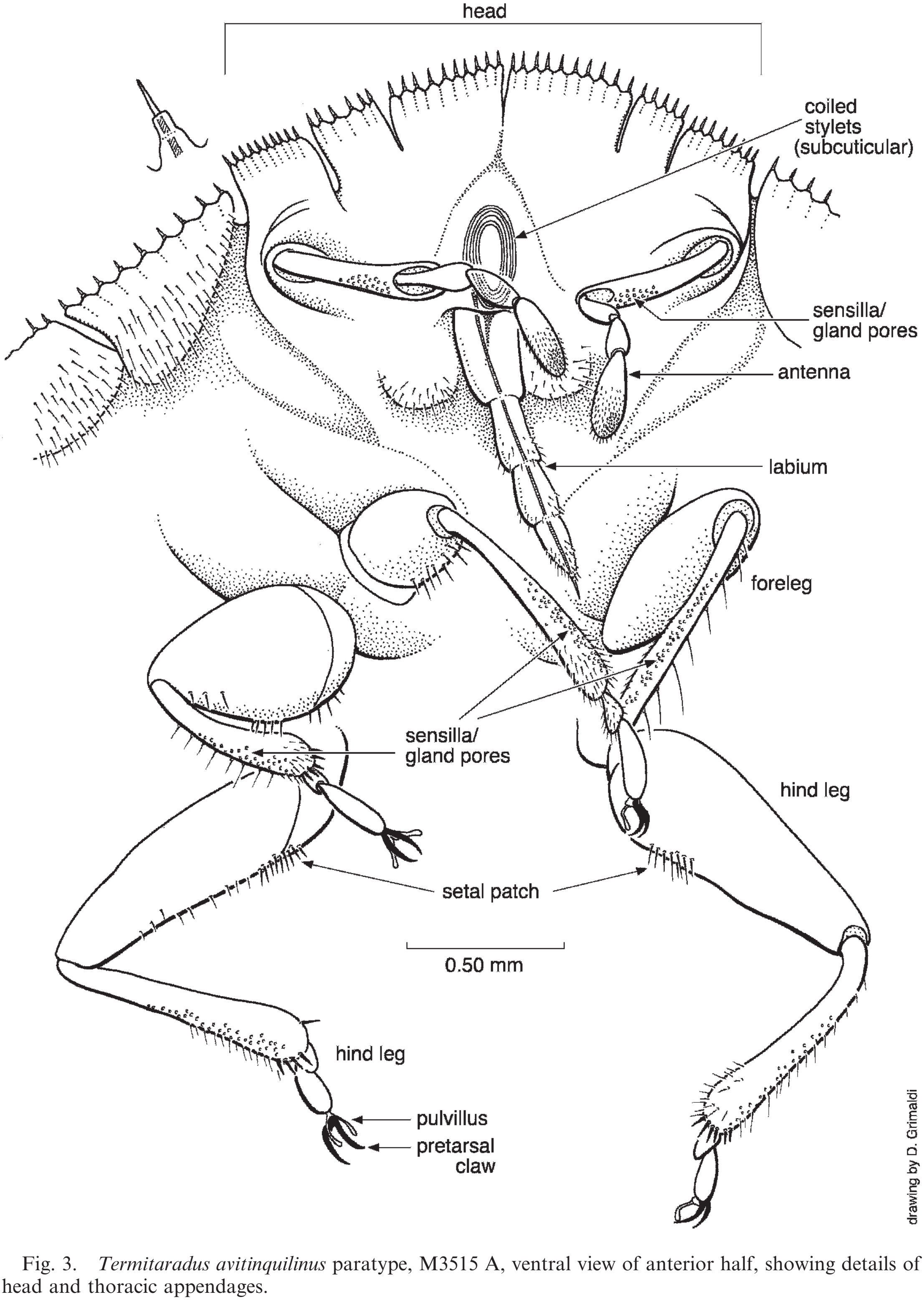

Fig. 3. *Termitaradus avitinquilinus* paratype, M3515 A, ventral view of anterior half, showing details of head and thoracic appendages.

