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Diverse Rhinotermitidae and Termitidae (Isoptera) in Dominican Amber

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ABSTRACT

The most diverse and best-preserved paleofauna of the higher termites heretofore known, all found in Miocene amber of the Dominican Republic, is described. The imago of *Coptotermes priscus* Emerson is redescribed, and the soldier of *C. priscus*, the first known fossil soldier of this genus, is described. The fauna includes the following 29 new species, all in existing genera, with Krishna and Grimaldi as authors of each: in the Rhinotermitidae, two new species based on imagoes of each—*Coptotermes hirsutus* and *C. paleodominicanus*; in the Termitidae, 23 new species based on imagoes—*Amitermes lucidus*, *Anoplotermes bohio*, *A. cacique*, *A. carib*, *A. maboya*, *A. naboria*, *A. nitaino*, *A. quisqueya*, *A. taino*, *Atlantitermes antillea*, *A. caribea*, *A. magnoculus*, *Microcerotermes insulanus*, *M. setosus*, *Nasutitermes amplioculatus*, *N. incisus*, *N. magnocellus*, *N. medioculatus*, *N. pilosus*, *N. seminudus*, *Subulitermes hispaniola*, *S. insularis*, and *Termes primitivus*; in the Nasutitermitinae four new species based on nasute soldiers—*Caribitermes hispaniola*, *Nasutitermes rotundicephalus*, *Parvitermes longinasus*, and *Velocitermes bulbus*. This brings the total termite fauna in Dominican amber to four families, 17 genera, and 39 species, a number that exceeds that of the present-day fauna of Hispaniola. Biogeographical, paleoecological, and phylogenetic implications of the Dominican amber termites are discussed.

INTRODUCTION

This is the last and largest report in a series of six papers on the fossil record of the order Isoptera. Prior papers have dealt with Cretaceous taxa (Engel et al., 2007a; Grimaldi et al., 2008), Eocene taxa in Baltic amber (Engel et al., 2007b; Engel, 2008), and Kalotermitidae in Miocene amber from the Dominican Republic (Engel and Krishna, 2007). Here, we describe the most diverse and best-preserved paleofauna, also in Dominican amber, of the so-called "higher" termites in the large family Termitidae, totaling 27 new species in 10 extant genera. In addition, two new species of Rhinotermitidae are described. The total

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TABLE 1
Hispaniolan Termites

FOSSIL	LIVING
Family Mastotermitidae	
Mastotermes electrodominicus Krishna and Grimaldi	
Family Kalotermitidae	
Cryptotermes glaesarius Engel and Krishna	*Cryptotermes brevis* (Walker)
Cryptotermes yamini Krishna and Bacchus	*Cryptotermes chasei* Scheffrahn
	Cryptotermes cavifrons Banks
	Cryptotermes sp. nr. *hemicyclius* Bacchus*
	Cryptotermes longicollis Banks
	Cryptotermes rotundiceps Scheffrahn and Křeček
Glyptotermes grimaldii Engel and Krishna	*Glyptotermes liberatus* (Snyder)
Glyptotermes paleoliberatus Engel and Krishna	
Incisitermes peritus Engel and Krishna	*Incisitermes bequaerti* (Snyder)
	Incisitermes milleri (Emerson)
	Incisitermes sp. near *snyderi* (Emerson)*
	Incisitermes sp. near *schwarzi* (Banks)*
	Neotermes castaneus (Burmeister)
	Neotermes jouteli (Banks)
	Neotermes mona (Banks)
	Procryptotermes corniceps (Snyder)
Family Rhinotermitidae	
Dolichorhinotermes dominicanus Schlemmermeyer and Cancello	
Coptotermes priscus Emerson	
Coptotermes paleodominicanus **n. sp.**	
Coptotermes hirsutus **n. sp.**	
	Heterotermes cardini (Snyder)
	Heterotermes convexinotatus (Snyder)
	Heterotermes tenuis (Hagen)
	Rhinotermes marginalis (Linnaeus)
Family Termitidae	
Amitermes lucidus **n. sp.**	
Anoplotermes bohio, **n. sp.**	*Anoplotermes meridianus* Emerson
Anoplotermes cacique, **n. sp.**	*Anoplotermes* sp. A*
Anoplotermes carib, **n. sp.**	*Anoplotermes* sp. B*
Anoplotermes maboya, **n. sp.**	
Anoplotermes naboria, **n. sp.**	
Anoplotermes nitaino, **n. sp.**	
Anoplotermes quisqueya, **n. sp.**	
Anoplotermes taino, **n. sp.**	
	Antillitermes subtilis (Scheffrahn and Křeček)
Atlantitermes antillea, **n. sp.**	
Atlantitermes caribea, **n. sp.**	
Atlantitermes magnoculus, **n. sp.**	
Caribitermes hispaniola, **n. sp.**	*Caribitermes discolor* (Banks)
Constrictotermes electroconstrictus Krishna	
Microcerotermes insulanus, **n. sp.**	*Microcerotermes arboreus* Emerson
Microcerotermes setosus **n. sp.**	
Nasutitermes amplioculatus, **n. sp.**	*Nasutitermes costalis* (Holmgren)
Nasutitermes electronasutus Krishna	*Nasutitermes hubbardi* Banks
Nasutitermes incisus, **n. sp.**	*Nasutitermes lividus* (Burmeister)
Nasutitermes magnocellus, **n. sp.**	

TABLE 1
(Continued)

FOSSIL	LIVING
Nasutitermes medioculatus, **n. sp.**	
Nasutitermes pilosus, **n. sp.**	
Nasutitermes rotundicephalus, **n. sp.**	
Nasutitermes seminudus, **n. sp.**	
Parvitermes longinasus, **n. sp.**	*Parvitermes toussainti* (Banks)
Subulitermes hispaniola, **n. sp.**	
Subulitermes insularis, **n. sp.**	
Termes primitivus, **n. sp.**	*Termes hispaniolae* (Banks)
Velocitermes bulbus, **n. sp.**	*Velocitermes antillarum* (Holmgren)

*from Scheffrahn et al., 1994

termite fauna in Dominican amber thus consists of four families, 17 genera, and 39 species, which exceeds that of the present fauna of Hispaniola, with three families, 15 genera, and 31 species (table 1). Later in this paper we discuss the biogeographic implications of this difference. The sum of fossil termite taxa from all six recent papers is 47 newly described species and a further 17 revised, which largely redefines what had previously been known (Nel and Paicheler, 1993; Thorne et al., 2000) of the fossil record of this ecologically fundamental group of insects. The purpose of these studies on termite fossils is to construct a phylogeny of the major lineages of termites, both living and extinct.

The main phylogenetic pattern emerging thus far for termites is that basal families (like Mastotermitidae, Hodotermitidae, and Termopsidae) and stem groups predominated in the Cretaceous. By the Eocene (i.e., Baltic amber), Kalotermitidae and Rhinotermitidae were diverse (Engel et al., 2007b). Interestingly, definitive fossils of the Termitidae—a family that comprises more than 75% of all termite species—did not appear until the Late Oligocene (Martins-Neto and Pesenti, 2006; Nel and Paicheler, 1993). Unfortunately, those records are preserved as compressions and impressions in rocks, which seriously compromises the interpretation of Isoptera, a group where taxonomically important structures are usually minute and subtle. As we report here, by the Miocene ca. 20 mya the Termitidae had evolved into essentially modern tropical groups, indicating that the radiation of the higher termites was relatively recent as well as rapid. Indeed, this radiation appears to be the most significant one among all insects that took place in the mid- to Late Tertiary (Grimaldi and Engel, 2005).

METHODS

Dominican amber is Miocene in age, approximately 17 myo (Iturralde-Vinent and MacPhee, 1996), and material in the AMNH collection derived from dealers in the Dominican Republic, as is all commercially available amber from that country. All of the amber comes from mines in the Cordillera Septentrional approximately 10 to 30 km NE of Santiago (Grimaldi, 1995), but the exact source (i.e., the mine) is generally impossible to determine for commercial amber. With the obvious exception of copal, there is little or no variation in composition or age among main amber mines of the Dominican Republic (Grimaldi, 1995; Iturralde-Vinent and MacPhee, 1996). Copal is immediately recognizable: it is lighter in color, softer, crazes readily, and the surface becomes tacky when a drop of solvent is applied. Recent ^{14}C dating found that Dominican copal is merely several hundred years old (Grimaldi, unpubl.). Thus, there is no doubt that all the material we studied is definitively Miocene in age. Unless the provenance of an amber specimen is specifically known and stated, it should be assumed that the locus typicus of all new species is the following: Hispaniola (Dominican Republic), Cordillera Septentrional near Santiago, specific provenance (mine) unknown, El Mamey Formation, Early to mid-Miocene.

Careful study of a termite in amber requires meticulous preparation. Particularly for Rhinotermitidae and Termitidae, identifying imagoes to genus and distinguishing among species depends upon proportions and shapes of the head, eyes, ocelli, clypeus, and pronotum. Details such as the position and structure of the fontanelle and the shape and setation of the head and pronotum require very close views of these structures. Thus, for this study, amber pieces were trimmed and polished for a full frontal view of the head and full dorsal view of the pronotum, where possible. Mandibular dentition is also significant, and fortuitously the labrum of some specimens was clear enough to observe the mandibles beneath. Where possible, a full view of the wings was also prepared so as to document venation. Amber pieces were trimmed with a small water-fed diamond saw (thickness ca. 1 mm), and the faceted surfaces were ground and polished with a water-fed lapidary wheel using emory papers of successively finer grits (first 400, then 600, 2400, and finally 4000). For optimal observation the amber specimen was mounted on a small piece of plasticene or dental wax applied to a glass slide, in the desired orientation, and a small drop of glycerine and a coverslip were applied to the surface of the amber. This last step obscures fine scratches on the surface that reduce visibility of minute structures. Microscope study used fiber optic illumination and either a Zeiss SV8 stereoscope (up to 64×) or a Leitz Wetzlar stereoscope (up to 144×); measurements were made with an ocular reticle on the Leitz stereoscope. Photomicrography used a Nikon D1X digital camera attached to either Infinity® lenses or a Nikon compound microscope, with fiber-optic flash illumination provided by a MicrOptics® system.

SYSTEMATICS

FAMILY RHINOTERMITIDAE Froggatt, 1897

SUBFAMILY COPTOTERMITINAE Holmgren, 1910

Genus *Coptotermes* Wasmann, 1896

The genus *Coptotermes* is found in all tropical areas of Earth. Many species of this genus have been introduced in various parts of the world, and some have become serious pests, most notoriously *Coptotermes formosanus* Shiraki. Of the total number of 75 living and two fossil species of the genus hitherto described, only four living (one introduced) and two fossil (one Dominican Republic amber and one Mexican amber) are found in the Neotropical Region (all others are in southeast Asia and Africa). In this paper we are adding two new species and describing the first soldier of the genus *Coptotermes* in the fossil record.

Coptotermes hirsutus, new species

Figures 1, 2, 3; table 2

DIAGNOSIS: The head, pronotum, and wing scale of the imago of this new species are densely covered with setae of various lengths, in contrast to *C. priscus* Emerson and *C. paleodominicanus*, n. sp., in which setae are sparse. It differs from *C. priscus* in having larger eyes and a wider head and from *C. paleodominicanus* in having a smaller head and smaller eyes.

DESCRIPTION: **Imago**: Head dark brown; pronotum, antennae, and legs lighter than head; wing scale brownish, about same color as pronotum; wings brownish yellow, membrane transparent. Head, pronotum, and wing scale densely covered with long bristles, longest about 0.19 mm; costal margin of forewing with several short hairs; wing membrane with fine short hairs. Head semicircular. Eyes medium sized, somewhat oval. Ocelli oval, very close to eyes. Fontanelle dot shaped; situated in middle of head, about 0.49 mm from posterior margin of head (in distorted specimen appearing closer to posterior margin). Postclypeus narrow, faintly arched; width four times length. Antennae with 18–19 articles; third shortest; second longer than fourth. Pronotum slightly narrower than head; front margin broadly concave; posterolateral corners broadly rounded; posterior margin emarginate, faintly angular. Forewing with costal margin heavily sclerotized; radius equally sclerotized, running parallel to costa; median weak, emerging separately from scale, running close to cubitus, with two or three distal subbranches; cubitus as weak as median, with about 11 subbranches to posterior border of wing. Hind wing with costal margin and radius as in forewing; median arising from radius outside

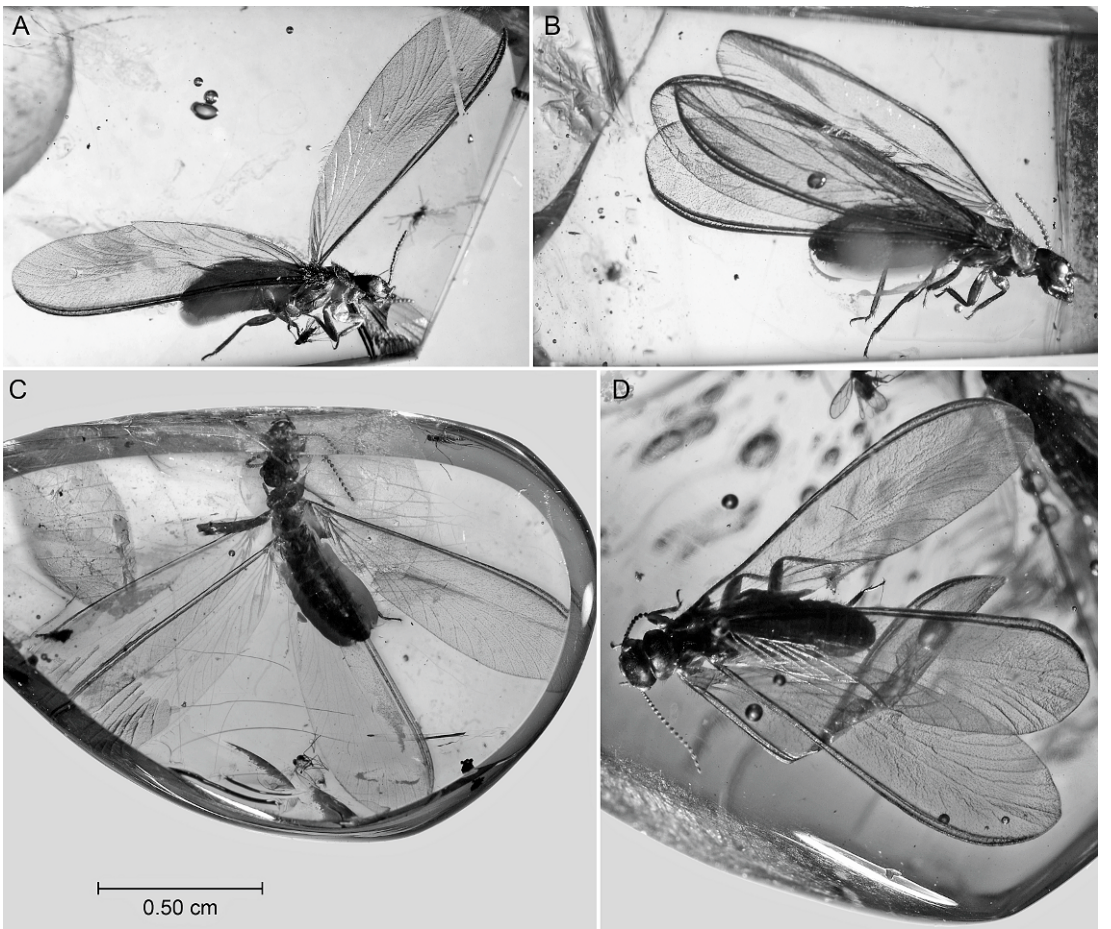

Fig. 1. Photomicrographs of *Coptotermes species* in Dominican amber. **A.** *Coptotermes hirsutus*, n. sp., AMNH DR-PB278. **B.** *Coptotermes hirsutus* AMNH DR10-1656. **C.** *Coptotermes paleodomincanus*, n. sp., AMNH DR10-1513. **D.** *Coptotermes priscus* Emerson, AMNH DR-PB279.

of the scale; median and cubitus as in forewing. Tibial spurs 3:2:2.

SPECIMENS: Holotype (imago) AMNH No. PB-278. Paratypes (imagoes) AMNH nos. DR8-343, DR10-1263, DR10-1518, DR10-1535, DR10-1561, DR10-1578, DR10-1643, DR10-1648, DR10-1656, PB-277.

ETYMOLOGY: This species is named after the Latin term *hirsutus*, ''hairy'', and refers to the characteristic dense covering of the head and pronotum.

Coptotermes paleodominicanus, new species

Figures 1, 2, 3; table 2

DIAGNOSIS: The imago of this new fossil species has a distinctly longer and wider head, larger eyes and ocelli, and a longer and wider pronotum than the other two fossil species of this genus: *C. priscus* Emerson and *C. hirsutus*, n. sp.

DESCRIPTION: **Imago**: Head rusty brown; postclypeus and labrum brownish, lighter than frons; pronotum brown, lighter than head; legs and antennae light brown; wings brownish yellow. Head with a few short and long bristles; pronotum surface and margins moderately covered with short and long setae, longest about 0.13 mm; sternites, tergites, tibiae, and tarsi covered with short and long bristles; forewing scale with several long bristles, longest about 0.15 mm; costal margin of forewing with several short hairs; wing surface with scattered short bristles. Head

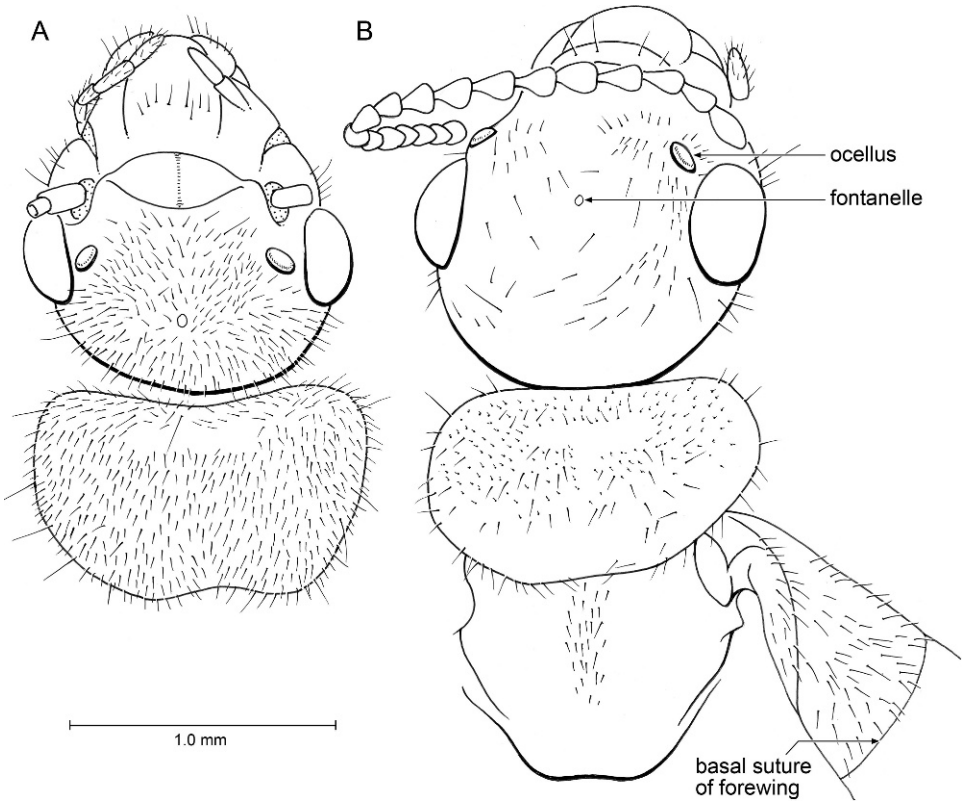

Fig. 2. Drawings of head and portions of thoraces of *Coptotermes* species in Dominican amber, dorsal views. **A.** *Coptotermes hirsutus*, n. sp., AMNH DR10-1656 (head), DR10-1698 (pronotum). **B.** *Coptotermes paleodominicanus*, n. sp., AMNH DR10-1513 (slightly oblique view).

much larger than those of *C. priscus* and *C. hirsutus*. Eyes large. Ocelli long, very close (0.02 mm) to eye; outer margin indented when viewed dorsally. Fontanelle small, dotlike; about 0.61 mm from posterior margin of head. Postclypeus short, faintly arched; width 3.8 times length. Antennae with 21 articles (only 10 articles visible in holotype); third article shortest; fourth subequal to second. Pronotum narrower than head; anterior margin broadly indented in middle; posterolateral margins broadly rounded; posterior margin emarginate. Forewing with costal margin heavily sclerotized; radius equally sclerotized, running parallel to costa; median weak, emerging separately from scale, running close to cubitus, with two or three distal subbranches; cubitus as weak as median, with about 15 subbranches to posterior border of wing. Hind wing with costal margin and radius as in forewing; median arising from radius outside of the scale; median and cubitus as in forewing. Tibial spurs 3:2:2.

SPECIMENS: Holotype (imago) AMNH DR10-1567. Paratype (imago) AMNH DR1-1513.

ETYMOLOGY: The species name is a combination of *paleo-*, "ancient", and *dominicanus*, for the Dominican Republic, the general locality where the amber fossil was collected.