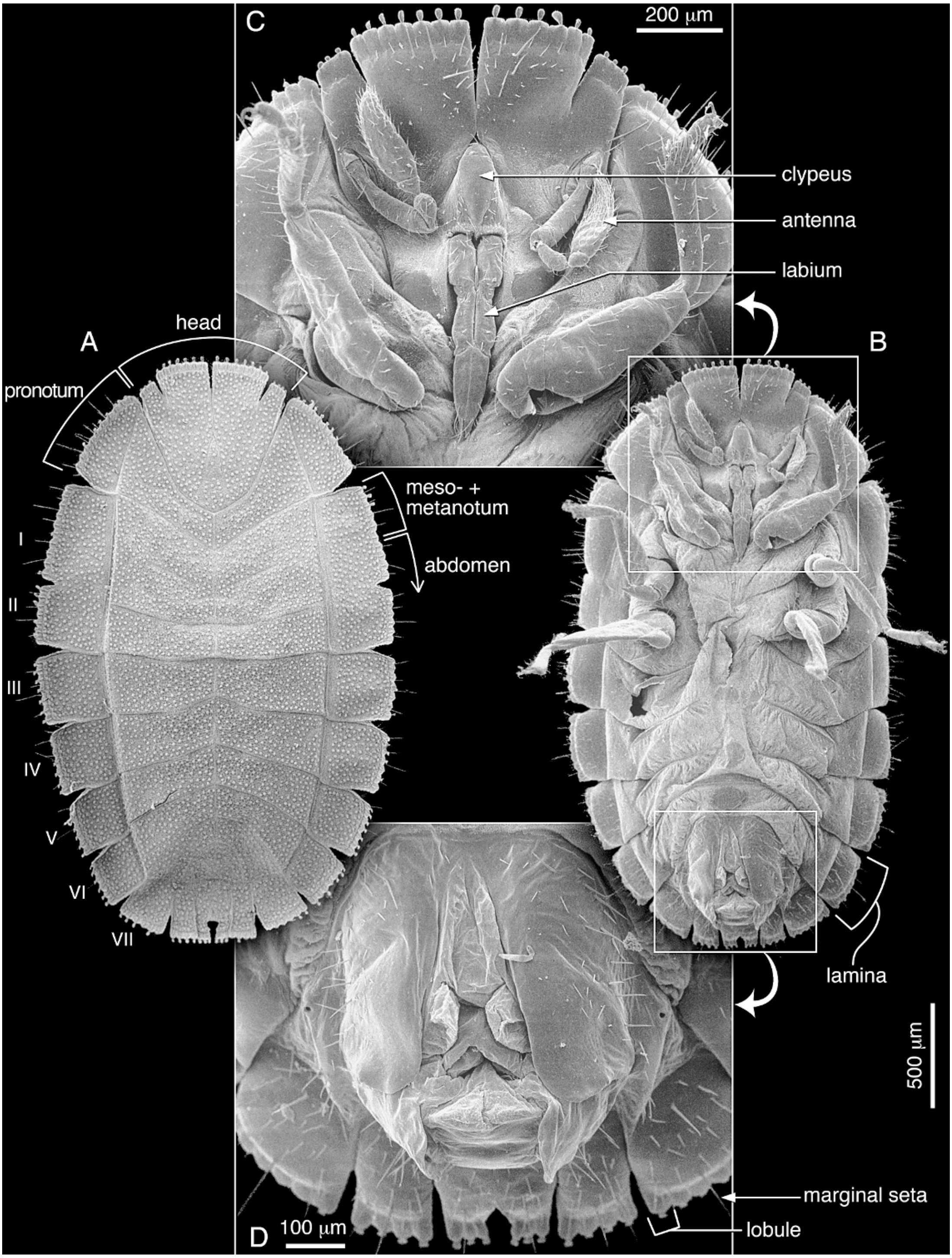

Fig. 4. *Termitaradus guianae*, scanning electron micrographs. **A, B.** Dorsal and ventral habitus, respectively. **C.** Detail of head (ventral). **D.** Detail of male genitalia.

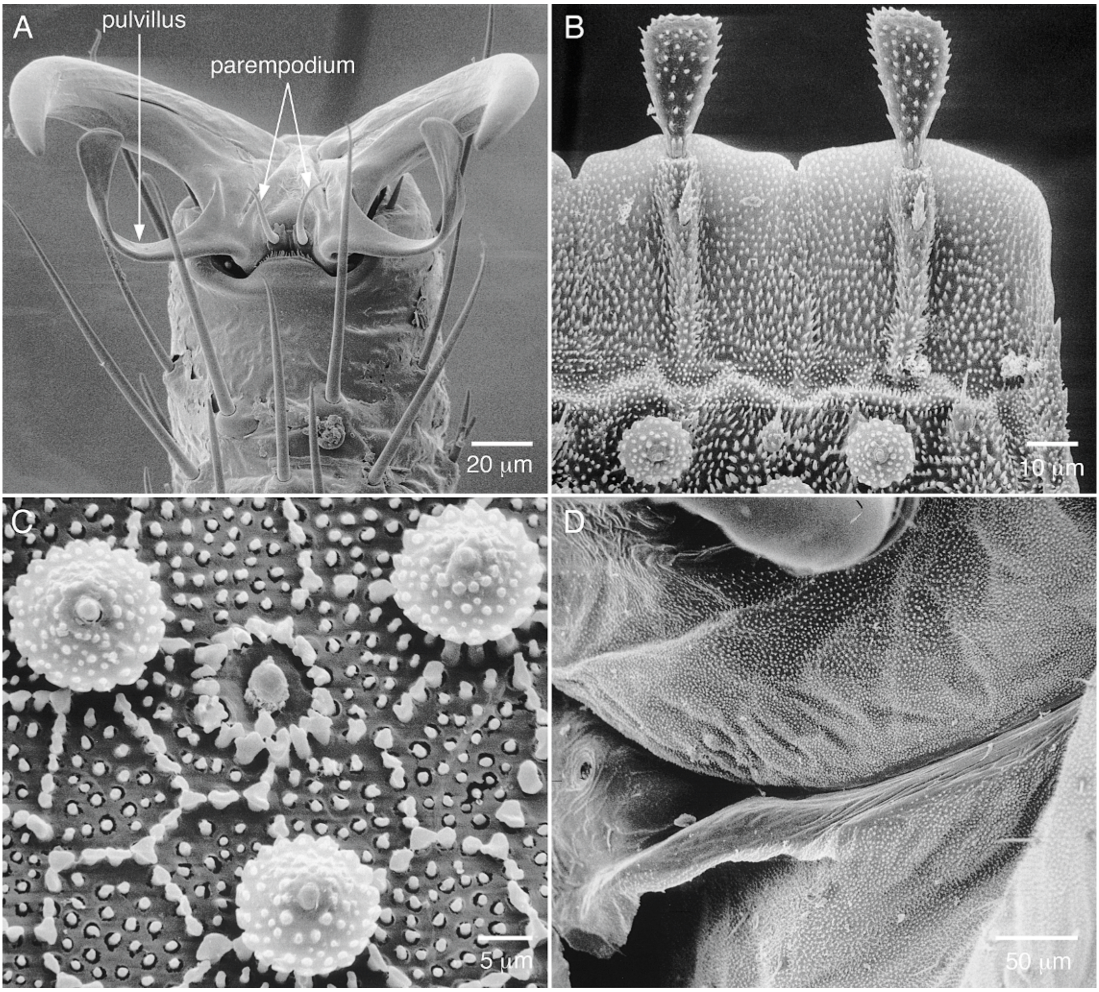

Fig. 5. *Termitaradus guianae*, scanning electron micrographs. **A.** Pretarsus, ventral view. **B.** Clavate marginal setae on margin of head lamina. **C.** Detail of cuticular nodules on dorsum. **D.** Metathoracic scent gland. (Figs. 4 and 5 adapted from fig. 65.1 in Schuh and Slater, 1995.)

ca. six fine, erect setae. Apices of mid- and hind tibiae with transverse row of approximately five short, stiff, sclerotized setae. Base of hind femur with ventral patch of ca. eight short, stiff setae.