Coptotermes priscus Emerson

Figures 1, 4, 5; tables 2, 3

REDESCRIPTION (based on new material): **Imago**: Head dark brown; pronotum, antennae, and legs lighter than head; wing scale and costal margin brown; wing mem-

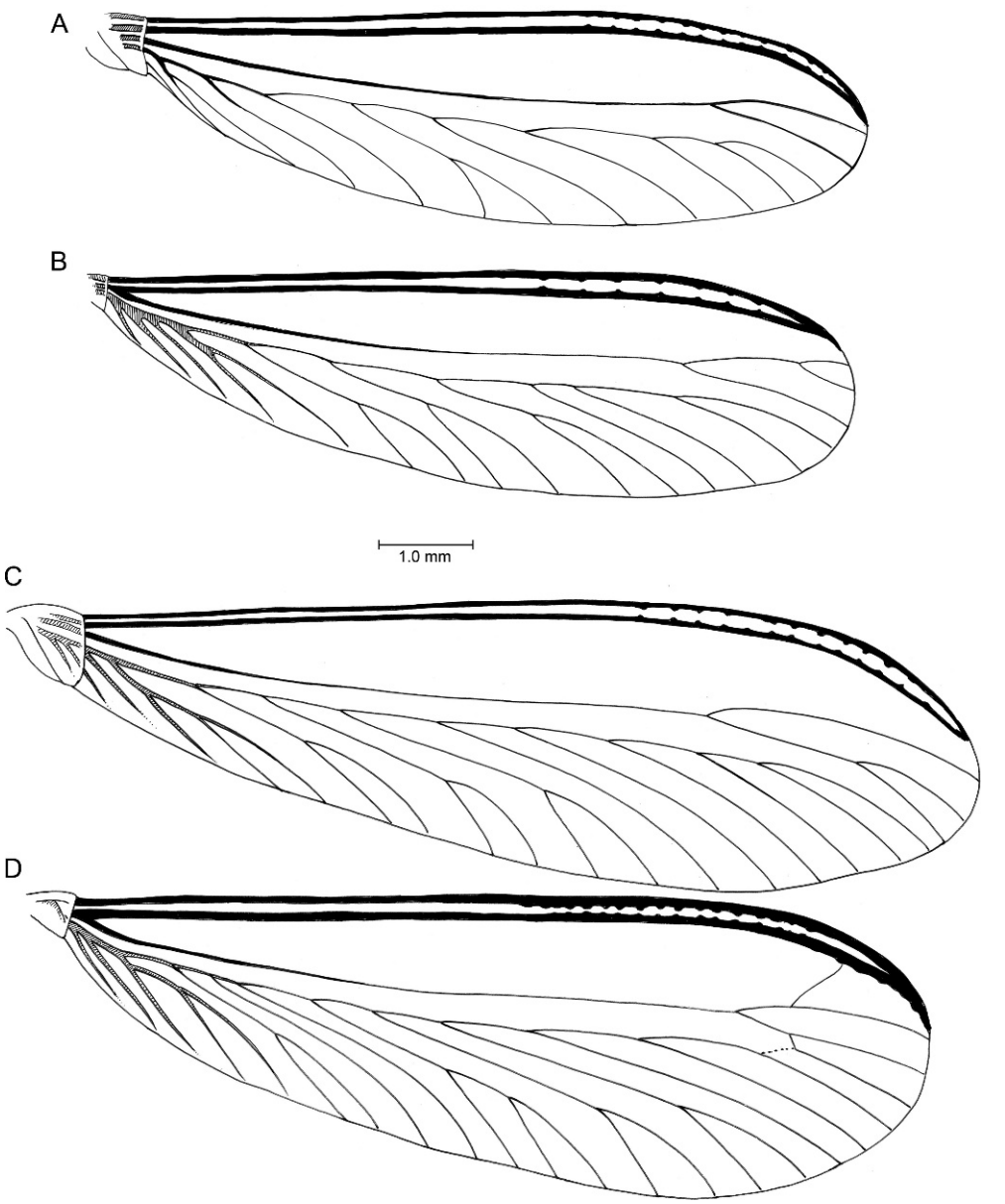

Fig. 3. Wings of *Coptotermes* species in Dominican amber. **A, B.** *Coptotermes hirsutus*, n. sp., AMNH PB278. A. forewing; B. hindwing. **C, D.** *Coptotermes paleodominicus*, n. sp., AMNH DR10-1513.

brane transparent. Head with many short hairs and several long bristles; pronotum surface moderately covered with short and medium-sized bristles, longer bristles along margin; wing scale with longer bristles than head and surface of pronotum; anterior margin of fore- and hind wing with a row of very short hairs; wing membrane moderately covered with very short hairs. Head circular. Eyes small, rounded, slightly protruded. Ocelli oval, oblique, very close to eyes. Fontanelle dotlike; in a slight depression in middle of head. Postclypeus short, slightly arched; four times as wide as long. Mandible dentition typical of *Coptotermes*: left mandible with an apical tooth and three marginal teeth; first

TABLE 2
Measurements (mm) of imagoes of three species of *Coptotermes*

	priscus (5 imagoes)		***paleodominicus***		***hirsutus*** (5 imagoes)		
	Range	Mean	Holotype	Paratype	Holotype	Range	Mean
Length of head to tip of labrum	1.28–1.32	1.30	1.83	1.78	1.42	1.25–1.42	1.38
Width of head with eyes	1.02–1.17	1.12	1.53	1.40	1.30	1.22–1.30	1.27
Diameter of eye	0.31–0.33	0.33	0.59	0.56	0.39	0.36–0.41	0.39
Eye from lower margin	0.08	0.08	—	—	0.06	0.05–0.07	0.06
Length of ocellus	0.14–0.15	0.14	0.23	0.17	0.18	0.15–0.18	0.16
Length of postclypeus	0.10–0.12	0.11	0.15	0.13	0.12	0.12	0.12
Width of postclypeus	0.43–0.44	0.41	0.56	0.53	0.49	0.49–0.51	0.50
Maximum length of pronotum	0.53–0.71	0.63	0.77	0.75	0.69	0.64–0.69	0.66
Width of pronotum	0.84–1.10	1.02	1.17	1.22	1.07	1.07–1.20	1.15
Length of hind tibia	1.07–1.12	1.10	—	—	0.99	0.99–1.14	1.04
Length of forewing scale	0.84–0.89	0.87	1.07	1.04	0.89	0.80–0.89	0.86
Length of forewing from suture	7.50–8.00	7.75	8.10*	8.70	7.50	7.30–8.50	7.66
Width of forewing	2.30	2.30	2.60	2.70	2.30	2.35–2.50	2.38

*approximate

marginal tooth shorter than both apical and second marginal tooth; second marginal tooth subequal to apical. Antennae with 21 articles; third shortest; second longer than fourth. Pronotum as wide as head; anterior margin broadly concave; lateral margins rounded; posterior margin emarginate. Forewing with costal margin heavily sclerotized; radius equally sclerotized, running parallel to costa; median weak, emerging separately from scale, running close to cubitus, with two or three subbranches in distal one-third; cubitus as weak as median, with 9–11 subbranches to posterior border of wing. Hind wing with costal and radius as in forewing; median arising from radius outside of scale; median and cubitus as in forewing. Tibial spurs 3:2:2.

Soldier (fig. 4) (first description of a *Coptotermes* soldier in the fossil record): Head brown to yellowish brown; pronotum, antennae and legs lighter than head; mandibles brown. Head and pronotum with a few short and medium-sized bristles; area around fontanelle with several short bristles; tergites covered with several medium-sized bristles; sternites with short bristles. Head pear shaped; fontanelle large, typical of *Coptotermes*, with a large, round opening near base of postclypeus. Labrum subtriangular, longer than broad, with a pointed hyaline tip. Mandibles saber shaped, gently incurved at tips. Postmentum club shaped, approximately twice as long as wide; sides narrowing posteriorly to form a ''waist'' slightly below middle. Antennae broken; with as least 13 articles; second longer than third. Pronotum flat, narrower than head; anterior margin with a notch in the middle; sides rounded; posterior margin emarginate.

Material Examined: AMNH DR15-280 (soldier and imago); DR10-1248 (soldier); DR14-1179 (soldier); DR10-1200 (imago); PB 280 and PB 281 (three imagoes in each). AMNH No. 11339 (a large, pear-shaped piece, 3″ × 1.5″, containing several imagoes and wings, along with a partial wing of *Mastotermes electrodominicus*, from La Toca mines).

FAMILY TERMITIDAE Latreille, 1802

subfamily apicotermitinae Grassé and Noirot, 1955

Genus *Anoplotermes* Müller, 1873

The genus *Anoplotermes* was first described by F. Müller in 1873, with *A. pacificus* Müller from Brazil as the type species. After Müller, a large number of species from the Ethiopian, Neotropical, and Nearctic regions were added by various authors (see Snyder, 1949). In a major revision, Sands (1972) removed all the species from the Ethiopian Region previously included in this genus, assigning them to several new genera and leaving only the Neo-

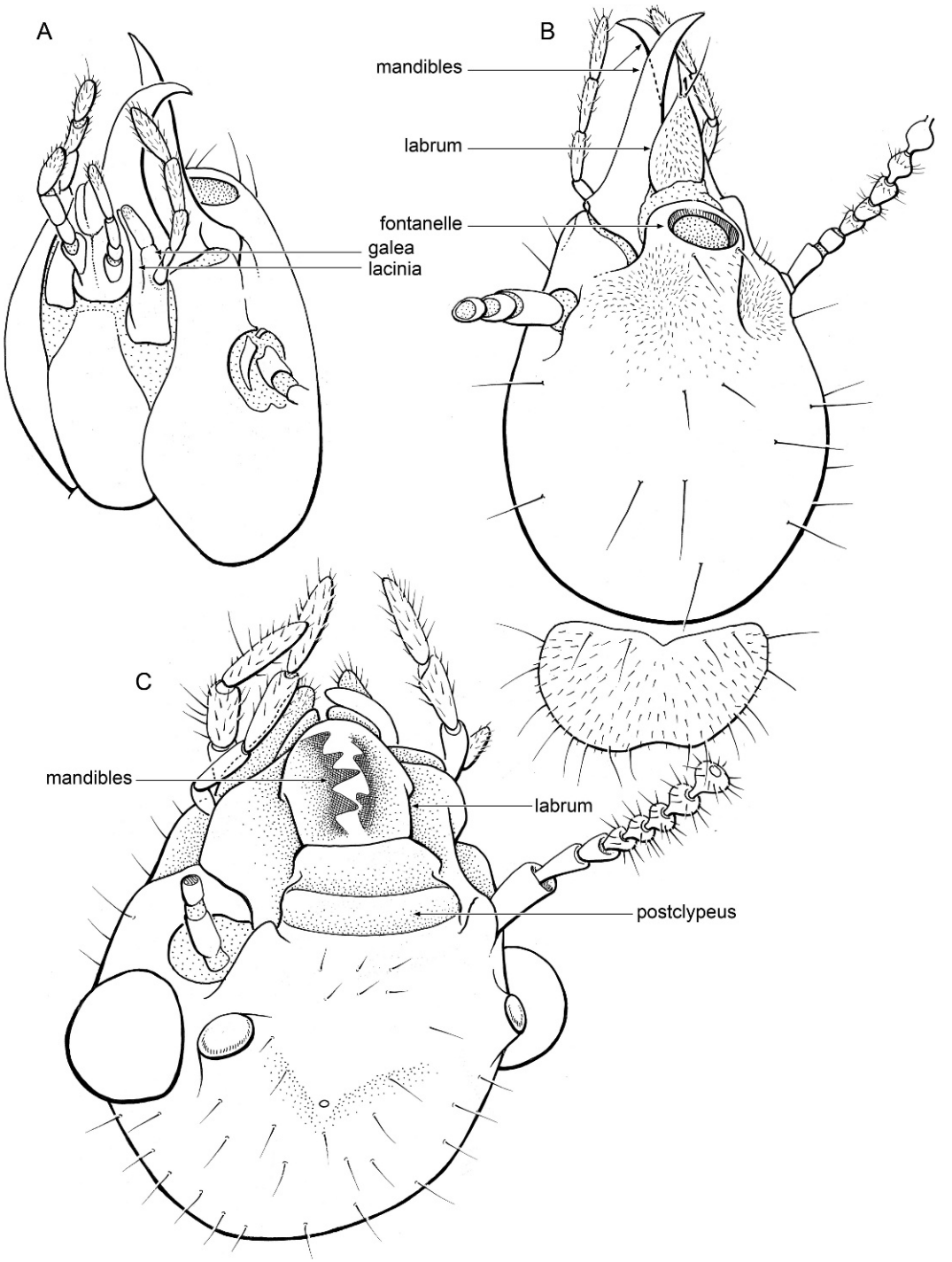

Fig. 4. *Coptotermes priscus* Emerson in Dominican amber, heads. **A, B.** Soldier, in ventrolateral view (A) and dorsal view (B, slightly oblique). AMNH DR10-1248. **C.** Alate, slightly oblique dorsal view, AMNH DR-PB277.

Fig. 5. A swarm of *Coptotermes priscus* Emerson in Dominican amber. This is the most common species of termite in Dominican amber, and is frequently preserved as swarms. AMNH DR-PB279.

tropical and Nearctic species in *Anoplotermes*. As soil and humus feeders, the genus *Anoplotermes* and the related African genera created by Sands are important constituents of the soil fauna in tropical forests (Sands, 1972). *Anoplotermes* and the African genera of this group are distinguished by having no soldier caste. The workers defend the colony by committing suicide: when encountering an enemy, they rupture their abdomens by muscular contractions, spilling the abdominal contents over the attacker. At present there

TABLE 3
Measurements (mm) of three soldiers of *Coptotermes priscus* Emerson

	Range	Mean
Length of head to side base of mandibles	1.00–1.07	1.03
Width of head (approx.)	0.77	0.77
Length of head to fontanelle	0.95–1.02	0.98
Height of head	0.61	0.61
Length of left mandible	0.53–0.56	0.59
Maximum width of postmentum	0.26	0.26
Minimum width of postmentum	0.23	0.23
Length of postmentum	0.54–0.59*	0.55*
Maximum length of pronotum	0.30–0.36	0.33
Width of pronotum	0.51–0.53	0.52
Length of hind tibia	0.74–0.76	0.75

*approximate

are 34 living species, along with several undescribed species in the AMNH collection. Of the 34 species, six are reported from the West Indies, of which only one is from Hispaniola (table 1). The Neotropical and Nearctic species presently placed in *Anoplotermes* need a revision along the lines of that done by Sands (1972), to include studies of the internal characters, such as gut anatomy and Malphigian tubules. Until that is done, we are including the fossil species in the genus *Anoplotermes*.

Anoplotermes bohio, new species
Figures 6, 8; table 4

DIAGNOSIS: *Anoplotermes bohio* differs from all of the other fossil species described here in having its head and pronotum densely covered with long setae. It is closest to *A. carib* and *A. maboya*, n. spp., in head size, but differs from *A. maboya* in having a wider head, slightly larger eyes, and a larger pronotum. It differs from *A. carib* in its narrower head, smaller eyes, and larger pronotum.

DESCRIPTION: **Dealate imago**: Head, pronotum, and wing scale dark brown; antennae yellowish. Head, pronotum, and wing scale densely covered with long, interspersed with short, setae. Head longer than wide. Eyes small, nearly oval. Ocelli oval, not touching eyes (0.05 mm from eye). Fontanelle not clearly visible, but apparently oval. Postclypeus arched; length equal to half its width (length to width index 0.50). Antennae with 15 articles; third slightly shorter than fourth; second subequal to fourth. Pronotum as wide as head; anterior margin raised in middle, forming two mild concavities on either side of median; posterolateral corners broadly rounded; posterior margin faintly emarginate.

SPECIMEN: Holotype (imago) AMNH PB-258.

ETYMOLOGY: This new species name is directly from the Taino word for *Hispaniola*. The Taino were a Greater Antillean tribe of the Arawaka people.

Anoplotermes cacique, new species
Figures 6, 8; table 4

DIAGNOSIS: This species is closest to *Anoplotermes naboria*, and *A. nitaino*, n. spp., in its head length. It differs from *A. naboria* in its narrower head, smaller eyes, larger pronotum, and longer and wider forewing. It differs from *A. nitaino* in its slightly wider head, larger eyes, and larger pronotum.

DESCRIPTION: **Imago**: Head and pronotum metallic brown appearing (coloration obscure due to preservation). Head and pronotum pilosity also obscure; anterior margin of forewing with a row of short setae; wing membrane with dotlike punctations. Head longer than wide. Eyes roundish, moderately sized, bulging. Ocelli not touching eye (about 0.03 mm from eye). Fontanelle not visible. Postclypeus arched, divided medially by a fine line; length slightly less than half its width (length to width index 0.47). Antennae with 15 articles; third very short; second subequal to fourth. Pronotum narrower than head; anterior margin very faintly emarginate; posterolateral corners widely rounded; posterior margin with a faint median indentation.

SPECIMEN: Holotype (imago) AMNH DR10-1512.

ETYMOLOGY: This new species is given the Taino name for *chief*.

Anoplotermes carib, new species
Figures 6, 9, 12; table 4

DIAGNOSIS: This new species is closest to *A. bohio* and *A. maboya*, n. spp., in its head

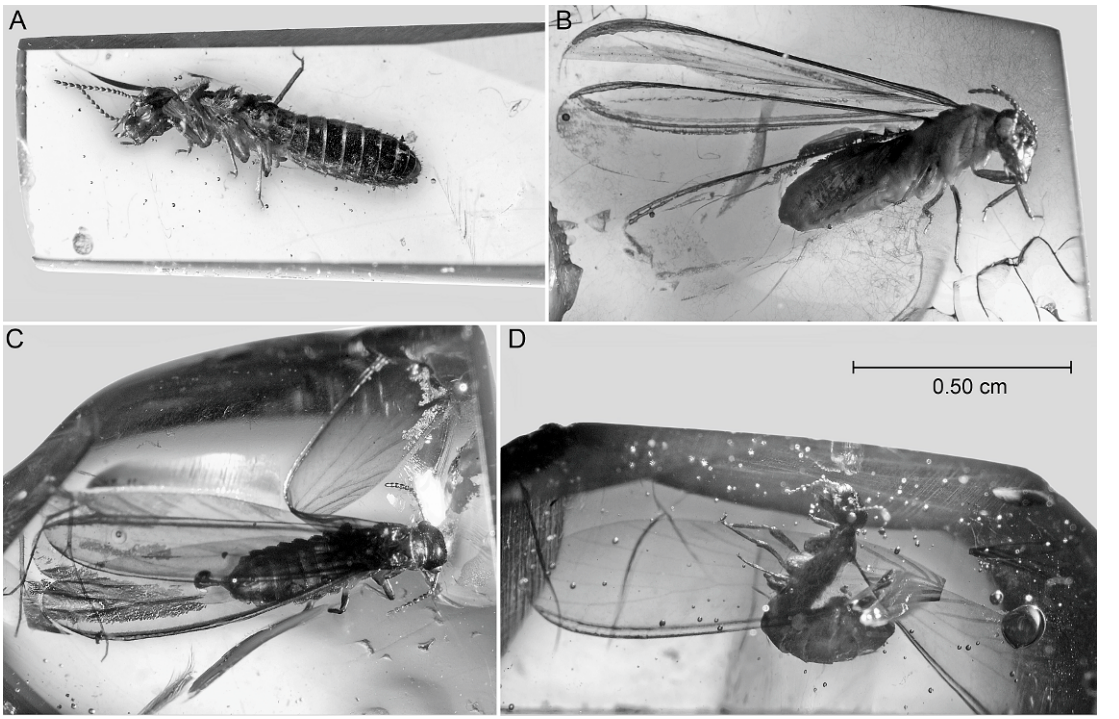

Fig. 6. Photomicrographs of *Anoplotermes* species in Dominican amber; all are holotypes. **A.** *A. bohio*, n. sp., AMNH DR-PB258. **B.** *A. cacique*, n. sp., AMNH DR10-1512. **C.** *A. carib*, n. sp., AMNH DR10-1541. **D.** *A. maboya*, n. sp., AMNH DR10-1567.

length, but differs from the latter in having a wider head, shorter and narrower forewings, and larger eyes. It differs from *A. bohio* in having shorter setae, slightly larger eyes, and a narrower pronotum.

DESCRIPTION: **Imago**: Head brown; pronotum, forewing scale brown, lighter than head; antennae brownish yellow. Head and pronotum densely covered with short setae, interspersed with a few long setae; forewing scale with several long setae; anterior margin of forewing with a row of short setae; wing membrane with dotlike punctations and a few short, scattered setae. Head slightly longer than wide. Eyes small, nearly round, faintly protruding. Ocelli oval, not touching eyes (about 0.03 mm from eyes). Fontanelle oval; width 0.03 mm; situated about 0.31 mm from posterior margin of head. Postclypeus arched; length equal to half its width (length to width index 0.50); medial line not clearly visible. Antennae with 15 articles; third shortest; fourth subequal to second. Pronotum narrower than head; anterior margin moderately concave; posterolateral corners broadly rounded; posterior margin faintly indented medially. Median vein branched into two apically.

SPECIMEN: Holotype (imago) AMNH DR10-1541.

ETYMOLOGY: This new species is given the name of the fierce, indigenous peoples of South America who invaded the Tainos.

Anoplotermes maboya, new species

Figures 6, 9, 12; table 4

DIAGNOSIS: *Anoplotermes maboya* is closest to *A. bohio* and *A. carib*, n. spp., in its head length and size of the eyes. It differs from *A. bohio* in having smaller eyes and sparse setae on its head and pronotum. It differs from *A. carib* in its longer and wider forewing and smaller eyes.