Marginal setae generally subtriangular to lanceolate in form, those of head slightly more elongate, in well-preserved setae margins are clearly serrate; none are clavate (e.g., fig. 5B), including ones on head. Fourteen marginal laminae present (three for head, first distinctly larger than second and with small separation; three for thorax [one lobule per thoracic segment]; and one each for the eight abdominal segments). Laminae with lobules arranged as follows: 13–15, 4–6, and 9–10 on head laminae; 8–10 on thoracic segments; 10 on first abdominal; 12 on second abdominal; 12 on third abdominal; 9 on fourth abdominal; 10 on fifth abdominal; 10 on sixth abdominal; 7 on seventh abdominal; and 4 on eighth abdominal. Abdomen dorsally with paramedial, longitudinal ridges.

HOLOTYPE: Female, AMNH DR-14-425, Miocene amber (Burdigalian), Dominican Republic; deposited in the Amber Fossil Collection, Division of Invertebrate Zoology, American Museum of Natural History, New York.

PARATYPES: Females, M-3515 A and B (see fig. 2), Miocene amber (Burdigalian), Dominican Republic; deposited in the Morone Amber Collection, Turin, Italy.

ETYMOLOGY: The specific epithet is a combination of the Latin terms *avitus* ("ancestral", literally "of or relating to a grandfather") and *inquilinus* ("lodger").

DISCUSSION

The most remarkable observation is the presence of two *T. avitinquilinus* specimens preserved in an amber piece with a worker termite of *Mastotermes electrodominicus* Krishna and Grimaldi (Mastotermitidae) (fig. 2). It is highly likely that this termite represents the host of the fossil species given that termitaphidids occur in isolation from their associated termites probably very infrequently. In fact, the specimen from Mexican amber (Poinar and Doyen, 1992) was reported in a piece also containing two wingless termites (it was not mentioned whether these were dealates or workers, and the termite genus was not identified). Given the difficulty in locating modern termitaphidids (which may be easily overlooked) and the scarcity of data available for them, it has to be wondered whether additional, modern termitaphidid species will eventually be discovered in the nests of other families of termites. Thus far, no termitaphidids have been found in the nests of the most basal living termite, *Mastotermes darwiniensis* Froggatt from Australia (N. Lo, personal commun.), so if the association indeed no longer exists then the fossilized association represents a dramatically new one and raises questions regarding the fidelity of termitaphidids with "higher" termite hosts.

Poinar and Doyen (1992) hypothesized that the termitaphidids were ancient and predate the breakup of Pangaea 175 Ma. The rationale for an estimate of such antiquity is based on what appears to be the extremely limited vagility of these bugs, but yet they are circumtropical, so their ancestral distribution was presumably fragmented by drifting continents. Most species of *Termitaradus* are known from Central and South America (*guianae* [Morrison], *jamaicensis* Myers, *mexicanus* [Silvestri], *panamensis* Meyers, and *trinidadensis* [Morrison]), but with one species each in India, Australia, and Africa (*annandalei* [Silvestri], *australiensis* [Mjörberg], and *subafra* Silvestri, respectively). Despite such a distribution, we maintain that a pre-Pangaean existence of termitaphidids is completely unrealistic, and that their distribution can be dated almost certainly to a time 100 Ma or more younger than that posited by Poinar and Doyen.

The Termitaphididae probably originated in the latest Cretaceous or Early Tertiary because, first, the Pentatomomorpha (to which the Aradoidea is the sister group) appears to have originated in either the latest Jurassic or earliest Cretaceous (Grimaldi and Engel, 2005). For example, the earliest and most primitive aradoid is *Archaearadus burmensis* Heiss and Grimaldi in mid-Cretaceous amber from Myanmar (Heiss and Grimaldi, 2001), so it is inconceivable that such a specialized group of pentatomomorphans would far predate the age of the infraorder. Second, the earliest fossil termites occur in the Barremian (Engel et al., 2007a), and termites as a whole did not originate until the latest Jurassic or earliest Cretaceous (Grimaldi and Engel, 2005). Indeed, the higher termites, upon which modern termitaphidids specialize, did not radiate until the Tertiary (Grimaldi and Engel, 2005; Engel et al., 2007a, 2007b). All of this evidence suggests that diversification of Termitaphididae was largely Tertiary, and in such case their circumtropical distribution could be a result of dispersion during globally tropical and subtropical conditions during the Eocene, as is known for myriad other insect groups (Grimaldi and Engel, 2005).

Perhaps most significantly, there are indications that termitaphidids phylogenetically may be highly derived members of the Aradidae. Termitaphidids have the same uniquely modified maxillary and mandibular stylets that are coiled within the head capsule that are characteristic of Aradidae (this is even seen in fossil M3515A, in which the external cuticle is translucent: fig. 3). Aradids have repeatedly become brachypterous and apterous, and in the subfamilies Mezirinae and Carventinae in particular many species are wholly apterous. Mezirinae and

Termitaphididae also share the derived feature of a rostral base situated within a closed atrium (fig. 4C), although four mezirine genera have an open atrium (*Chiastoplonia* China, *Daulocoris* Usinger and Matsuda, *Euchelonocoris* Hoberlandt, and *Pseudomezira* Heiss), and four Carventinae genera have a closed atrium (*Apteraradus* Drake, *Libiocoris* Kormilev, *Neocarventus* Usinger and Matsuda, and *Notoplocaptera* Usinger and Matsuda). Also, the seventh abdominal ventrite in female termitaphidids and Mezirinae is divided into hemiventrites. Many mezirines have lateral lobes on the pronotum and/or abdomen that extend beyond the body, such as *Chlonocoris* Usinger and Matsuda, *Dysodiellus* Hoberlandt, *Oroessa* Usinger, and Matsuda, and *Rossius* Usinger and Matsuda (Usinger and Matsuda, 1959). Many of these even have small setigerous tubercles on the dorsal surface of the body and the lateral margins, much like the lobules and marginal setae (e.g., fig. 5B) of termitaphidids. Furthermore, the arrangement of segments within tagmata of termitaphidids is essentially the same as that of apterous genera of Mezirinae and Carventinae (E. Heiss, personal commun., 2007). Lastly, the structure of the male genital capsules in some mezirines and in termitaphidids is similar.

Circumstantial biological evidence for a termitaphidid-mezirine relationship lies in the fact that several mezirine aradids are apparently facultative inquilines in the colonies of termites, and one species (*Aspisocorus termitophilus* Kormilev, from southwest Australia) is morphologically specialized and thus appears to be an obligate inquiline in the nests of a "higher" termite, *Occasitermes occasus* (Silvestri) (Isoptera: Termitidae: Nasutitermitinae) (Kormilev, 1967; Monteith, 1997). *Aspisocoris* has distinctively reduced compound eyes and hemelytra (such reduction is taken to an extreme in termitaphidids, where they are lost altogether), pale coloration, and small size. Other putative termitophiles in Mezirinae are not morphologically specialized and have also been found away from termites under decaying bark. Interestingly, though, those facultative inquilines occur in the nests of primitive termites such as *Zootermopsis* (e.g., *Mezira reducta* Van Duzee) or *Archotermopsis* (e.g., *Pseudomezira termitophila* [Kormilev]), both of the basal family Termopsidae. The presently documented hosts of modern termitaphidids are exclusively among the higher termites (Rhinotermitidae and Termitidae).