DESCRIPTION: **Imago**: Head and pronotum brown; antennae yellowish brown; wings brownish. Head and pronotum with a few

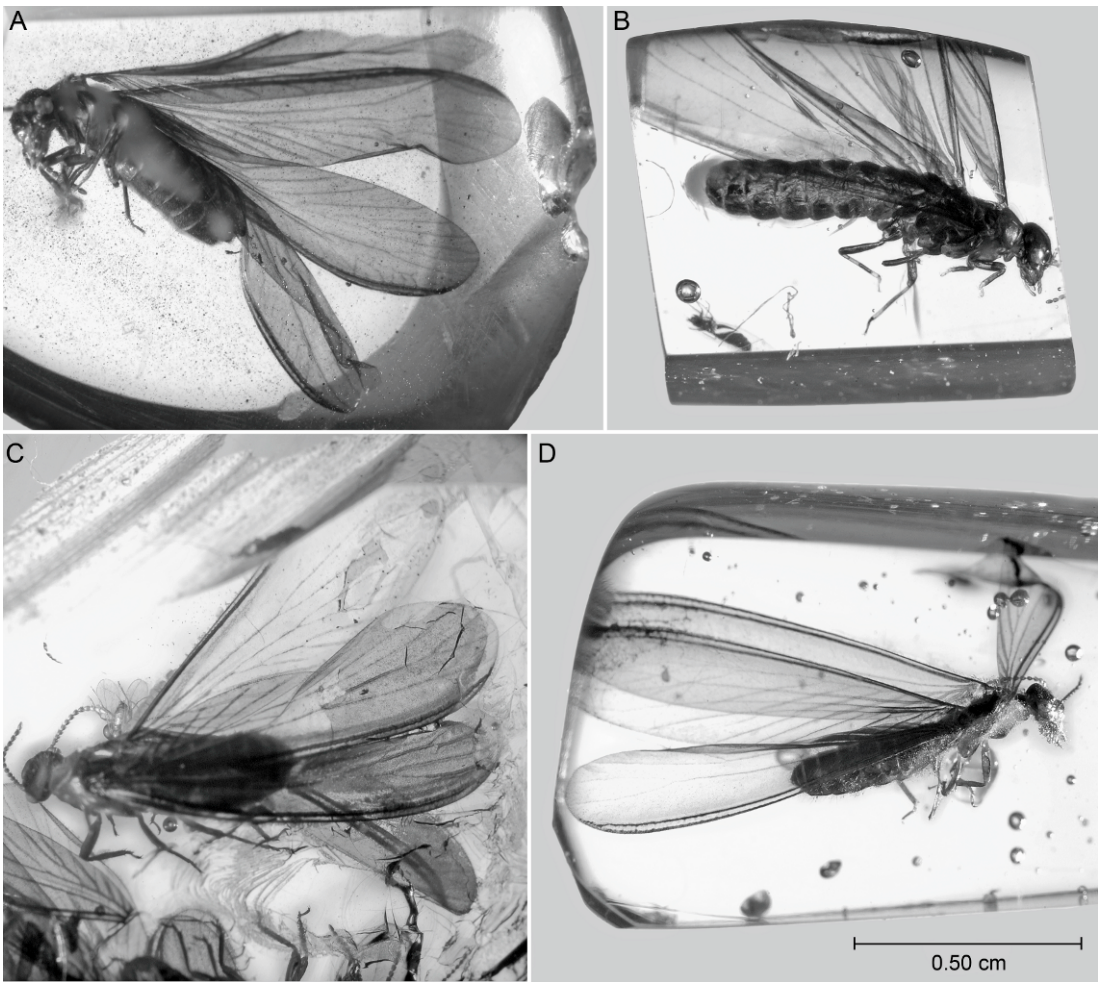

Fig. 7. Photomicrographs of *Anoplotermes* species in Dominican amber. **A.** *A. naboria*, n. sp., AMNH DR10-1537 (holotype). **B.** *A. nitaino*, n. sp., AMNH DR-PB260 (holotype). **C.** *A. quisqueya*, n. sp., AMNH DR-PB255 (paratype). **D.** *A. taino*, n. sp., AMNH DR-PB257 (holotype).

short setae; forewing with a row of short setae; wing membrane with dotlike punctations. Head poorly preserved, compressed laterally; longer than wide. Eyes small, round, protruding slightly. Ocelli oval, small, not touching eyes (0.02 mm from eye). Fontanelle small, oval; width 0.03 mm; situated about 0.31 mm from posterior margin of head; medial line faintly visible. Postclypeus arched; length equal to half its width (length to width index 0.50). Mandibles visible, characteristic of *Anoplotermes*. Antennae with 15 articles; third shortest; fourth subequal to second. Pronotum not clearly visible, apparently narrower than head; anterior margin apparently angular.

SPECIMEN: Holotype (imago) AMNH DR10-1567.

ETYMOLOGY: This new species is given the Taino name of the nocturnal god and destroyer of crops.

Anoplotermes naboria, new species
Figures 7, 10, 12; table 4

DIAGNOSIS: *Anoplotermes naboria* is closest to *A. nitaino* and *A. quisqueya*, n. spp., in its

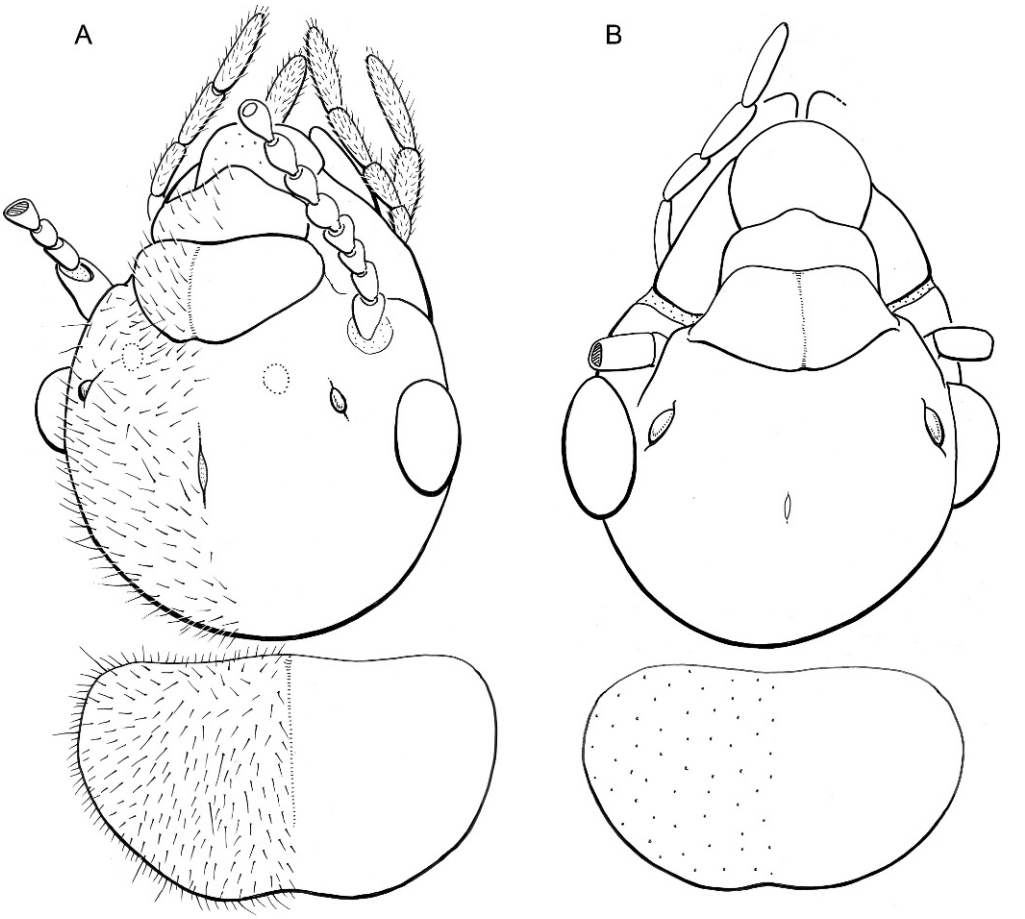

Fig. 8. Heads and pronota of *Anoplotermes* spp. in Dominican amber, dorsal views. **A.** *A. bohio*, n. sp. (head slightly oblique), AMNH DR-PB258. **B.** *A. cacique*, n. sp., AMNH DR10-1512.

pilosity and its head length. It differs from *A. quisqueya* in having a narrower head and fontanelle, larger eyes, a smaller pronotum, and a shorter and narrower forewing. It differs from *A. nitaino* in having a wider head, larger eyes, and narrower forewing.

DESCRIPTION: **Imago**: Head and pronotum dark brown; postclypeus brown, slightly lighter than head; antennae brown. Head densely covered with very short setae; pronotum densely covered with short setae, like head, with a few long setae along margins; anterior margin of forewing with a row of short setae; wing membrane with dotlike punctations. Head longer than wide. Eyes of moderate size, roundish, bulging. Ocelli oval, not touching eye (0.03 mm from eye). Fontanelle oval; width 0.03 mm; situated about 0.26 mm from posterior margin. Postclypeus flat; length slightly less than half its width (length to width index 0.47); medial line very faint. Antennae with 15 articles; third shortest; fourth subequal to second. Pronotum narrower than head; anterior margin deeply angular; posterolateral corners broadly rounded; posterior margin slightly indented medially. Forewing with median unbranched; Cu with 10 branches.

SPECIMEN: Holotype (imago) AMNH DR10-1537.

ETYMOLOGY: This new species is given the name for *worker* in the Taino language.

TABLE 4
Measurements (mm) of imagoes of eight new species of *Anoplotermes*

	bohio holotype	*cacique* holotype	*carib* holotype	*maboya* holotype	*naboria* holotype	*nitaino* holotype	*quisqueya* holotype	*taino* holotype
Length of head to tip of labrum	1.05	1.10	1.04	1.05	1.10	1.10	1.12	0.87
Length of head to postclypeus	0.64	0.56	0.61	0.56*	0.61	0.56	0.69	0.56
Width of head with eyes	0.79	0.91	0.92	0.64*	0.99	0.89	1.02	0.79
Diameter of eye	0.23	0.31	0.26	0.21	0.33	0.26	0.27	0.20
Eye from lower margin	0.05	0.03	—	0.03	0.05	0.08	0.03	0.05
Length of ocellus	0.10	0.10	0.07	0.08	0.10	0.08	0.10	0.09
Length of postclypeus	0.18	0.20	0.20	0.18	0.20	0.20	0.23	0.15
Width of postclypeus	0.36	0.43	0.41	0.36	0.43	0.43	0.48	0.33
Maximum length of pronotum	0.51	0.51	0.49	0.33*	0.43	0.46	0.54	0.51
Width of pronotum	0.81*	0.81	0.69	—	0.77	0.77	0.87	0.69
Length of hind tibia	0.92	0.66	0.69	—	0.89	0.87	0.56	0.87
Length of forewing scale	0.43	0.43	0.41	—	0.49	0.51	0.49	0.38
Length of forewing from suture	—	6.60	5.60	7.00	6.30	6.10*	6.50*	6.70*
Width of forewing	—	1.63	1.58	2.04	1.50	1.63	1.93*	1.83

*approximate

Anoplotermes nitaino, new species
Figures 7, 10; table 4

DIAGNOSIS: *Anoplotermes nitaino* is distinguished from all the other fossil species by its small, round, dotlike fontanelle (vs. oval or teardrop shaped in all the other species).

DESCRIPTION: **Imago**: Head and pronotum chestnut brown; antennae brownish. Head and pronotum densely covered with short setae, bases of setae appearing as small dots; anterior margin of forewing with a row of setae; wing membrane with dotlike punctations. Head longer than wide. Eyes nearly round, bulging. Ocelli small, oval, not touching eyes (0.03 mm from eye). Fontanelle small, round, dotlike; situated about 0.33 mm from posterior margin of head. Postclypeus flat; length slightly less than half its width (length to width index 0.47). Mandibles partially visible, suggestive of *Anoplotermes* (see Ahmad, 1950: fig. 12). Antennae with 15 articles; third shortest; second subequal to fourth. Pronotum narrower than head; anterior margin concave; posterior margin broadly emarginate.

SPECIMEN: Holotype (imago), AMNH PB-260.

ETYMOLOGY: This new species is given the Taino name for *nobleman* or *subchief*.

Anoplotermes quisqueya, new species
Figures 7, 11; table 4

DIAGNOSIS: This species differs from all the other fossil species of this genus in having a large, teardrop-shaped fontanelle (width 0.05 mm vs. 0.03 mm in all other species).

DESCRIPTION: **Imago**: Head, pronotum, and wing scale brown; antennae brown, lighter than head. Head and pronotum densely covered with short setae, interspersed with a few long setae; anterior margin of forewing with a row of setae; wing membrane with dotlike punctations. Head longer than wide. Eyes medium sized, nearly oval, bulging. Ocelli oval, not touching eyes (0.06 mm from eye). Fontanelle large, teardrop shaped; width 0.05 mm; situated about 0.36 mm from posterior margin of head. Postclypeus very slightly arched; length slightly less than half its width (length to width index 0.48); divided by a medial line. Antennae with 15 articles; third shortest; second subequal to fourth. Pronotum narrower than head; anterior margin widely concave; posterolateral corners widely rounded; posterior margin almost straight. Partial forewing showing median with four branches.

SPECIMENS: Holotype (imago) AMNH DR10-1528. Paratypes (imagoes) AMNH DR10-1255, AMNH PB-255, PB-261.

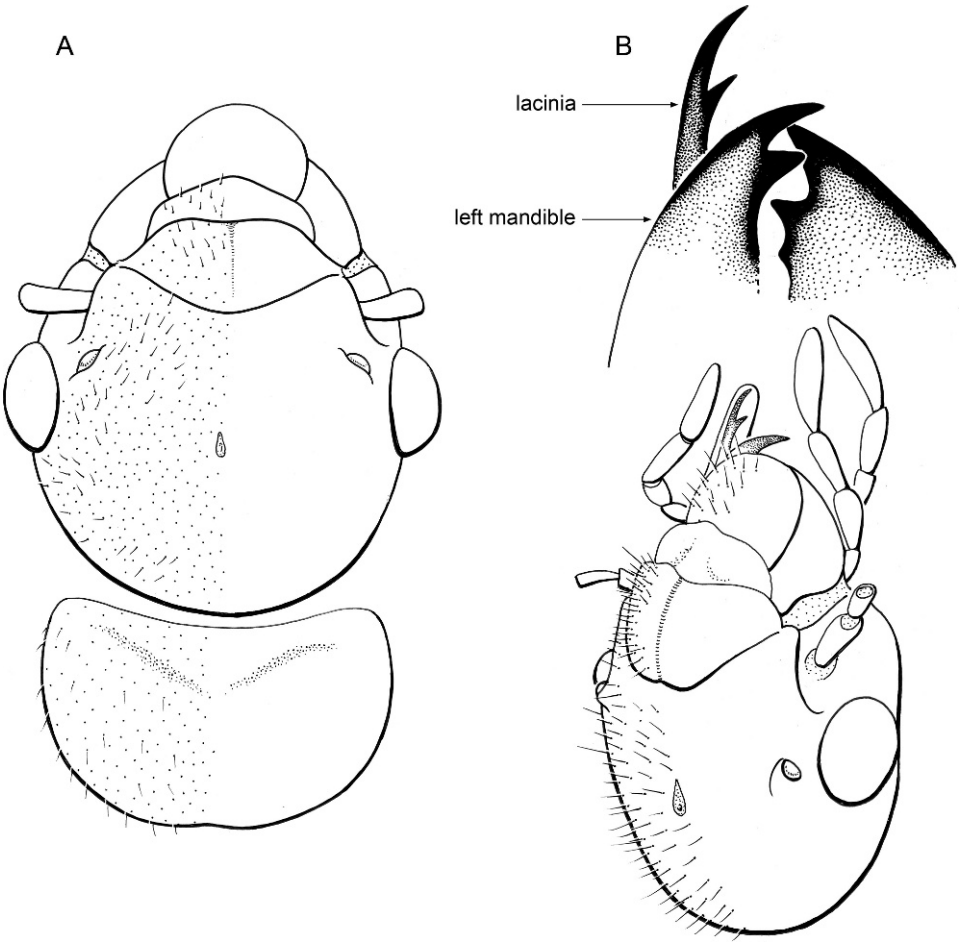

Fig. 9. Heads and pronotum of *Anoplotermes* spp. in Dominican amber; both are holotypes. **A.** *A. carib*, n. sp., dorsal view. AMNH DR10-1541. **B.** *A. maboya*, n. sp., dorsolateral view of head (pronotum not fully visible), with detail of mandibles and lacinia. AMNH DR10-1567.

ETYMOLOGY: This new species is given the Taino name for *Hispaniola*, also meaning "mother of the earth."

Anoplotermes taino, new species
Figures 7, 11, 12; table 4

DIAGNOSIS: *Anoplotermes taino* is close to *A. quisqueya*, n. sp., in its fontanelle size, but differs from it in having small eyes, a narrower head, and a narrower pronotum.

DESCRIPTION: **Imago**: Head and pronotum dark brown; antennae brown; wings brownish. Head covered with numerous short setae interspersed with moderate-sized setae; tergites, sternites, and legs with short setae; anterior margin of forewing with a row of short setae; wing membrane with dotlike punctations. Head longer than wide. Eyes small, round, bulging. Ocelli oval, not touching eyes (about 0.03 mm from eye). Fontanelle large, pear shaped; situated posteriorly below level of eyes, close (0.10 mm) to posterior margin of head. Postclypeus arched; length slightly less than half its width (length to width index 0.45). Antennae with 16 articles (apparently): third very short; second subequal to fourth. Pronotum narrower than head; anterior margin roundish (somewhat unclear); posterolateral corners widely rounded; poste-

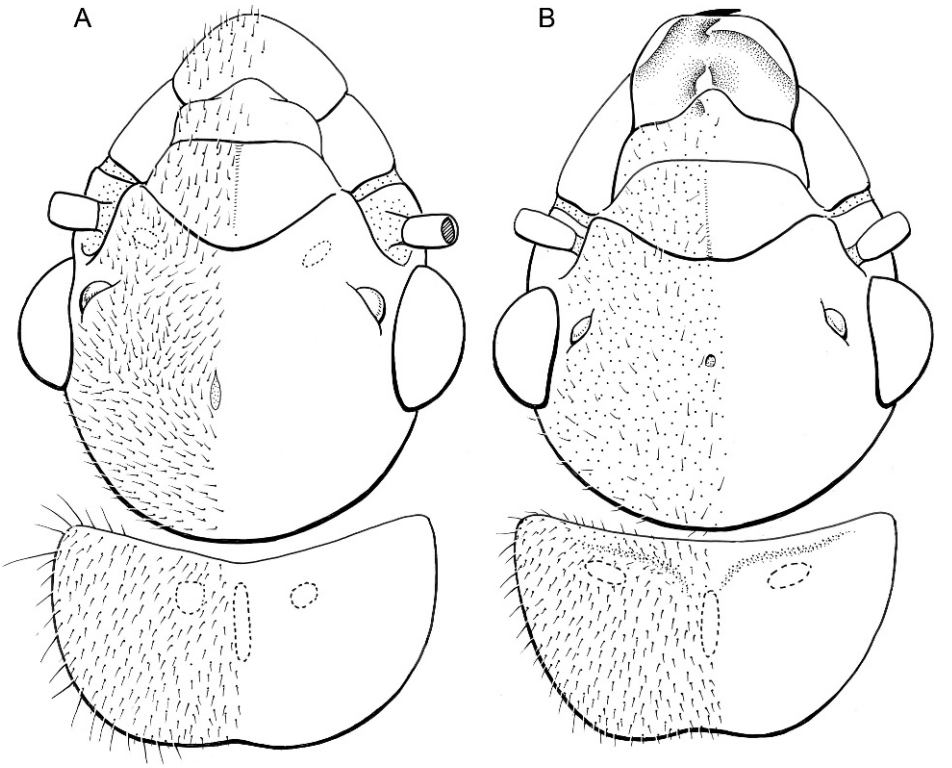

Fig. 10. Heads and pronota of *Anoplotermes* spp. in Dominican amber, dorsal views. **A.** *A. naboria*, n. sp., AMNH DR10-1537. **B.** *A. nitaino*, n. sp., AMNH DR-PB260.

rior margin with a faint median indentation. Forewing with median vein branched apically; cubitus with 11 branches.

SPECIMEN: Holotype (imago) AMNH PB-257.

ETYMOLOGY: This new species is given the name of the Taino, the indigenous people of the Greater Antilles.

Key to the species of *Anoplotermes* in Dominican amber

1. Fontanelle dotlike or not visible 2
— Fontanelle teardrop shaped, oval, or slitlike 3
2. Eye diameter 0.31 mm; pronotal width 0.81 mm; pronotum with posterolateral corners widely rounded (fig. 8B). . . . . *A. cacique*
— Eye diameter 0.26 mm; pronotal width 0.77 mm; pronotum with posterolateral corners narrowly rounded (fig. 10B) . . . . *A. nitaino*
3. Head densely covered primarily with long setae (fig. 8A) . . . . . *A. bohio*
— Head densely covered with short setae or very few setae. 4
4. Fontanelle small, width 0.03 mm 5
— Fontanelle large, width 0.05 mm 7
5. Eye diameter 0.21 mm; head with few setae; forewing length 7.00 mm (fig. 9B) . . . . *A. maboya*
— Eye diameter 0.26 to 0.33 mm; head densely covered with setae; forewing length 5.60 to 6.30 mm 6
6. Eye diameter 0.26 mm; pronotal width 0.69 mm; forewing length 5.60 mm forewing width 1.58 mm (fig. 9A). . . . . *A. carib*
— Eye diameter 0.33 mm; pronotal width 0.77 mm forewing length 6.30 mm; forewing width 1.50 mm (fig. 10A) . . . . . *A. naboria*
7. Eye diameter 0.20 mm; head width 0.79 mm; pronotal width 0.69 mm (fig. 11B) . . . . . *A. taino*
— Eye diameter 0.27 mm; head width 1.02 mm; pronotal width 0.87 mm (fig. 11A) . . . . . *A. quisqueya*

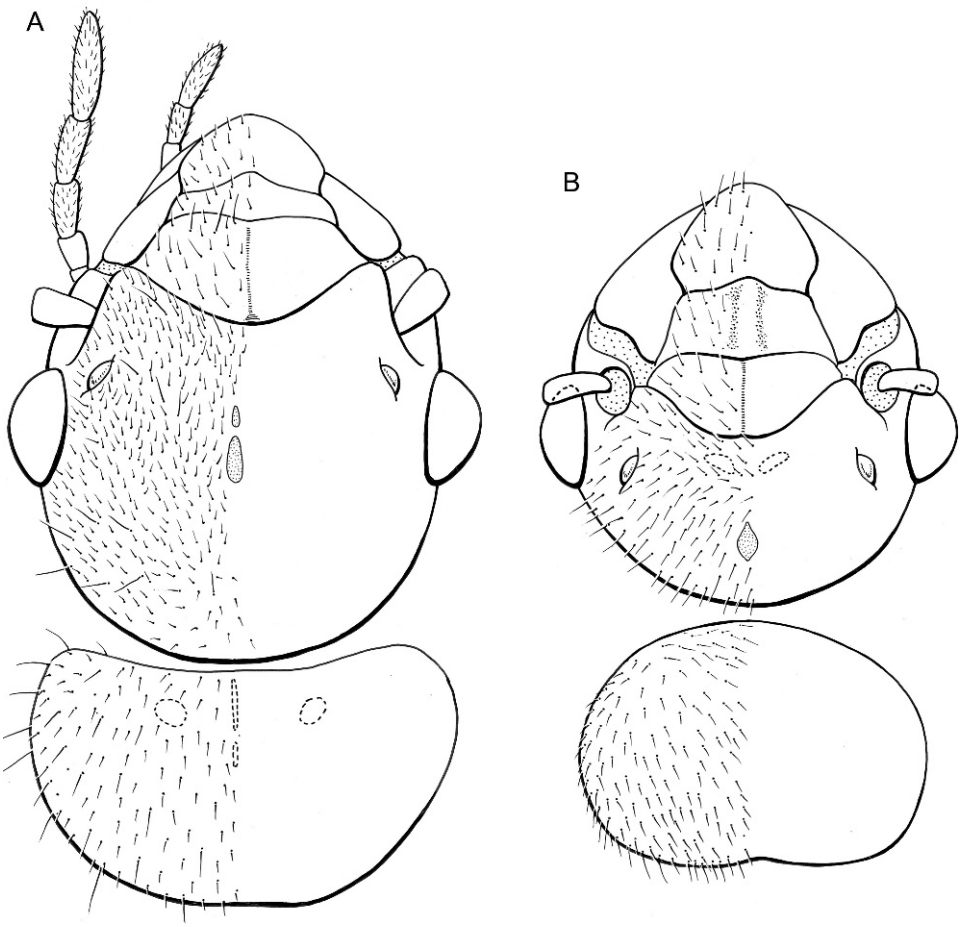

Fig. 11. Heads and pronota of *Anoplotermes* spp. in Dominican amber, dorsal views. **A.** *A. quisqueya*, n. sp., AMNH DR10-1528 (paratype). **B.** *A. taino*, n. sp. (dorsofrontal view of head), AMNH DR-PB257 (holotype).

SUBFAMILY TERMITINAE Latreille, 1802

Genus *Amitermes* Silvestri, 1901

The genus *Amitermes* is a mostly circumtropical genus, with 16 living species reported from the Neotropical Region, of which only one is from the West Indies (Cuba) (table 1). *Amitermes* species generally feed on wood and are found in a variety of habitats, from desert to savannah to rainforest. Some nest underground and others are mound builders, most notably *Amitermes excellens* (Silvestri 1923) from Brazil, reported to build mounds up to 15 feet (5 m) high. No living species has been reported from Hispaniola. *Amitermes lucidus*, n. sp., is the first record of this genus, living or fossil, from Hispaniola and the first fossil record of this genus from any deposit.

Amitermes lucidus, new species

Figure 13; table 5

DIAGNOSIS: The imago of this new fossil species has a narrower head and pronotum, smaller eyes, and a larger fontanelle than the living species *A. beaumonti* Banks from Cuba, the only species of *Amitermes* heretofore known from the West Indies.

DESCRIPTION: **Imago**: Head light yellow; pronotum yellowish, darker than head; antennae yellowish; wings brownish. Head, postclypeus, and pronotum densely covered with

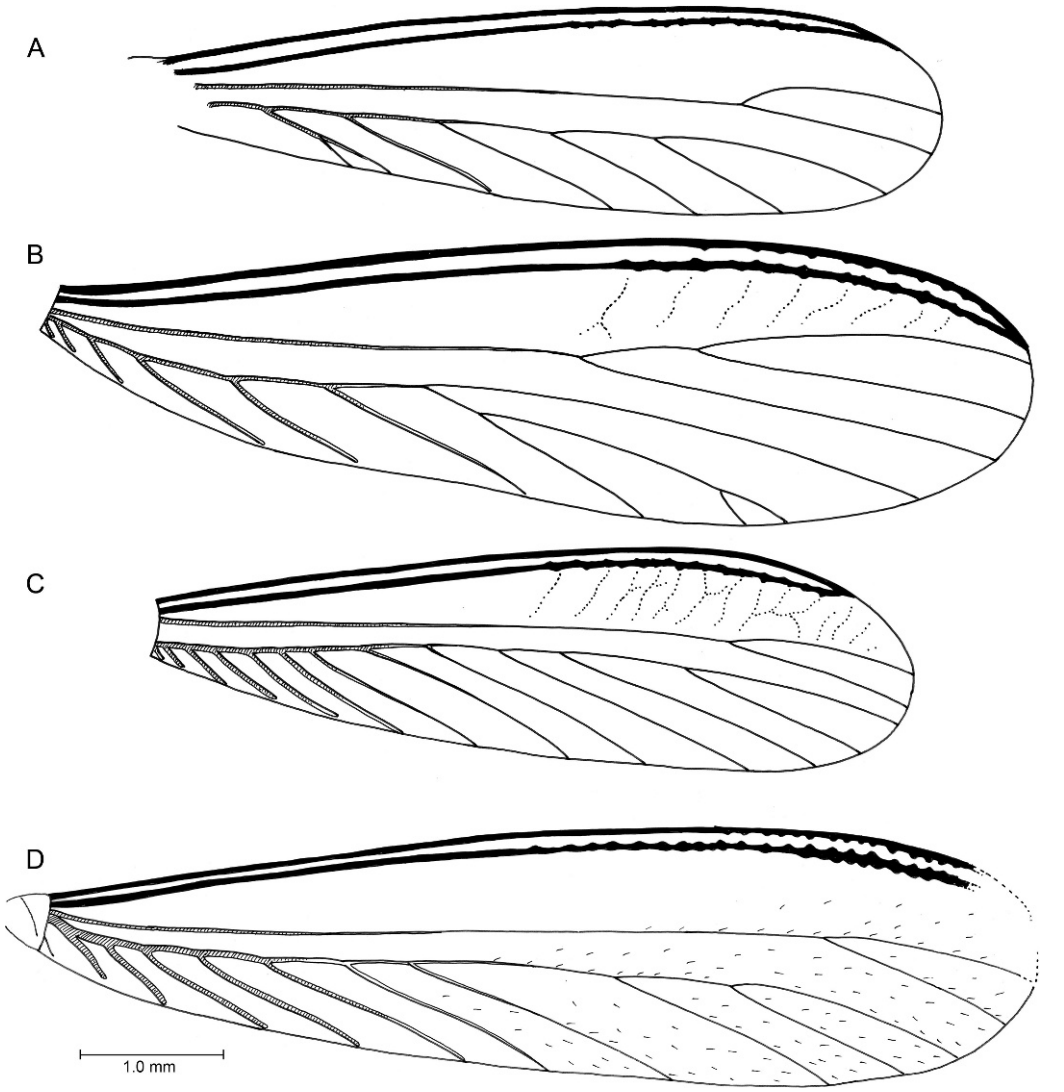

Fig. 12. Forewings of *Anoplotermes* spp. in Dominican amber. **A.** *A. carib*, n. sp., AMNH DR10-1541. **B.** *A. maboya*, n. sp., AMNH DR10-1567. **C.** *A. naboria*, n. sp., AMNH DR10-1537. D. *A. taino*, n. sp., AMNH PB257.

short bristles interspersed with several long ones; wing scale with several short bristles; wing membrane with a few hairs and pigmented punctations. Head longer than wide. Eyes small, nearly oval, protruding. Ocelli small, oval, not touching eyes (0.05 mm from eye). Fontanelle large, teardrop shaped; 0.39 mm from posterior margin of head. Postclypeus arched; width slightly less than half its length (length to width index 0.53), with a faint median line. Left mandible faintly visible; dentition characteristic of the genus *Amitermes* (see Ahmad, 1950: fig. 12). Antennae with 15 articles; third very short; second subequal to fourth. Pronotum narrower than head; anterior margin slightly raised medially; posterolateral corners broadly rounded; posterior margin distinctly emarginate. Forewing with costa thickly sclerotized; radius equally sclerotized, running parallel to costa; median weak, emerging separately from scale, running close to cubitus, with six branches, joining

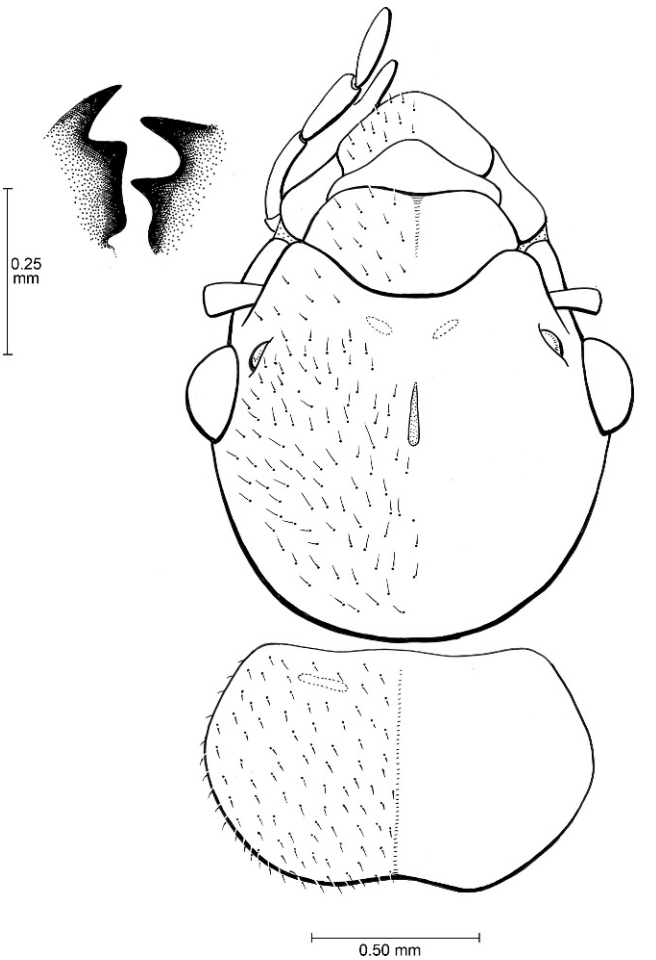

Fig. 13. Head, pronotum (dorsal view) and detail of manidibles (as preserved in Dominican amber) of *Amitermes lucidus*, n. sp., AMNH DR10-1563.

apical margin; cubitus weak, approximately 8 branches to lower margin.

SPECIMENS: Holotype (imago) AMNH DR-10-1255. Paratype (imago), AMNH DR10-1855.

ETYMOLOGY: This new species is named after the Latin *lucidus*, "light", referring to the coloration of the head.

Genus *Microcerotermes* Silvestri, 1901

Microcerotermes is a genus most abundant in the tropical regions of the world, with seven living species from the Neotropical Region, two of which are reported from the West Indies, of which one is from Hispaniola (Haiti only) (table 1). Most species are wood feeders and build hard carton nests of fecal matter. The two species described here, *Microcerotermes insulans* and *M. setosus*, are, with the exception of a dubious species in gum copal, the first record of this genus, living or fossil, from the Dominican Republic and the first fossil record of this genus.

Microcerotermes insulanus, new species

Figures 14–16; table 6

DIAGNOSIS: The imago of this species differs from *M. setosus*, n. sp., in having

TABLE 5
Measurements (mm) of imago of *Amitermes lucidus*, new species

	Holotype
Length of head to tip of labrum	1.04
Length of head to postclypeus	0.69
Width of head with eyes	0.94
Diameter of eye	0.23
Eye from lower margin	0.05
Length of ocellus	0.08
Length of postclypeus	0.23
Width of postclypeus	0.43
Maximum length of pronotum	0.51
Width of pronotum	0.79
Length of hind tibia	0.79
Length of forewing scale	0.43
Length of forewing from suture	—
Width of forewing	—

smaller eyes, shorter and narrower forewings, a narrower pronotum, and its head and pronotum less densely covered with setae.

DESCRIPTION: **Imago**: Head and pronotum dark brown; antennae lighter brown; wings light brown. Head and pronotum covered with a moderate number of short setae; forewing scale with numerous long setae; wing membrane with a few short setae and dotlike punctations (microtrichia). Head with sides subparallel below eyes. Eyes small, nearly round. Ocelli barely visible (appear oval), approximately 0.05 mm from eyes. Fontanelle not clearly visible due to whitish film over head (appears dotlike). Postclypeus faintly arched; length half its width (length to width index 0.50). Antennae with 15 articles; third shortest; second subequal to fourth. Pronotum distorted in preservation, narrower than head; anterior margin concave; posterolateral corners broadly rounded. Forewing with median vein unbranched.

SPECIMEN: Holotype (imago) AMNH DR10-1526.

ETYMOLOGY: This new species is named after the Latin *insulanus*, ''islander''.

Microcerotermes setosus, new species
Figures 14–16; table 6

DIAGNOSIS: The imago of this species differs from *M. insulanus*, n. sp., in having larger eyes, longer and wider forewings, and its head and pronotum densely covered with setae.

DESCRIPTION: **Imago**: Head and pronotum blackish brown; antennae brownish, lighter than head; forewing scale yellowish brown. Head with a dense mat of short setae, with many long setae interspersed; pronotum densely covered with short setae and longer setae along its margin; wing scale, tergites, sternites heavily covered with setae; anterior margin of forewing with a row of short setae; wing membrane with dotlike punctations (microtrichia). Head oblong, with sides subparallel below eyes. Eyes nearly round. Ocelli oval, very close (0.03 mm) to eyes. Fontanelle not visible due to debris on surface of head (in one specimen appears dotlike). Postclypeus apparently flat, perhaps distorted in preservation; length more than half its width (length to width index 0.58). Antennae with 15 articles; third shortest; second subequal to fourth. Pronotum narrower than head; anterior margin concave; anterolateral corners narrow; posterior margin faintly emarginate. Forewing with median vein with five branches.

SPECIMENS: Holotype (imago) AMNH DR10-1553. Paratypes (imagoes), AMNH DR10-1559, PB-256.

ETYMOLOGY: This new species name is from the Latin *setosus*, for its being densely covered with setae.

Genus *Termes* Linnaeus, 1758

The genus *Termes* is a circumtropical genus with a wide range of nesting habits. Of the 28 living species, nine have been recorded from the Neotropical Region, with four from the West Indies, only one of which is from Hispaniola (table 1). *Termes fatalis*, a living species from Surinam, was the first named termite, described by Linnaeus in 1758. One impression fossil species is known from the Oligocene of France, diagnosed on the basis of wing venation. The species described here, *Termes primitivus*, is the first amber fossil of this genus to be described and the first *Termes* fossil to be reported from the Dominican Republic.

Termes primitivus, new species
Figures 17, 18; table 7

DIAGNOSIS: The imago of this new fossil species has a narrower head and pronotum

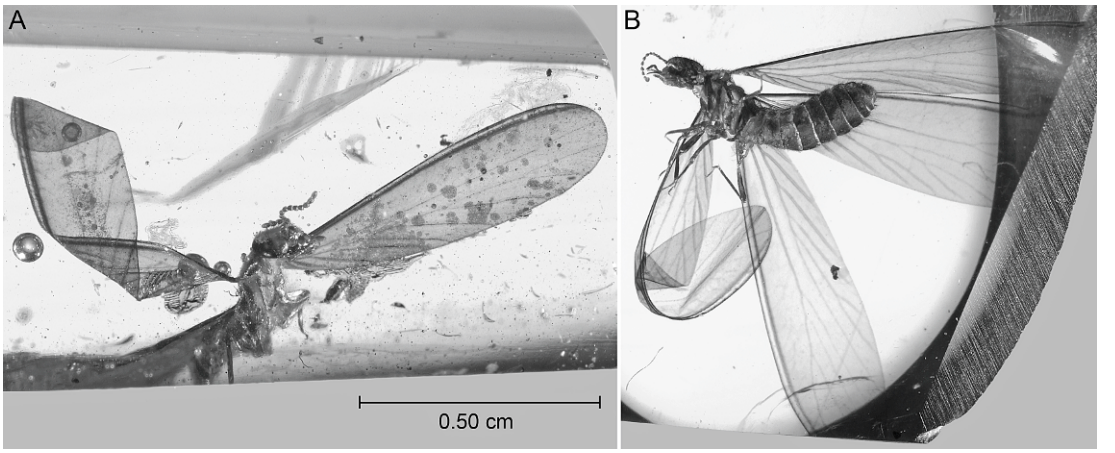

Fig. 14. Photomicrographs of *Microcerotermes* spp. in Dominican amber. **A.** *M. insulanus*, n. sp., AMNH DR10-1526. **B.** *M. setosus*, n. sp., AMNH DR10-1559.

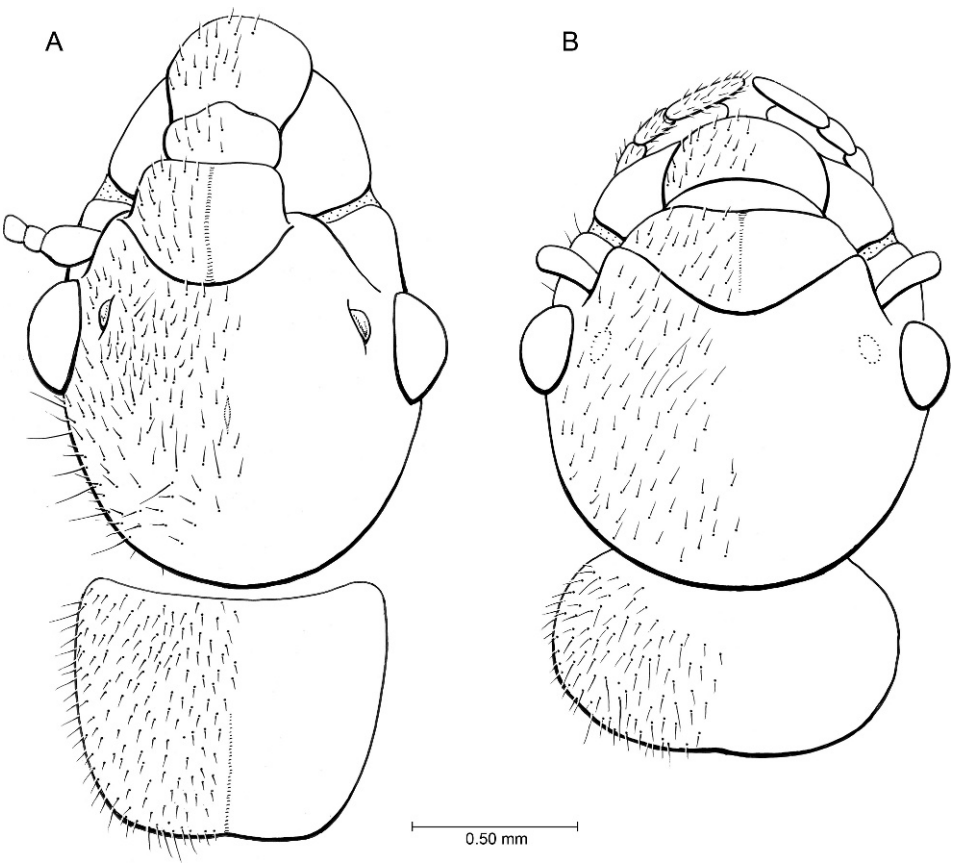

Fig. 15. Heads and pronota of *Microcerotermes* spp. in Dominican amber (dorsal views). **A.** *M. setosus*, n. sp., AMNH DR10-1553. **B.** *M. insulanus*, n. sp., AMNH DR10-1526.

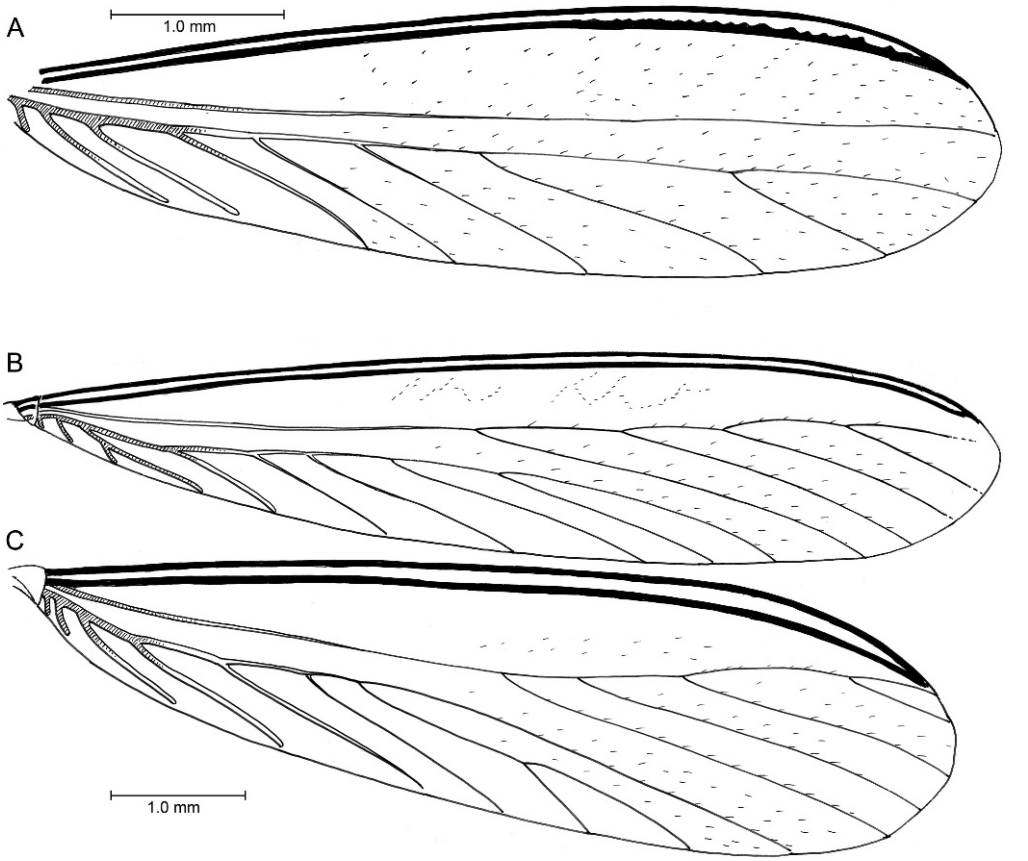

Fig. 16. *Wings of Microcerotermes* spp. in Dominican amber. **A.** *M. insulanus*, n. sp., forewing, AMNH DR10-1526. **B, C.** Fore- and hindwing, respectively, of *M. setosus*, n. sp., AMNH DR10-1559.

and larger eyes than the living species *T. hispaniolae*, the only species of *Termes* heretofore reported from Hispaniola.