Thus, the possibility should be considered that termitaphidids are highly specialized aradids, in or near the Mezirinae or Carventinae. In such a scenario, and with the exception of the fossilized host association we report here, the termite host associations of modern aradioids roughly reflect a phylogenetic pattern: those mezirines (presumably basal to termitaphidids) facultatively occur in colonies of Termopsidae (one species obligately with a termitid), and the more derived and younger termitaphidids subsist in colonies of higher termites of the Rhinotermitidae and Termitidae. There is even divergence between the two main lineages of termitaphidids: *Termitaphis* is known from Termitidae, and this genus is clearly the sister group to the more specialized, flattened, laminate, and monophyletic *Termitaradus*, which live with Rhinotermitidae.

Unfortunately, the only phylogenetic hypotheses for Aradidae are slim and superficial, using only 15–25 characters and treating subfamilies as terminal taxa (Vásárhely, 1987; Grozeva and Kerzhner, 1992). The monophyly of these subfamilies cannot be assumed. So, confronting a putative mezirine-termitaphidid relationship must await a comprehensive phylogenetic analysis, but our ignorance is far more profound that this. The last extant termitaphidid to have been described was by Myers (1932), even though vast expanses of forests from the Andean and Amazonian regions, the Congo Basin, and the IndoPacific are unexplored. While it is intriguing to consider how such intimate symbiosis as that between termitaphidids and termites could be evolving for much of the Tertiary, even more fundamental is what alliances have yet to be discovered.

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REFERENCES

Engel, M.S., D.A. Grimaldi, and K. Krishna. 2007a. Primitive termites from the Early Cretaceous of Asia (Isoptera). Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie) 371: 1–32.

Engel, M.S., D.A. Grimaldi, and K. Krishna. 2007b. A synopsis of Baltic amber termites (Isoptera). Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie) 372: 1–20.

Grimaldi, D., and M.S. Engel. 2005. Evolution of the insects. Cambridge: Cambridge University Press, xv+755 pp.

Grozeva, S.M., and I.M. Kerzhner. 1992. On the phylogeny of aradid subfamilies (Heteroptera, Aradidae). Acta Zoologica Hungarica 38: 199–205.

Heiss, E., and D. Grimaldi. 2001. *Archearadus burmensis* gen. n., sp. n., a remarkable Mesozoic Aradidae in Burmese amber (Heteroptera, Aradidae). Carolinea 59: 99–102.

Kormilev, N.A. 1967. Aradidae in the South Australian Museum, Adelaide. II. Hemiptera—Heteroptera. Records of the South Australian Museum 15: 513–550.

Kormilev, N.A., and R.C. Froeschner. 1987. Flat bugs of the world: a synonymic list (Heteroptera: Aradidae). Entomography 5: 1–246.

Monteith, G.B. 1997. Revision of the Australian flat bugs of the subfamily Mezirinae (Insecta: Hemiptera: Aradidae). Memoirs of the Queensland Museum 41: 1–169.

Myers, J.G. 1924. On the systematic position of the family Termitaphididae (Hemiptera, Heteroptera), with a description of a new genus and species from Panama. Psyche 31: 259–278.

Myers, J.G. 1932. Observations on the family Termitaphididae (Hemiptera-Heteroptera), with the description of a new species from Jamaica. Annals and Magazine of Natural History (10)9: 366–372.

Poinar, G.O., Jr., and J.T. Doyen. 1992. A fossil termite bug, *Termitaradus protera* sp. n. (Hemiptera: Termitaphididae), from Mexican amber. Entomologica Scandinavica 23(1): 89–93.

Schuh, R.T., and J.A. Slater. 1995. True Bugs of the world (Hemiptera: Heteroptera). Classification and Natural History. Ithaca NY: Cornell University Press, xii + 336 pp.

Usinger, R.L. 1942. Revision of the Termitaphididae (Hemiptera). Pan-Pacific Entomologist 18: 155–159.

Usinger, R.L., and R. Matsuda. 1959. Classification of the Aradidae (Hemiptera–Heteroptera). London: British Museum (Natural History), vii + 410 pp.

Vásárhelyi, T. 1987. On the relationships of the eight aradid subfamilies (Heteroptera). Acta Zoologica Hungarica 32: 377–383.

Wilson, E.O. 1971. The insect societies. Cambridge, MA: Belknap Press, x + 548 pp.

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