DESCRIPTION: **Imago**: Head and pronotum dark brown; legs brown; wing scale brown, lighter than head. Head, postclypeus, and pronotum covered with a dense mat of short bristles and a few long ones; wing scale with several short bristles; wing membrane with a few hairs and pigmented punctations; femur and coxa densely covered with short hairs. Head longer than wide; posterior margin broadly concave. Eyes medium sized, circular. Ocelli oval, arched, very close to eyes. Fontanelle ovalish, with a faint slit in front. Postclypeus arched, with a faint median line; length about half its width (length to width index 0.49). Left mandible faintly visible; apical tooth long, about 0.13 mm from anterior margin of first marginal tooth, characteristic of the genus *Termes*. Antennae with 15 articles; third shortest; second subequal to fourth. Pronotum flat, narrower than head; anterior margin concave, lateral sides broadly rounded; posterior margin angular, emarginate. Forewing suture faintly arched. Forewing with costa thickly sclerotized; radius equally sclerotized, running parallel to costa; median weak, emerging separately from scale, running close to cubitus, unbranched, joining apical margin; cubitus weak; approximately 14–16 branches to lower margin. Hind wing, costa, and radius similar to forewing; median weak, arising from radius, outside of scale. Tibial spurs 3:2:2.

SPECIMENS: Holotype (imago) AMNH DR10-1521. Paratype (imago) AMNH DR10-1520.

TABLE 6
Measurements (mm) of imagoes of two species of *Microcerotermes*

	insulanus	***setosus*** (3 imagoes)		
	Holotype	Holotype	Range	Mean
Length of head to tip of labrum	1.02	1.14	1.07–1.14	1.10
Length of head to postclypeus	0.63	0.63	0.58–0.63	0.61
Width of head with eyes	0.91	0.84	0.84–0.86	0.85
Diameter of eye	0.26	0.23	0.22–0.23	0.23
Eye from lower margin	0.05	0.03	0.03	0.03
Length of ocellus	0.10	0.08	0.08	0.08
Length of postclypeus	0.20	0.23	0.20–0.23	0.22
Width of postclypeus	0.41	0.40	0.40–0.43	0.42
Maximum length of pronotum	0.31*	0.53	0.53–0.56	0.54
Width of pronotum	0.59	0.71	0.69–0.71	0.70
Length of hind tibia	0.71*	—	0.82	0.82
Length of forewing scale	0.38*	0.41	0.41	0.41
Length of forewing from suture	5.60	7.00	7.00	7.00
Width of forewing	1.63	1.83	1.83	1.83

*approximate

ETYMOLOGY: This new species is named after the Latin *primitivus*, "first", earliest of its kind.

SUBFAMILY NASUTITERMITINAE Hare, 1937
Genus *Atlantitermes* Fontes, 1979

The genus *Atlantitermes* was first described by Fontes in 1979 for three new species and later expanded (Fontes, 1982) to include five species previously included in the genus *Subulitermes*. As this exclusively Neotropical genus is comprised today, only one living species of the eight is reported from the West Indies, which is actually from the subcontinental island of Trinidad (table 1). Like *Subulitermes*, the *Atlantitermes* species are tropical soil dwellers, feeding on soil rich in humus. No fossil species of this genus has been hitherto reported. The three new fossil species described here are the first record of this genus, living or fossil, from Hispaniola.

Atlantitermes antillea, new species
Figures 19, 20; table 8

DIAGNOSIS: *Atlantitermes antillea* is close to *A. caribea*, n. sp., but differs from it in having a wider head and pronotum, smaller eyes and ocelli, and a shorter fontanelle.

DESCRIPTION: **Imago**: Head and pronotum chestnut brown; postclypeus brown, lighter than head; antennae brown; wings brownish, membrane clear. Head and pronotum sparsely covered with short setae; anterior margin of forewing with a row of short setae; wing membrane with dotlike punctations. Head longer than wide. Eyes medium-sized, round, bulging. Ocelli large, oval, very close (0.01 mm) to eyes. Fontanelle ovalish, extended as a faint line in front; located between eyes, 0.28 mm from posterior margin of head. Postclypeus arched; length less than half its width (length to width index 0.42); with a median line. Antennae with 15 articles; third shortest; second subequal to fourth. Pronotum narrower than head; anterior margin almost straight; lateral margains angular posteriorly; posterior margin almost straight.

SPECIMEN: Holotype (imago) AMNH DR10-1543.

ETYMOLOGY: This new species name is derived from *Antilles*, another name for the Caribbean Islands.

Atlantitermes caribea, new species
Figures 19, 20; table 8

DIAGNOSIS: *Atlantitermes caribea* is close to *A. antillea*, n. sp., but differs from it in

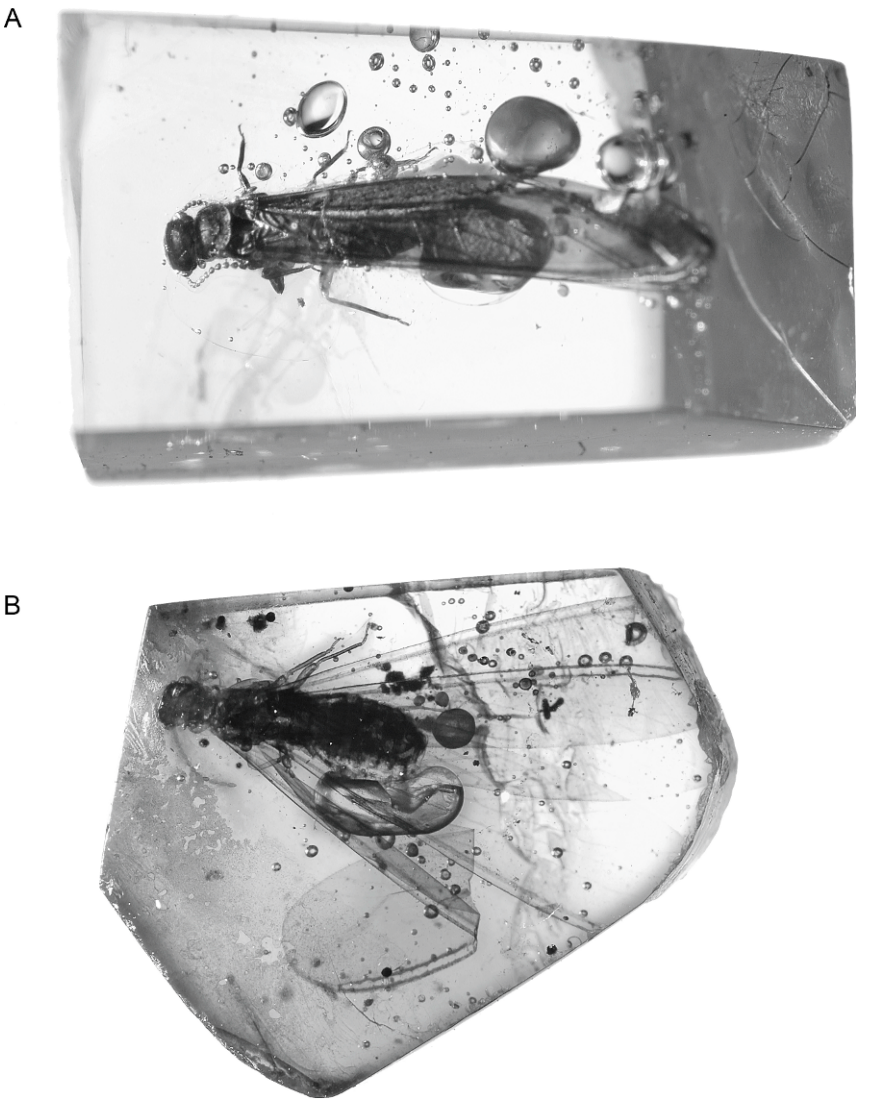

Fig. 17. Photomicrographs of **A.** *Termes primitivus*, n. sp., AMNH DR 10-1521 (paratype). **B.** *Subulitermes insularis*, n. sp., in Dominican amber, AMNH DR8-332 (holotype).

having a narrower head and pronotum, larger eyes and ocelli, and a longer fontanelle.

DESCRIPTION: **Imago**: Head and pronotum brown; postclypeus brown, lighter than head; antennae yellowish brown; wings brownish, membrane clear. Head densely covered with short setae; pronotum densely covered with short setae, longer setae along margins; anterior margin of forewing with a row of short setae; wing membrane with dotlike punctations. Head longer than wide. Eyes medium-sized, roundish, bulging. Ocelli large, oval, long, almost touching (0.03 mm) eyes. Fontanelle long, ovalish, located between eyes, 0.28 mm from posterior margin of head. Postclypeus arched, with a faint median line; length less than half its width (length to width index 0.43). Antennae with 15 articles; third shortest; second subequal to fourth. Pronotum narrower than head; anterior margin concave; posterolateral corners broadly rounded; posterior margin distinctly emarginate.

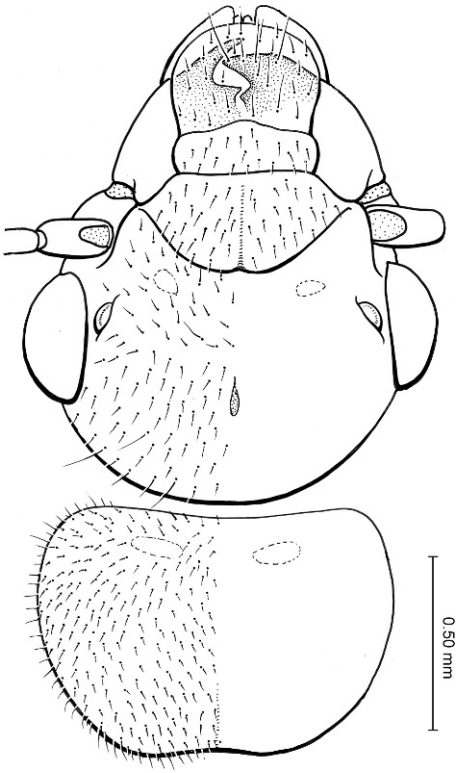

Fig. 18. Head and pronotum of *Termes primitivus*, n. sp., in Dominican amber, AMNH DR10-1521.

TABLE 7
Measurements (mm) of imago of *Termes primitivus*, new species

	Holotype
Length of head to tip of labrum	1.04
Length of head to postclypeus	0.57
Width of head with eyes	0.87
Diameter of eye	0.30
Eye from lower margin	—
Length of ocellus	0.10
Length of postclypeus	0.20
Width of postclypeus	0.41
Maximum length of pronotum	0.56
Width of pronotum	0.76
Length of hind tibia	0.84
Length of forewing scale	0.36
Length of forewing from suture	—
Width of forewing	1.33

SPECIMENS: Holotype (imago) AMNH DR10-1555.

ETYMOLOGY: This new species name is from the stem of *Caribbean*, in reference to the extralimital occurrence of the fossil species in this area.

Atlantitermes magnoculus, new species
Figures 19, 20; table 8

DIAGNOSIS: *Atlantitermes magnoculus* differs from all other fossil species of *Atlantitermes* in being much larger in all respects, notably the head, pronotum, and eyes. In eye size, fontanelle shape, and overall appearance it is close to the living species *A. osborni* Emerson, from Guyana.

DESCRIPTION: **Imago**: Head brown; pronotum brownish; postclypeus brownish, lighter than head; wings brownish, membrane clear. Head densely covered with short setae; pronotum densely covered with short setae, longer setae along margins; anterior margin of forewing with a row of short setae; wing membrane with dotlike punctations. Head (partially damaged in preservation) longer than wide. Eyes very large, oval, bulging. Ocelli large, oval, touching eyes. Fontanelle damaged, apparently narrow, slitlike, forked at tip; located between eyes, about 0.38 mm from posterior margin of head. Postclypeus arched; length less than half its width (length to width index 0.35); median line not visible. Left mandible dentition visible, *Atlantitermes*-type (Fontes, 1979). Antennae with 15 articles; second article equal to third; fourth subequal to second and third. Pronotum narrower than head; anterior margin faintly concave; lateral margins angular posteriorly; posterior margin faintly emarginate.

SPECIMEN: Holotype (imago) AMNH DR-10-1259.

ETYMOLOGY: This new species name is a combination of the root of the Latin *magnus*, "large", and *oculus*, "eye".

Genus *Nasutitermes* Dudley, 1890

Nasutitermes is the largest genus of the order Isoptera, with a circumtropical distribution. Of the total of 262 living species and subspecies, 71 are Neotropical, 10 of which are found in the West Indies, with three species from Hispaniola (table 1). The species of this

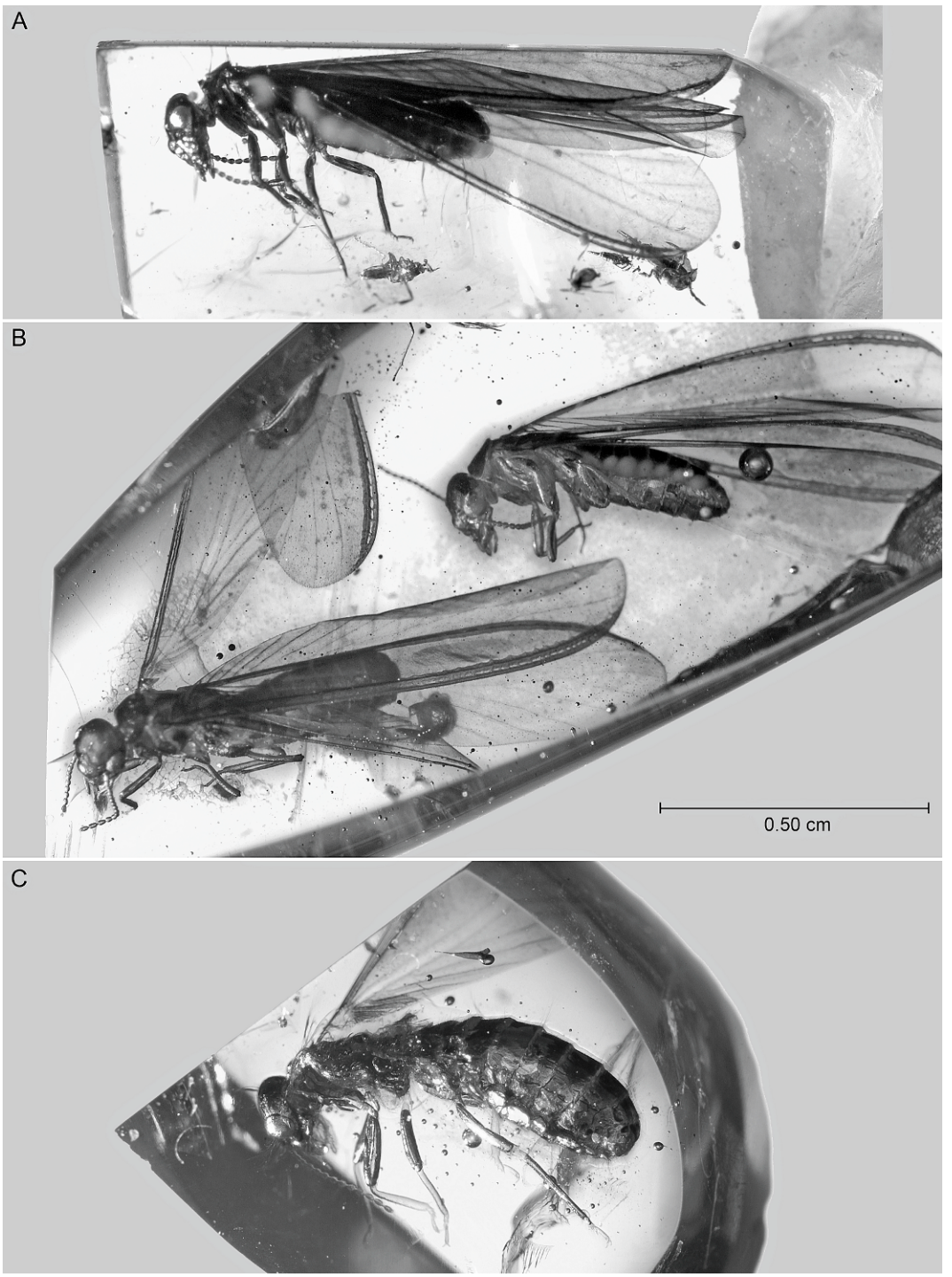

Fig. 19. Photomicrographs of *Atlantitermes* spp. in Dominican amber; all are holotypes. **A.** *A. antillea*, n. sp., AMNH DR10-1543. **B.** *A. caribea*, n. sp., AMNH DR10-1555. **C.** *A. magnoculus*, n. sp., AMNH DR10-1259.

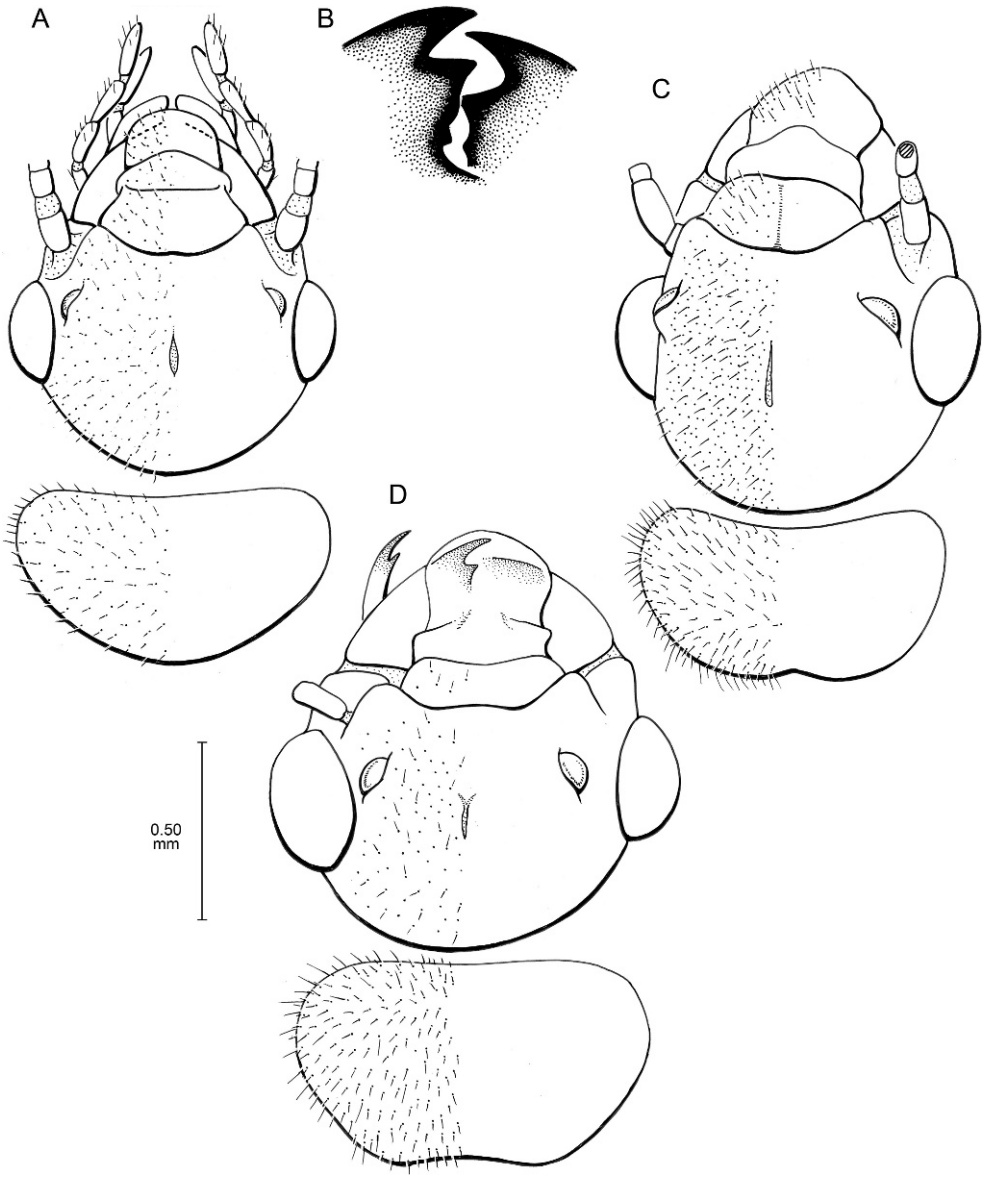

Fig. 20. Heads and pronota of *Atlantitermes* spp. in Dominican amber. **A.** *A. antillea*, n. sp. (reconstructed), AMNH DR10-1543. **B.** Detail of mandibles of *A. antillea*, n. sp., as observed through labrum, AMNH DR10-1543. **C.** *A. caribea*, n. sp., AMNH DR10-1555 (slightly oblique view). **D.** *A. magnoculus*, n. sp., AMNH DR10-1259.

genus are found in a variety of ecological habitats, with a great variation in feeding habits and nest construction. Many construct large terrestrial mounds, others build underground or arboreal nests. Their preferred diet is wood, and many species build runways of soil and carton to get to the wood source. Until now, one fossil species from Dominican amber, based on the soldier caste, and one fossil species from Mexican amber, based on the imago caste, have been known. Seven new fossil species, six based on the imago caste and one on the soldier, are described here.

TABLE 8
Measurements (mm) of imagoes of three new species of *Atlantitermes*

	magnoculus holotype	***caribea*** holotype	***antillea*** holotype
Length of head to tip of labrum	1.40	1.17	1.05
Length of head to postclypeus	0.82	0.59	0.64
Width of head with eyes	1.38	0.89	0.92*
Diameter of eye	0.49	0.33	0.31
Length of ocellus	0.13	0.13	0.10
Length of postclypeus	0.18	0.18	0.18
Width of postclypeus	0.51	0.41	0.43
Maximum length of pronotum	0.66	0.51	0.46
Width of pronotum	1.17	0.69	0.82
Length of hind tibia	1.53	0.92	0.89
Length of forewing scale	0.82	0.49	0.54
Length of forewing from suture	—	6.60	5.50
Width of forewing	2.50*	1.53	1.68

*approximate

Nasutitermes amplioculatus, new species
Figures 21, 23; table 9

DIAGNOSIS: *Nasutitermes amplioculatus* resembles *N. magnocellus* and *N. incisus*, n. spp., in having large eyes. It differs from both in having slightly smaller eyes and a small, dotlike fontanelle (vs. oblong in *N. magnocellus* and large and round in *N. incisus*).

DESCRIPTION: **Imago**: Head and pronotum dark brown; postclypeus lighter than head; antennae brownish. Head densely covered with short setae; pronotum with several short setae, longer setae along margins; tergites and sternites densely covered with long setae; forewing scale with several long setae; anterior margin of forewing with a row of short setae; wing membrane with dotlike punctations. Head longer than wide. Eyes large, oval, bulging laterally. Ocelli oval viewed dorsally, almost touching eyes. Fontanelle very small; located on a level with the dorsal margin of eyes, 0.28 mm from posterior margin of head. Postclypeus arched; length less than half its width (length to width index 0.41). Antennae broken, with 15 articles visible; third shorter than second and fourth; second subequal to fourth. Pronotum narrower than head; anterior margin slightly concave; posterolateral margins widely rounded; posterior margin with a faint medial indentation.

SPECIMEN: Holotype (imago) AMNH DR10-1680.

ETYMOLOGY: This new species name is a combination of the Latin prefix *ampli-* "large", and *oculatus*, "of eyes".

Nasutitermes incisus, new species
Figures 21, 23; table 9

DIAGNOSIS: *Nasutitermes incisus* differs from all of the other *Nasutitermes* fossil species described here in having very large eyes and the anterior margin of the pronotum deeply incised.

DESCRIPTION: **Imago**: Head and pronotum dark brown; wings light brown, membrane clear. Head and pronotum densely covered with long setae; legs, tergites, and sternites densely covered with setae; wing scales with long setae; anterior margin of forewing with a row of short setae; wing membrane with dotlike punctations. Head oblong. Eyes large, ovalish, bulging. Ocelli from side view round, touching eyes. Fontanelle round; diameter 0.08 mm; located between eyes, about 0.56 mm from posterior margin of head. Postclypeus arched; length less than half its width (length to width index 0.37). Antennae with 15 articles visible; second longer than third or fourth; third subequal to fourth. Pronotum narrower than head; anterior margin deeply incised; posterior margin with a deep medial indentation.

SPECIMEN: Holotype (imago) AMNH PB-263.

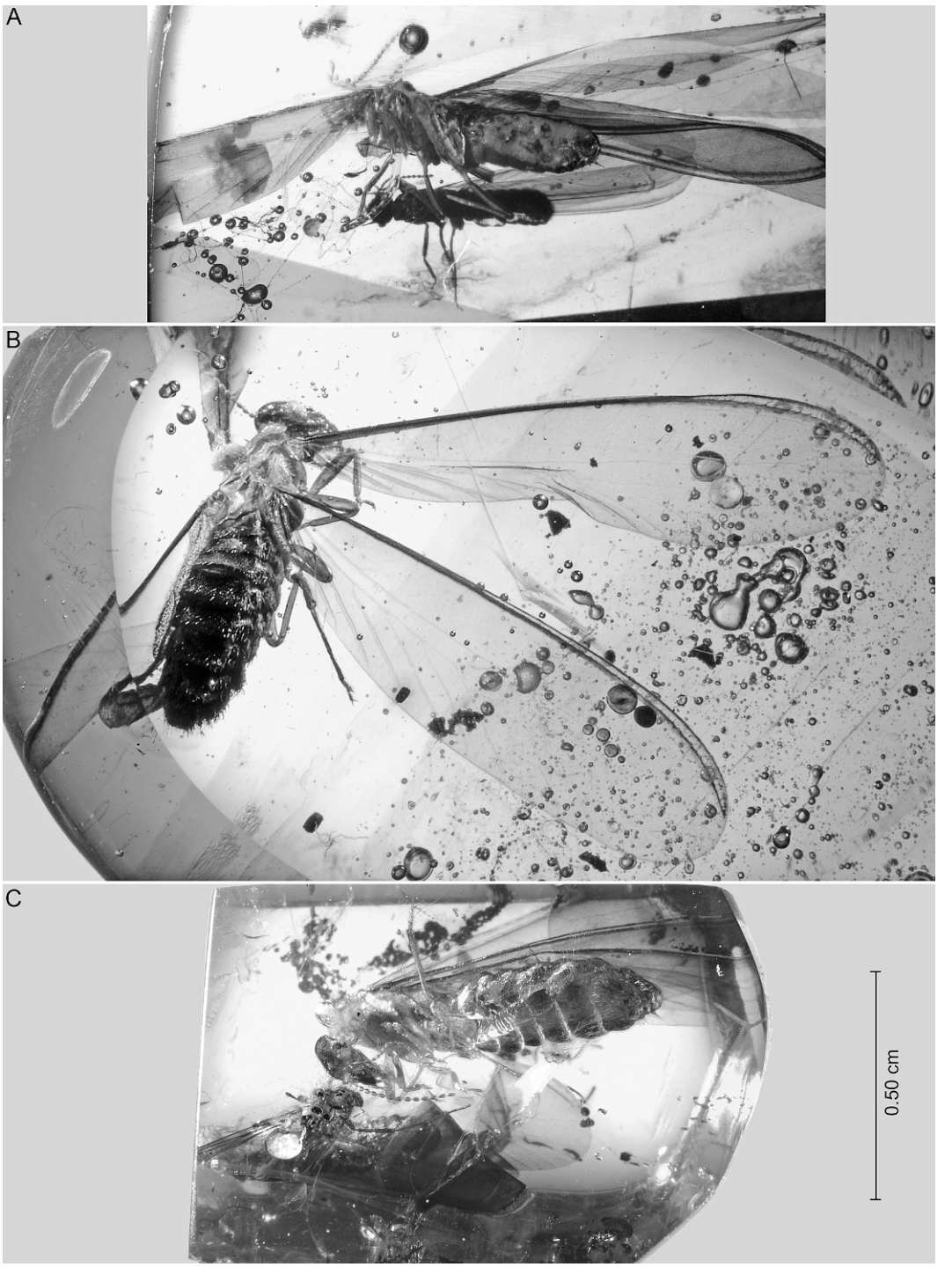

Fig. 21. Photomicrographs of imagoes of *Nasutitermes* spp. in Dominican amber; all are holotypes. **A.** *N. amplioculatus*, n. sp., AMNH DR10-1680. **B.** *N. incisus*, n. sp., AMNH DR-PB263. **C.** *N. medioculatus*, n. sp., AMNH DR14-643.

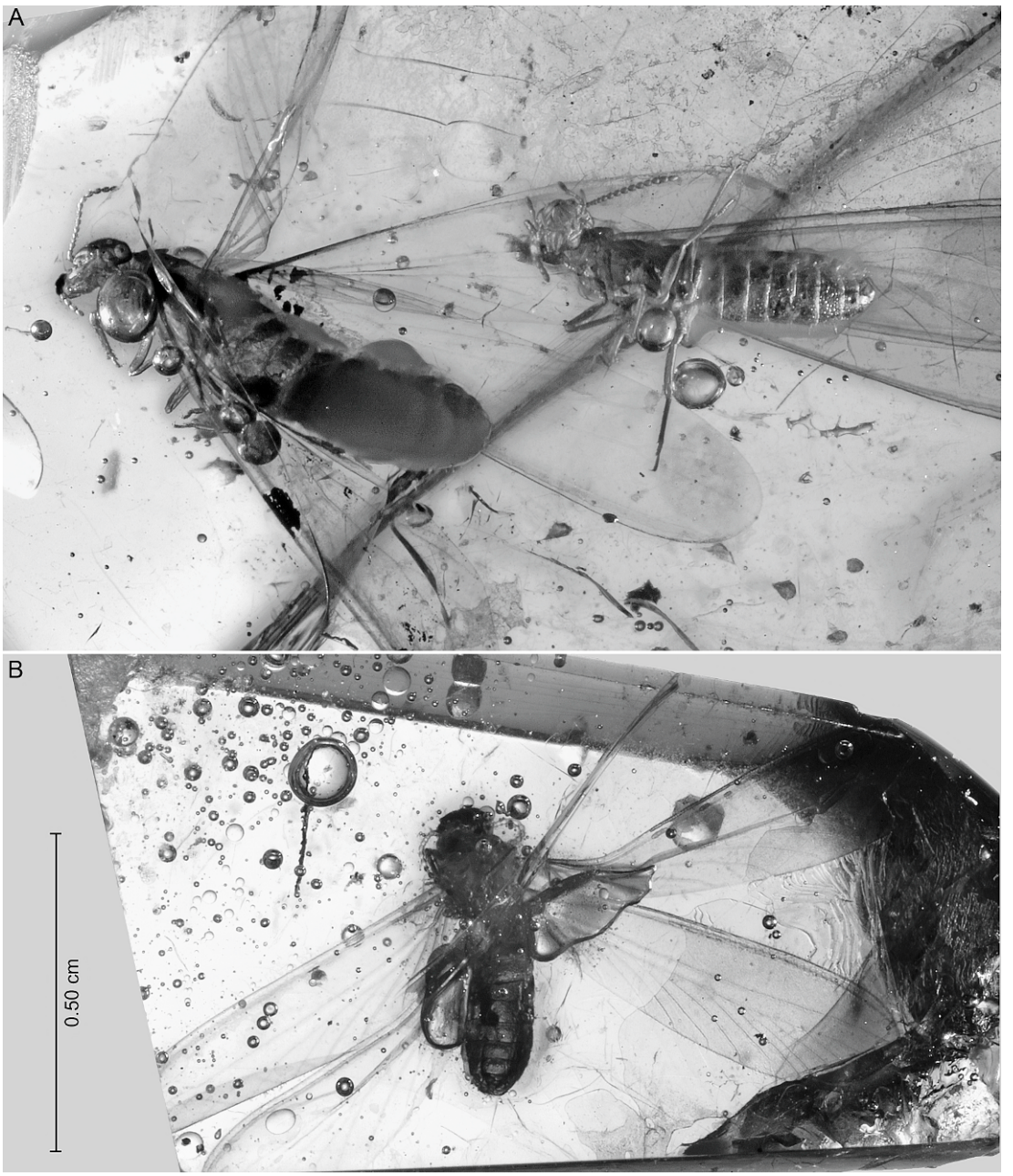

Fig. 22. Photomicrographs of imagoes of *Nasutitermes* spp. in Dominican amber; both are holotypes. **A.** *N. pilosus*, n. sp., AMNH DR10-1627. **B.** *N. seminudus*, n. sp., AMNH DR10-1574.

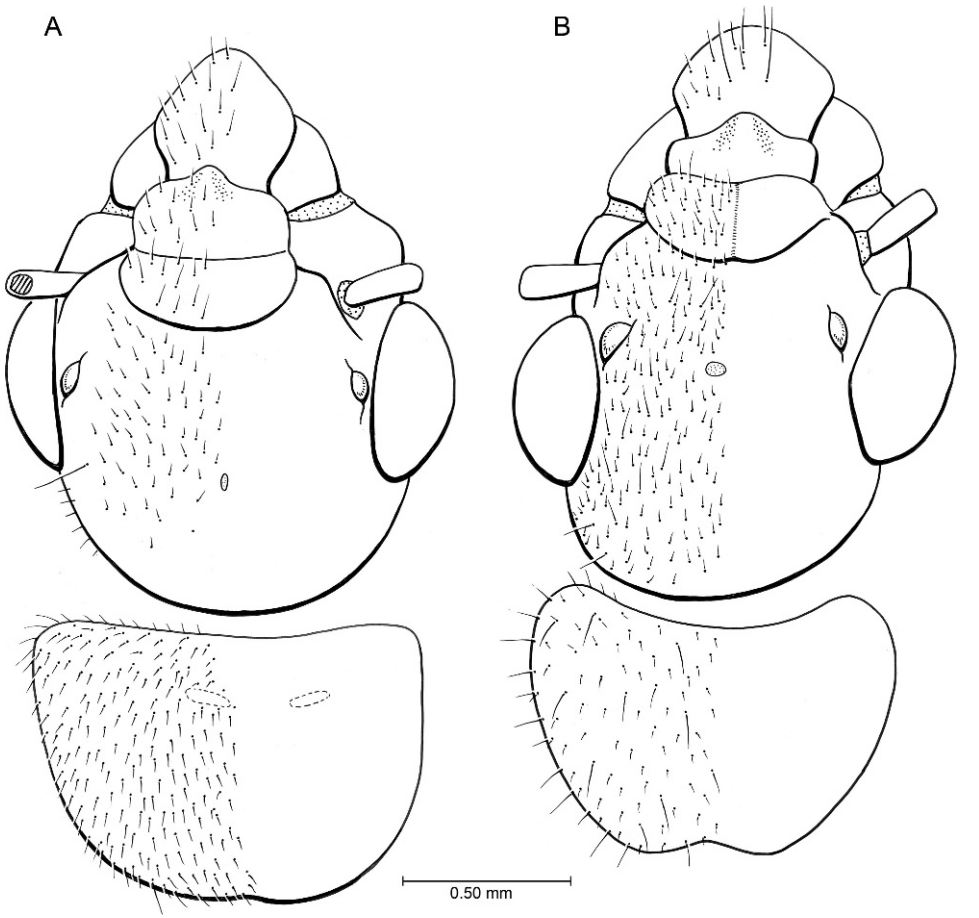

Fig. 23. *Nasutitermes* imagoes in Dominican amber, heads and pronota, dorsal views. **A.** *N. amplioculatus*, n. sp., AMNH DR10-1680. **B.** *N. incisus*, n. sp., PB263 (head slightly distorted).

ETYMOLOGY: This new species name is from the Latin *incisus*, "incised", referring to the deeply incised pronotum.

Nasutitermes magnocellus, new species
Figure 24; table 9

DIAGNOSIS: *Nasutitermes magnocellus*, n. sp., differs from all the other fossil species of this genus in having a very large ocellus that is also forked at the anterior end.

DESCRIPTION: **Imago**: Head brown; pronotum and postclypeus brown, lighter than head; antennae brownish; wings yellowish. Head densely covered with short setae, interspersed with a few longer setae; pronotum with several short setae, longer setae along margins; sternites, tergites, and legs densely covered with setae; forewing scale with several long setae; anterior margin of forewing with a row of short setae; wing membrane with dotlike punctations. Head longer than wide; right side not visible due to poor preservation. Eyes large, roundish, bulging laterally. Ocelli large, oval, almost touching eyes (about 0.02 mm). Fontanelle large, oblong, faintly forked at tip; located between eyes, about 0.56 mm from posterior margin of head. Postclypeus faintly arched; length less than half its width (length to width index 0.33). Antennae with 15 articles; articles appear elongated, due to poor preservation; second, third, and fourth appear equal in size. Pronotum narrower than head; anterior margin widely concave; posterolateral

TABLE 9
Measurements (mm) of imagoes of six new species of *Nasutitermes*

	pilosus holotype	*seminudus* holotype	*medioculatus* holotype	*amplioculatus* holotype	*magnaocellus* holotype	*incisus* holotype
Length of head to tip of labrum	1.02	0.89	1.17	1.19	1.53	1.65
Length of head to postclypeus	0.63	0.66	0.74	0.61	1.04	1.00
Width of head with eyes	0.87	0.89	0.94	0.95	1.25	1.25
Diameter of eye	0.26	0.28	0.37	0.41	0.51	0.56
Length of ocellus	0.09	0.13	0.13	0.13	0.23	0.15
Length of postclypeus	0.17	0.13	0.15	0.18	0.15	0.20
Width of postclypeus	0.43	0.38	0.38	0.43	0.45	0.54
Maximum length of pronotum	0.49	0.49	0.51	0.56	0.66	0.79
Width of pronotum	0.77	0.71*	0.79	0.79	1.15	1.10
Length of hind tibia	0.82	—	—	0.64*	1.53	0.82
Length of forewing scale	0.54	0.43	—	0.49	0.69	0.77
Length of forewing from suture	8.00	5.80*	—	7.80*	—	11.50
Width of forewing	1.94	1.53*	—	1.68*	—	3.20

*approximate

corners broadly rounded; posterior margin with a deep medial indentation. Hind tibia long. Forewing (partial) 10.00 mm long.

SPECIMEN: Holotype (imago) AMNH DR15-1252.

ETYMOLOGY: This new species name is a combination of the root of Latin *magnus*, "large", and *ocellus*.

Nasutitermes medioculatus, new species
Figures 21, 24; table 9

DIAGNOSIS: *Nasutitermes medioculatus* is close to *N. pilosus* and *N. seminudus*, n. spp., in the size of its eyes. It differs from *N. pilosus* in having a larger fontanelle, larger eyes, a wider head, and longer ocelli. It differs from *N. seminudus* in having a larger fontanelle, larger eyes, and its head and pronotum more densely covered with setae.

DESCRIPTION: **Imago**: Head and pronotum chestnut brown; postclypeus lighter than head; antennae brownish; legs yellowish. Head moderately covered with short setae, along with a few longer setae; pronotum with several short setae, longer setae along margins; forewing scale with several long setae; anterior margin of forewing with a row of short setae; wing membrane with dotlike punctations. Head oval. Eyes roundish, bulging laterally. Ocelli oval, close to eyes (about 0.03 mm). Fontanelle long, ovalish, forked at tip; located between eyes, about 0.36 mm from posterior margin of head. Postclypeus faintly arched; length less than half its width (length to width index 0.39). Antennae broken, with only five articles visible; third very short; fourth subequal to second. Pronotum narrower than head; anterior margin widely concave; posterolateral corners broadly rounded; posterior margin with a deep medial indentation.

SPECIMEN: Holotype (imago) AMNH DR14-643.

ETYMOLOGY: This new species name is a combination of the Latin prefix *medi-*, "medium", and *oculatus*, "of eyes".

Nasutitermes pilosus, new species
Figures 22, 25, 26; table 9

DIAGNOSIS: *Nasutitermes pilosus* resembles *N. seminudus*, n. sp., but differs from it in having smaller eyes, a differently shaped fontanelle (round vs. oval in *N. seminudus*), a pronotum with its posterior margin broadly emarginate (vs. deeply notched medially in *N. seminudus*), and its head and pronotum densely covered with setae.

DESCRIPTION: **Imago**: Head brown; postclypeus lighter than head; pronotum, antennae, and legs yellowish. Head and pronotum densely covered with a fine mat of short setae, along with several longer setae; forewing scale with a few long setae; anterior margin of forewing with

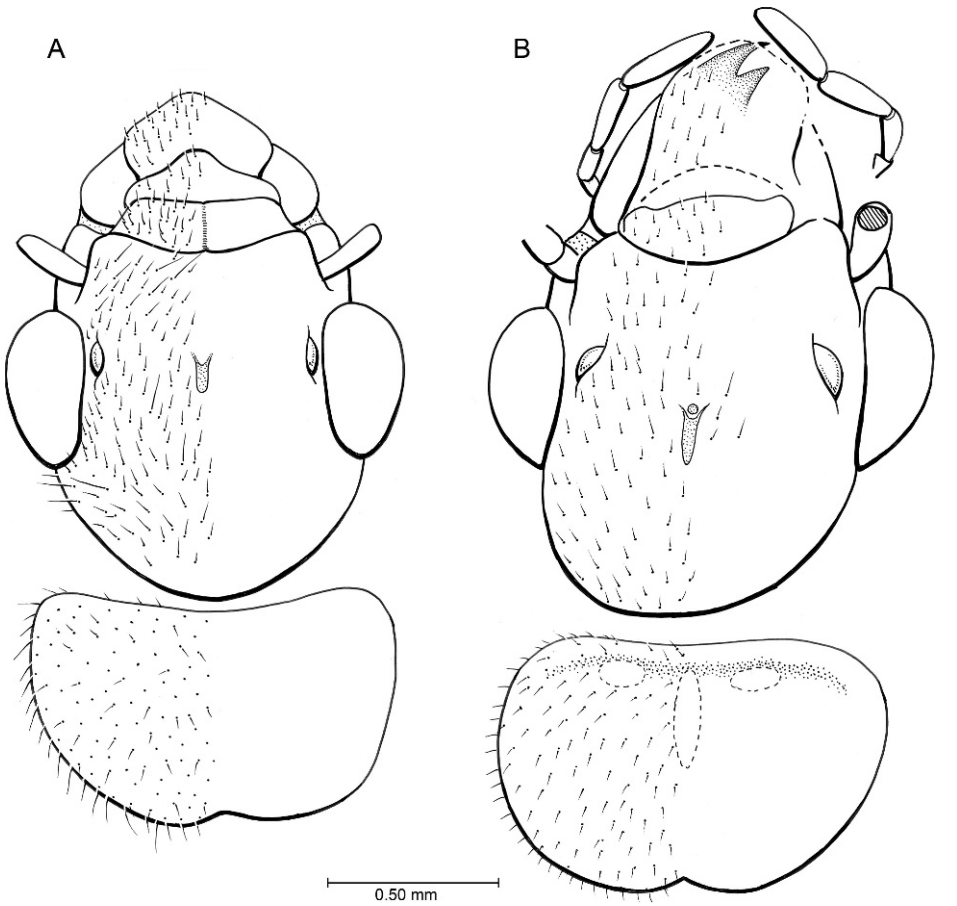

Fig. 24. *Nasutitermes* imagoes in Dominican amber, heads and pronota, dorsal views. **A.** *N. magnoculus*, n. sp., AMNH DR15-1252. **B.** *N. mediocculatus* n. sp., AMNH DR14-643 (head slightly distorted).

a row of short setae; wing membrane with dotlike punctations. Head oblong. Eyes small, nearly round. Ocelli small, oval, close (about 0.03 mm) to eyes. Fontanelle small, circular, located between eyes, about 0.36 mm from posterior margin of head. Postclypeus nearly flat; length less than half its width (length to width index 0.40). Antennae with 15 articles; third very short; fourth subequal to second. Pronotum narrower than head; anterior margin widely concave; posterior margin broadly emarginate. Forewing with median vein branched (four branches); cubitus with 6–7 branches.

SPECIMEN: Holotype (imago) AMNH DR10-1627.

ETYMOLOGY: This new species is named from the Latin *pilosus*, "hairy".

Nasutitermes seminudus, new species

Figures 22, 25, 26; table 9

DIAGNOSIS: *Nasutitermes seminudus* resembles *N. pilosus*, n. sp., but differs from it in having larger eyes, a differently shaped fontanelle (oval, vs. round in *N. pilosus*), a pronotum deeply notched medially, and its head and pronotum with few setae.

DESCRIPTION: **Imago**: Head and pronotum brown; postclypeus lighter than head; antennae yellowish; forewing scale brownish. Head with very few setae; pronotum with a few short setae on surface, a few long setae along margins; forewing scale with a few moderately sized setae; anterior margin of forewing with a row of short setae; wing membrane with punctations, no setae visible. Head nearly

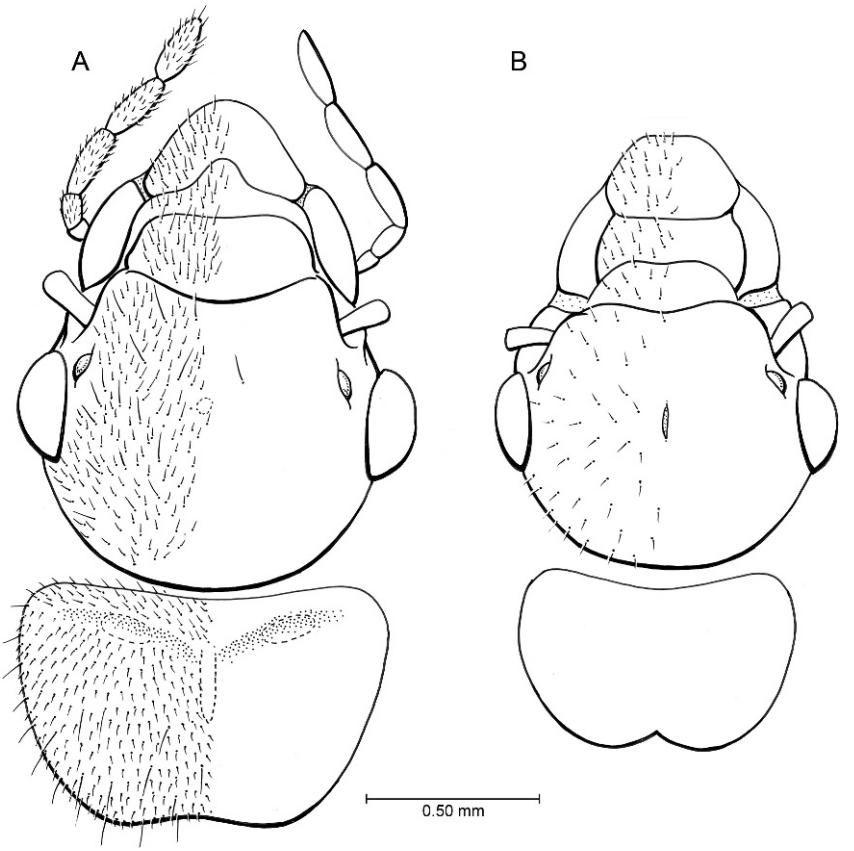

Fig. 25. *Nasutitermes* imagoes in Dominican amber, heads and pronota, dorsal views. **A.** *N. pilosus*, n. sp., AMNH DR10-1627 (fontanelle not fully visible). **B.** *N. seminudus*, n. sp., AMNH DR10-1574 (pronotum reconstructed slightly, setulae not fully visible).

oval. Eyes small, roundish. Ocelli ovalish, not touching eyes (0.03 mm from eyes). Fontanelle slitlike; located about 0.38 mm from posterior margin of head. Postclypeus arched; length less than half its width (length to width index 0.34). Antennae with 15 articles; third shortest; fourth subequal to second. Pronotum narrower than head; anterior margin broadly concave; posterior margin with a deep medial indentation. Forewing with median branched apically. Cubitus with 10 branches.

SPECIMEN: Holotype (imago) AMNH DR10-1574.

ETYMOLOGY: This new species is a combination of the Latin prefix *semi-*, "partially", and *nudus*, "naked, bare".

Key to the species of *Nasutitermes* imagoes in Dominican amber

1. Eyes large; diameter 0.41–0.56 mm. 2
— Eyes medium-sized or small; diameter 0.26–0.37 mm 4
2. Ocelli small; length 0.13–0.15 mm 3
— Ocelli large; length 0.23 mm; eye diameter 0.51 mm; fontanelle oblong, forked on front (fig. 24A) . . . . . *N. magnocellus*
3. Eye diameter 0.56 mm; fontanelle large, round; pronotal width 1.10 mm; anterior margin of pronotum deeply incised (fig. 23B) . . . . . *N. incisus*
— Eye diameter 0.41 mm; fontanelle small, dotlike; pronotal width 0.79 mm; anterior margin of pronotum not deeply incised (fig. 23A) . . . . . *N. amplioculatus*

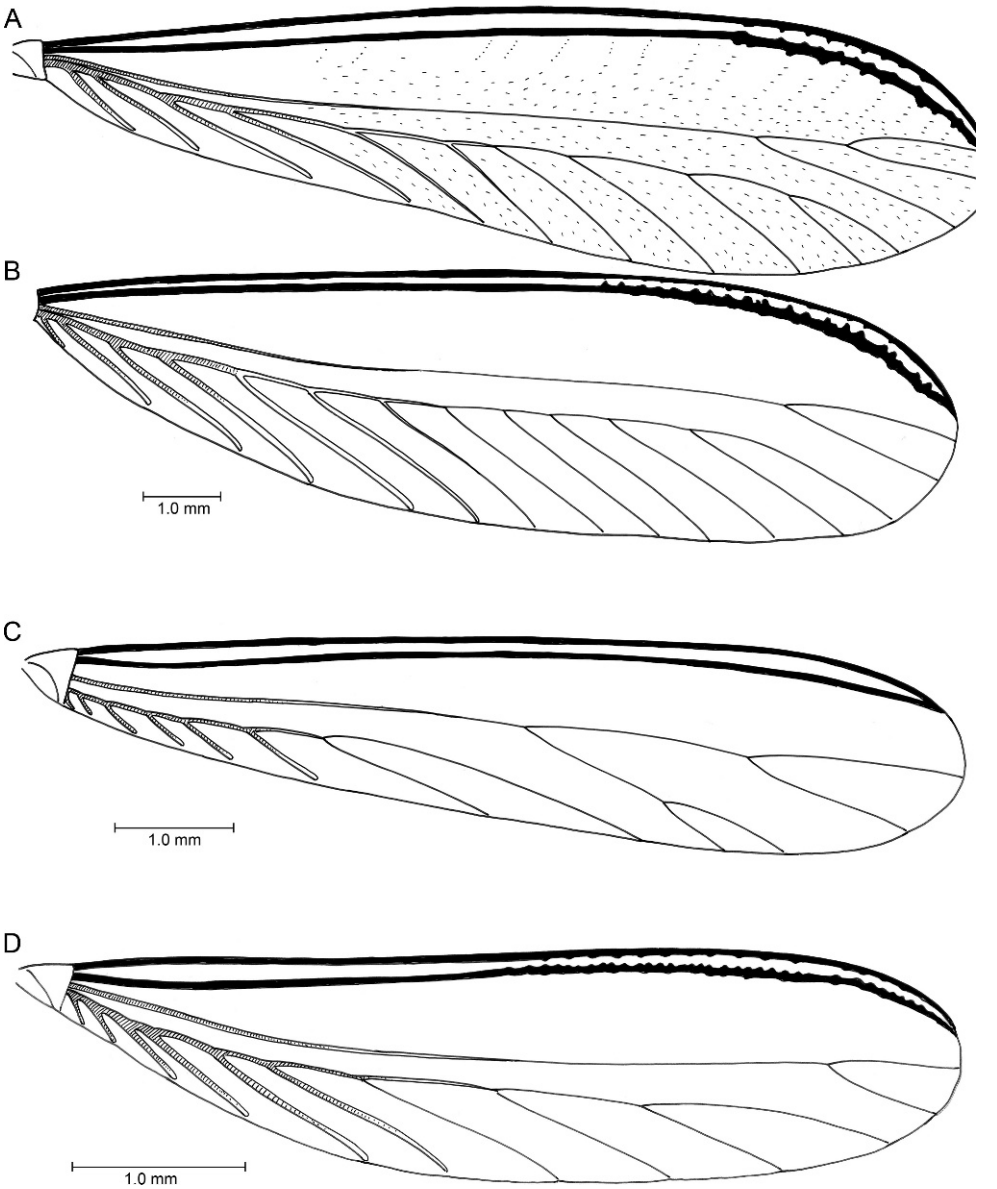

Fig. 26. Wings of *Nasutitermes* spp. in Dominican amber. **A, B.** *N. incisus*, n. sp., AMNH PB263, fore- (A) and hind wing (B). Microtrichia shown only for forewing. **C.** *N. pilosus*, n. sp., AMNH DR10-1627, forewing. **D.** *N. seminudus*, n. sp., AMNH DR10-1574, forewing.

4. Head and pronotum densely covered with setae. 5
— Head and pronotum sparsely covered with setae (fig. 25B) . . . . . *N. seminudus*
5. Eye diameter 0.26 mm; fontanelle small; head width 0.87 mm; ocellus length 0.09 mm (fig. 25A) . . . . . *N. pilosus*
— Eye diameter 0.31 mm; fontanelle large; head width 0.94 mm; ocellus length 0.13 mm (fig. 24B) . . . . . *N. medioculatus*

Genus *Subulitermes* Holmgren, 1910

The genus *Subulitermes*, treated today in a more restricted sense than that of Snyder

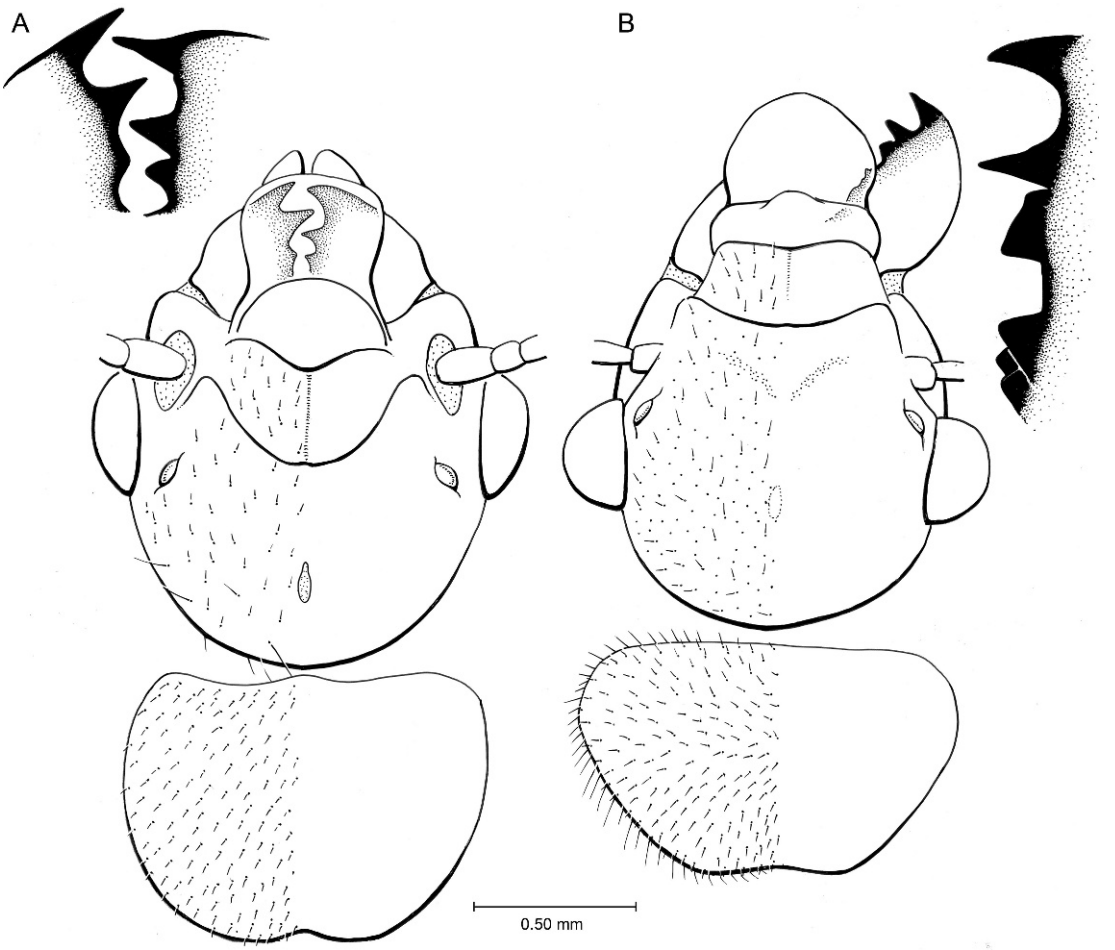

Fig. 27. Heads and pronota (dorsal views) with details of visible portions of mandibles of *Subulitermes* spp. in Dominican amber; both are holotypes. **A.** *S. hispaniola*, n. sp., AMNH DR8-341. **B.** *S. insularis*, n. sp., AMNH DR8-332.

(1949) and Emerson (1955), presently consists of six living species from the Neotropical Region. The distribution is very similar to that of *Atlantitermes*, with only one species reported from the West Indies, also from the subcontinental island of Trinidad (table 1). Species of *Subulitermes* are tropical soil dwellers, feeding on soil rich in humus. No fossil species of this genus has been hitherto reported. The two new fossil species described here are the first record of this genus, living or fossil, from Hispaniola.

Subulitermes insularis, new species
Figure 27; table 10

DIAGNOSIS: *Subulitermes insularis* differs from *S. hispaniola*, n. sp., in having smaller eyes, a wider head, a wider pronotum with angular sides and posterior margin almost straight.

DESCRIPTION: **Imago**: Head and pronotum brown; postclypeus lighter than head; wings light brown, membrane clear. Head densely covered with short setae; pronotum densely covered with short setae, longer setae along

margins; anterior margin of forewing with a row of short setae; wing membrane with dotlike punctations. Head longer than wide. Eyes small, round, bulging. Ocelli ovalish, very close (0.03 mm) to eyes. Fontanelle not clearly visible, apparently narrow and oblong; located between eyes, about 0.23 mm from posterior margin of head. Postclypeus arched; length less than half its width (length to width index 0.37). Mandible dentition visible, *Subulitermes*-type (see Ahmad, 1950: fig. 11). Antennae with 15 articles; second article longer than third or fourth; third subequal to fourth. Pronotum narrower than head; anterior margin straight; lateral margins narrowing posteriorly at an angle; posterior margin faintly emarginate.

SPECIMEN: Holotype (imago) AMNH DR8-332.

ETYMOLOGY: This new species name is based on *insular*, referring to the island origin.

Subulitermes hispaniola, new species

Figure 27; table 10

DIAGNOSIS: *Subulitermes hispaniola* differs from *S. insularis*, n. sp., in having larger eyes, a narrower head, narrower forewings, and a narrower pronotum, with its posterolateral corners more broadly rounded and its posterior margin with a medial indentation.

DESCRIPTION: **Imago**: Head and pronotum reddish brown; postclypeus light brown, lighter than head; antennae brownish; wings light brown, membrane clear. Head densely covered with short setae; pronotum densely covered with short setae, longer setae along margins; anterior margin of forewing with a row of short setae; wing membrane with dotlike punctations. Head longer than wide. Eyes small, ovalish, bulging. Ocelli oval, 0.05 mm from eyes. Fontanelle oval; about 0.31 mm from posterior margin of head. Postclypeus arched; length less than half its width (length to width index 0.39). Mandible dentition visible, *Subulitermes* type (Ahmad, 1950: fig. 11). Antennae with 15 articles; second longer than third or fourth; third subequal to fourth. Pronotum narrower than head; anterior margin undulating, with a faint median projection; posterolateral corners rounded; posterior margin with a distinct medial indentation.

TABLE 10
Measurements (mm) of imagoes of two new species of *Subulitermes*

	insularis holotype	***hispaniola*** holotype
Length of head to tip of labrum	1.02	1.02
Length of head to postclypeus	0.61	0.49
Width of head with eyes	0.89	0.87
Diameter of eye	0.23	0.26
Length of ocellus	0.10	0.09
Length of postclypeus	0.15	0.15
Width of postclypeus	0.41	0.38
Maximum length of pronotum	0.46	0.54
Width of pronotum	0.77	0.74
Length of hind tibia	0.82	0.87
Length of forewing scale	0.51	0.41
Length of forewing from suture	6.50*	—
Width of forewing	2.20	1.63*

*approximate

SPECIMEN: Holotype (imago) AMNH DR8-341.

ETYMOLOGY: This new species name is derived directly from the island of origin.

NASUTITERMITINAE SOLDIERS

Four new species of nasutitermitines are described below based on the soldiers, which, with two other Dominican amber species described previously (*Nasutitermes electronasutus* Krishna and *Constrictotermes electroconstrictus* Krishna), brings to six the total of nasutitermitine species in Dominican amber known from soldiers. The two species of *Nasutitermes* described on the basis of soldiers may be synonymous with two of the six species of this genus described from imagoes. The other four species of nasute soldiers belong to the genera *Caribitermes*, *Constrictotermes*, *Parvitermes*, and *Velocitermes*, so it is unlikely that any of these species are synonymous with any described species since imagoes of these genera are as yet unknown in Dominican amber.

Nasutitermes rotundicephalus, new species

Figures 28, 30; table 11

DIAGNOSIS: *Nasutitermes rotundicephalus* has a much longer, wider, and more rounded head compared to *N. electronasutus* Krishna,

the only soldier of *Nasutitermes* hitherto known from the fossil record.

DESCRIPTION: **Soldier**: Head chestnut brown; antennae, pronotum, and legs yellowish. Head with two long setae at base of nasus; four or five shorter setae at tip of nasus; tergites and sternites with very few short setae. Head dorsally viewed very wide and round behind nasus; posterior margin widely concave; nasus at base wide; dorsal margin of head in profile faintly sloping toward tip of nasus. Mandibles with short points. Antennae with 13 articles; third longer than second or fourth; second subequal to fourth. Pronotum saddle shaped; anterior margin with slight indentation in middle; posterior margin almost straight.

SPECIMEN: Soldier (holotype) AMNH DR-10-1789.

ETYMOLOGY: This new species name is a combination of Latin *rotundus*, ''round'', and Latin *cephalus* (borrowed from Greek), ''head''.

Genus *Parvitermes* Emerson, 1949

The genus *Parvitermes* consists of nine living species, all from the West Indies. Of these eight, six are from Hispaniola exclusively (table 1). *Parvitermes* species are tropical-forest soil dwellers and feed on soil rich in humus. The new species described here, based on the soldier, is the first species of this genus known for the fossil record.

Parvitermes longinasus, new species
Figures 28, 30; table 11

DIAGNOSIS: *Parvitermes longinasus* differs from all the living species of *Parvitermes* in having a long nasus and the constriction behind the head not as prominent.

DESCRIPTION: **Soldier**: Head chestnut brown; antennae and tergites brown; legs yellowish brown. Head with four setae at base of nasus, two behind constriction, a few shorter setae at tip of nasus. Head slightly constricted behind antennal fossae; in profile vertex raised in front of constriction; sides of head round behind constriction; in lateral view constriction 0.66 mm from posterior margin of head; nasus long, wide at base. Antennae with 13 articles; third longest, almost double the length of second; second subequal to fourth. Pronotum saddle shaped; slight indentation in middle; posterior margin straight.

SPECIMEN: Soldier (holotype) AMNH DR15-1255.

ETYMOLOGY: This new species name is a combination of the root of Latin *longus*, ''long'', and *nasus*, ''nose''.

Genus *Caribitermes* Roisin, 1996

Caribitermes was described by Roisin et al. (1996) as a monotypic genus for the species *C. discolor* from the West Indies, previously placed in *Parvitermes*. The new species described here, based on the soldier, is the first report of this genus in the fossil record.

Caribitermes hispaniola, new species
Figures 28, 29; table 11

DIAGNOSIS: *Caribitermes hispaniola* resembles *C. discolor* (Banks), a living species from the Caribbean of the hitherto monotypic genus *Caribitermes*, both species having the head capsule very slightly constricted behind the antennae. The genus was described based on this character, the imago mandibles, and the gut anatomy, the latter of which cannot be studied in this fossil specimen. *Caribitermes hispaniola* differs from *C. discolor* in having a longer and wider head and nasus, fewer setae, and a longer third antennal article.

DESCRIPTION: **Soldier**: Head chestnut brown; antennae and legs yellowish brown; sternites and tergites dark brown. Head capsule with no setae visible; nasus with two or three short bristles at tip. In dorsal view constriction of head below antennal fossae not very prominent; head capsule below constriction round and wide in holotype specimen; in paratype specimen head not as bulbous (head width 0.79 mm vs. 0.82 in holotype); in lateral view constriction 0.51–0.53 mm from posterior margin of head; in profile vertex raised in front of constriction; nasus long and narrow, broad at base. Mandibles with points. Antennae with 13 articles; third slightly longer than fourth; fourth shorter than second or third. Pronotum saddle-shaped; anterior margin arched; sides angular; posterior margin faintly emarginate.

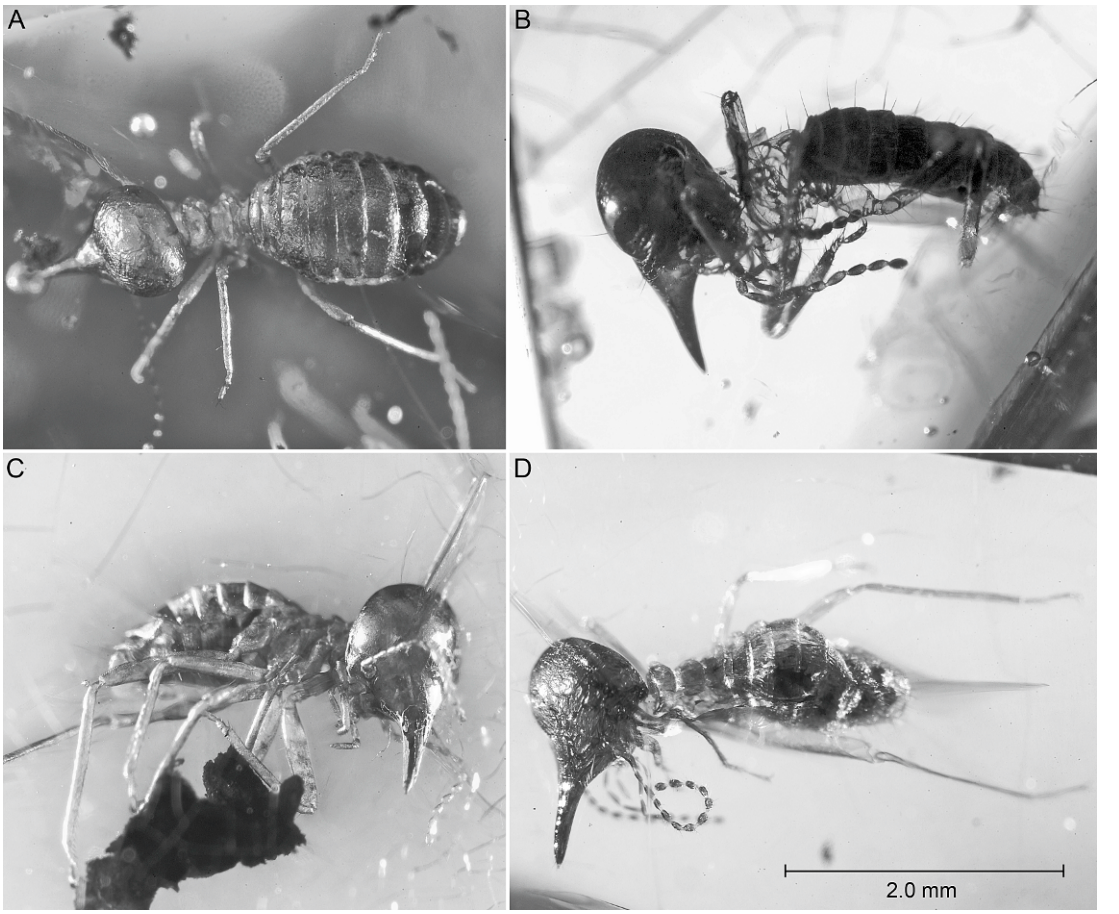

Fig. 28. Photomicrographs of Nasutitermitinae soldiers in Dominican amber. **A.** *Caribitermes hispaniola*, n. sp., AMNH DR15-1256A. **B.** *Parvitermes longinasus*, n. sp., AMNH DR15-1255. **C.** *Nasutitermes rotundicephalus*, n. sp., AMNH DR10-1789. **D.** *Velocitermes bulbus*, n. sp., AMNH DR15-1257.

SPECIMENS: Soldier (holotype) AMNH DR15-1256A. Paratype AMNH No. DR15-1256B (in same pieces as holotype).

ETYMOLOGY: This new species named after the island of Hispaniola (Dominican Republic and Haiti).

Genus *Velocitermes* Holmgren, 1912

The tropical genus *Velocitermes* consists of 10 species, all from the Neotropical Region, none of which are reported from the West Indies. *Velocitermes* species live in savannah and forested areas, feeding on leaf litter (Matthews, 1977). This new species, based on the soldier caste, is the first report of the genus *Velocitermes* from the West Indies (Hispaniola) and the first report of this genus in the fossil record.

Velocitermes bulbus, new species

Figures 28, 30; table 11

DIAGNOSIS: *Velocitermes bulbus*, differs from all living species of *Velocitermes* in having a less constricted head and a more prominent posterior lobe of the head.

DESCRIPTION: **Soldier**: Head brown; antennae brown; abdomen blackish. Head capsule with four or five long setae and four or five short setae at tip of nasus; tergites with very short setae. Head in dorsal view constricted below base of nasus; head below constriction large and bulbous in profile;

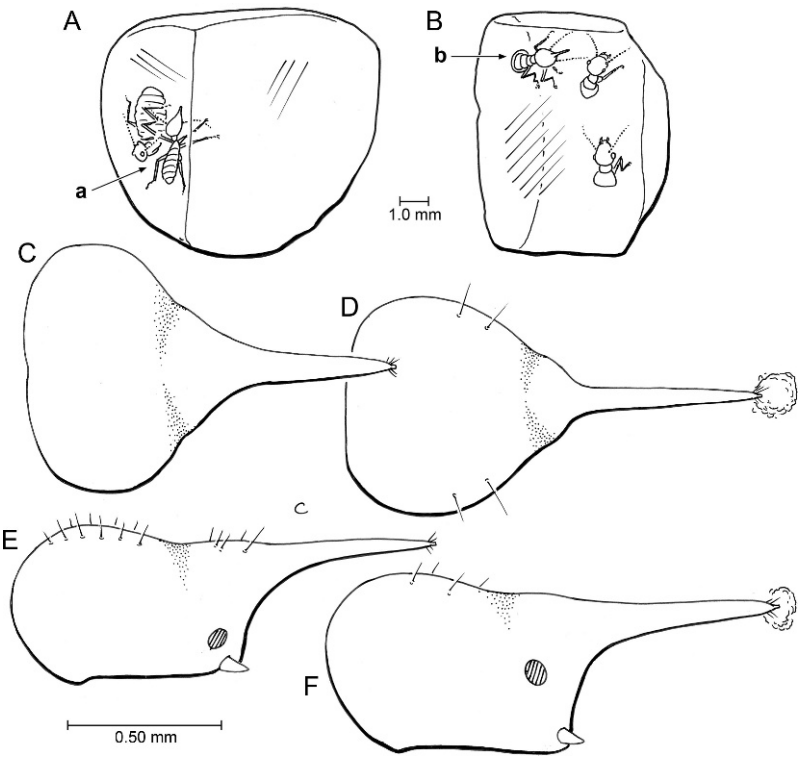

Fig. 29. *Caribitermes hispaniola*, n. sp. soldiers in Dominican amber, AMNH DR15-1256, pieces **A** and **B**, showing locations of soldier **a** (head shown in figs. C, D) and soldier **b** (shown in figs. E, F). Figs. **C, E.** head in dorsal view. **D, F.** Head in lateral view.

concavity between base of nasus and head; nasus narrow and slender, in profile upper margin bending downward anteriorly to tip. Mandibles with points. Antennae with 13 articles; third longest, second subequal to fourth. Pronotum saddle shaped; front margin slightly indented medially; posterior margin straight.

SPECIMEN AND TYPE LOCALITY: Soldier (holotype) AMNH DR15-1257.

ETYMOLOGY: This new species name is from Latin *bulbus*, "bulb", and describes the shape of the soldier's head.

DISCUSSION

In comparing the extant and extinct termite faunas on Hispaniola, it is crucial to first estimate sampling biases. The extant fauna is rather well surveyed for the Caribbean (Roisin et al., 1996; Scheffrahn and Křeček, 1993; Scheffrahn et al., 1994; Scheffrahn and Roisin, 1995; Scheffrahn et al., 1998, 2003, 2006; Snyder, 1956). The paleofauna preserved in Dominican amber, however, is undoubtedly a fraction of the entire paleofauna from Hispaniola. Hispaniola today is 76,480 km^2, and the amber deposits are localized within the Cordillera Septentrional of the Dominican Republic to an area of approximately 400 km^2 (Grimaldi, 1995). Like most fossil deposits, globules of amber are typically concentrated by tides and waves in shore and near shore sediments prior to burial, so the total area that originally produced the resin was certainly larger than 400 km^2. Even if that area was, say, 1000 km^2, it is still a small fraction of Hispaniola's present size. Given this fact, plus the bias that resin has in capturing forest arthropods associated with trees, it would not be surprising if 30% or less of the species in the original paleofauna of Hispaniola is actually represented in large samples of Dominican amber.

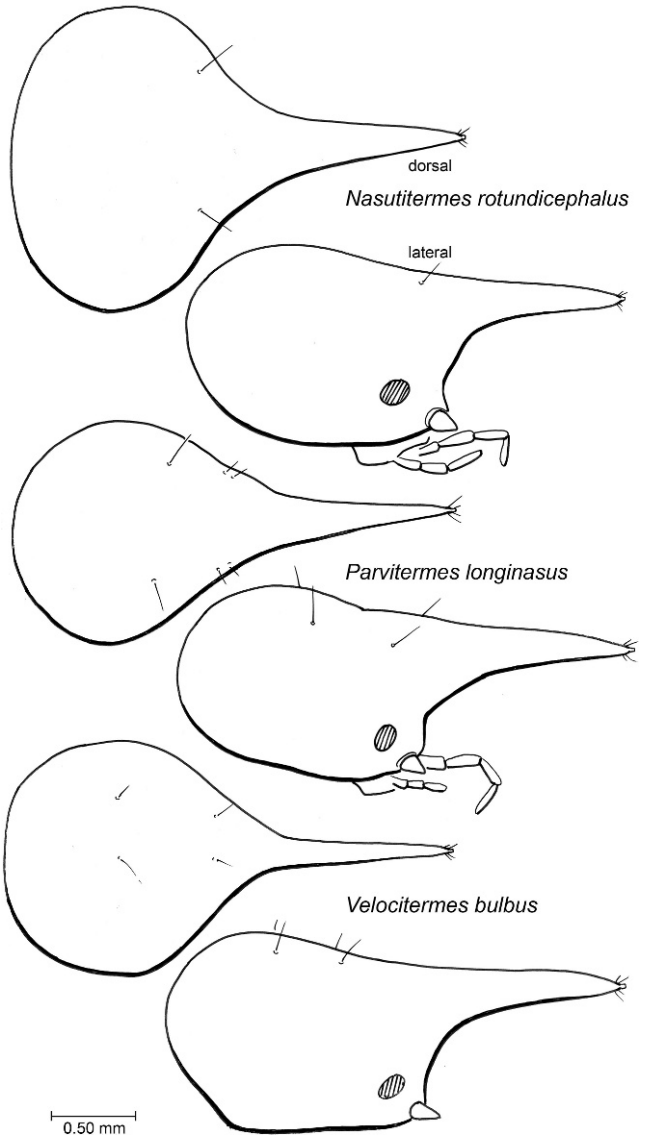

Fig. 30. Heads in dorsal and lateral views of nasutitermitine soldiers in Dominican amber.

Despite the biased undersampling, species diversity of termites in Dominican amber is approximately the same as is known for the entire island of Hispaniola (table 1). In order to examine the relationship between termite species number and island size for the Caribbean, we plotted extant termite species diversity on 46 Caribbean islands against a $\log_{10}$-transformed value of island area (in km^2) (table 12; fig. 31). The islands of Trinidad and Tobago were plotted in figure 31 but excluded from the regression analysis since they are virtually a peninsula of the Venezuelan mainland and, not surprisingly, have a disproportionately high number of termite species. Trinidad, for example, has 18 more termite species than Cuba, even though its size is 4% that of Cuba. There were several clear outliers in the species-area plot (fig. 31), namely two with disportionately high species numbers (Guana Island and Montserrat), and six with disproportionately few (St. Kitts,

TABLE 11
Measurements (mm) of soldiers of new species of Nasutitermitinae in Dominican amber

	Nasutitermes rotundicephalus holotype	*Parvitermes longinasus* holotype	*Caribitermes hispaniola* holotype	*Velocitermes bulbus* holotype
Lateral length of head with nasus	1.73	1.76	1.50	1.81
Lateral length of nasus	0.79	0.92	0.69	0.77
Width of head	1.30	0.91	0.81	0.89
Height of head	0.66	0.66	0.51	0.82
Maximum length of pronotum	0.26	0.26	0.15	0.28
Width of pronotum	0.41	0.38	0.33	0.41
Length of hind tibia	1.35	1.14	0.89	1.40

Curaçao, and a group of four Bahamas [Andros, Dry Key/Eleuthera, Grand Bahama, and San Salvador]). Guana Island is a small (3.4 km^2) island close to Tortola (95 km^2), both in the British Virgin Islands; the former is dry and low and has eight species, the latter is higher and even with cloud forest at the highest ridge and has five known species. The discrepancy may be due to the intensive collecting over many years (by Margaret Collins and Barbara Thorne), which may also explain the anomalous diversity reported for Montserrat. Intensive sampling plausibly uncovers rare, newly colonized species that may not become perennial inhabitants of an island. The paucity of termite species in the six islands that are low outliers is probably due to undersampling.

Despite the outliers and confounding factors (explained below), we found a strong, general relationship between termite species diversity and island, defined by the linear relationship $y = -1.85 = 4.39x$ ($r = 0.74$, $p < 0.01$), which follows general patterns of species numbers and island area (MacArthur and Wilson, 1967; Williamson, 1981). Though species-area relationships are explained by hypothetical rates in colonization and extinction, there are confounding factors, such as distance of islands from the mainland, age of islands, and the fact that larger islands usually have more topographic relief (Williamson, 1990), the mountains of which are usually forested and wet—conditions that sustain termites well. The Bahamas, Turks and Caicos, and smaller islands of the Virgin Islands group are low, desert islands, which may explain their paucity of termites. Nonetheless, the species-area relationship applies to islands within a group of low, dry islands as well as to a group that consists of high, forested ones (table 12; fig. 31).

By extrapolation, the large size of Hispaniola's termite paleofauna compared to that of present day suggests the island had a much larger area or a connection to the mainland. The latter possibility is supported by the presence in Dominican amber of taxa that are known to be poor dispersers over water, like stingless and orchid bees, which do not naturally occur in the Caribbean today with the exception of Trinidad and Tobago. (*Melipona beecheii*, occurring in Cuba, was introduced from Central America and Mexico by islanders for honey production.)

Ecologically, there appear to be significant differences in taxonomic composition between the living and extinct Hispaniolan termite faunas. Specifically, there is an unexpected diversity of soil- and humus-feeding termites in Dominican amber, such as *Atlantitermes*, *Anoplotermes* (8 species in amber and 3 living), and *Subulitermes*. Also, there are significantly more species of nasutitermitines in the amber (17 species) than are presently living in Hispaniola (6 species). Lastly, there are few kalotermitids in the amber (5 species), but 15 species in the Recent fauna. Kalotermitids feed and nest in sound wood, and so would be expected to have been living in close proximity to copious resin, since *Hymenaea* trees (the genus to which the Dominican amber tree belongs) bleed profusely in response to damage such as wind and insect attacks (Langenheim, 2003). Thus the scarcity of kalotermitids in Dominican amber may reflect

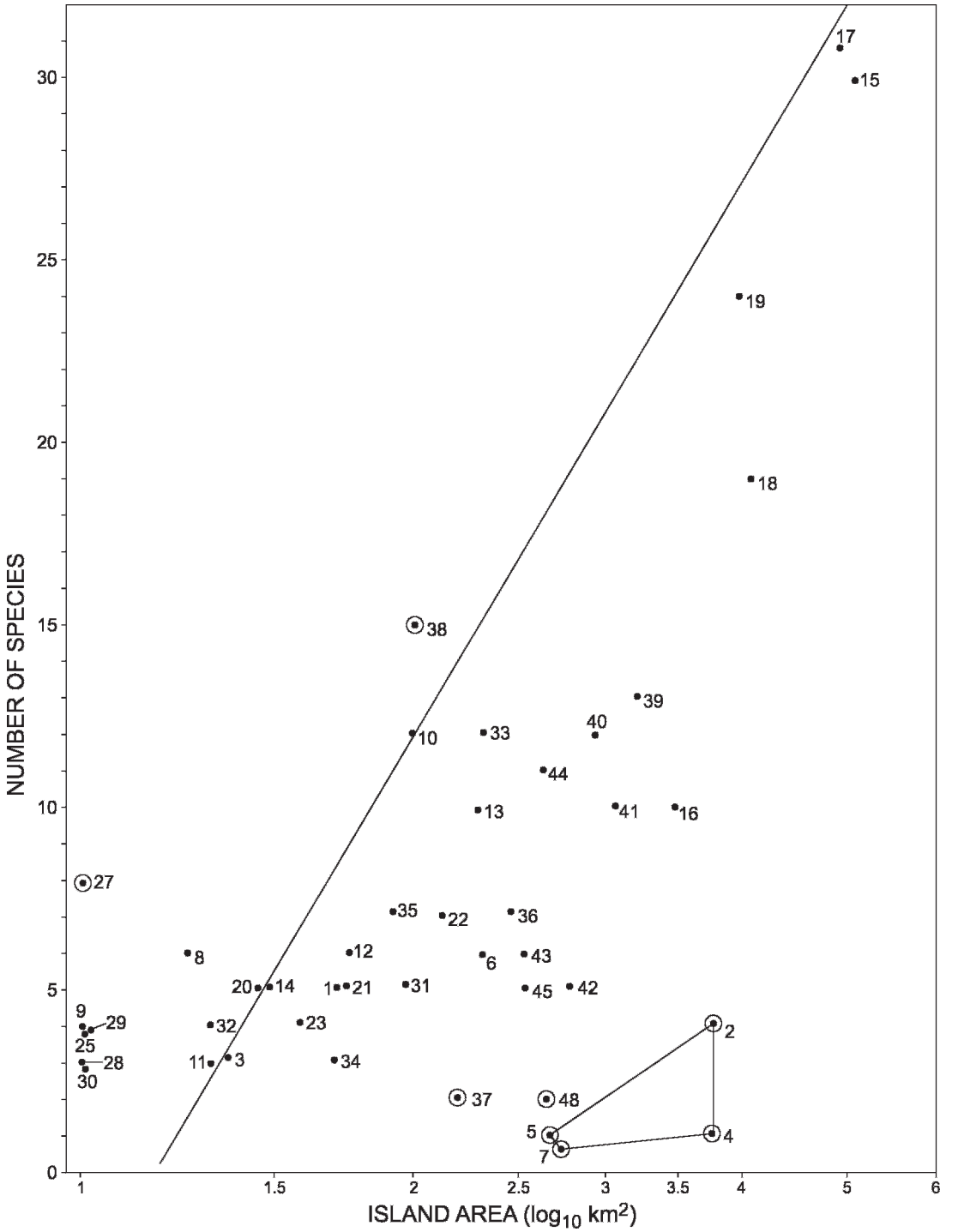

Fig. 31. Simple regression of island size ($\log_{10}$ km^2) and termite species number for 48 Caribbean islands ($y = 1.85 + 4.39x$, $r = 0.74$, $p < 0.01$). The number for each dot corresponds to the islands listed in table 12.

TABLE 12
Termite species diversity on Caribbean islands

Island Group/Island	Data #	# Termite Species	Area (km^2)
Bermuda	1	5	53
BAHAMAS			
Andros	2	4	6000
Bimini	3	3	23
Grand Bahama	4	1	1373
Dry Key, Eleuthera	5	1	470
New Providence	6	6	207
San Salvador	7	1	526
TURKS & CAICOS			
Grand Turk	8	6	18
Parrot Cay	9	4	4
Providenciales	10	12	98
South Caicos	11	3	21
CAYMAN ISLANDS			
Cayman Brac	12	6	36
Grand Cayman	13	10	196
Little Cayman	14	5	30
GREATER ANTILLES			
Cuba	15	30	105,006
Isla de Piños (Cuba)	16	10	3,056
Hispaniola	17	31	76,480
Jamaica	18	19	10,991
Puerto Rico	19	24	9,104
Culebra Is.	20	5	28
Mona Is.	21	5	52
Vieques	22	7	135
VIRGIN ISLANDS			
Anegada	23	4	38
Eustatia	24	3	0.1
Great Camanoe	25	4	3.2
Great Thatch/Necker	26	4	0.3
Guana	27	8	3.4
Lesser Jost Van Dyke	28	3	8
Peter	29	4	7.1
Scrub	30	3	7.7
Tortola/Beef	31	5	95
Virgin Gorda	32	4	21
St. Croix	33	12	207
St. John	34	3	51
St. Thomas	35	7	81
LESSER ANTILLES (N > S)			
Antigua	36	7	281
St. Kitts	37	2	168
Montserrat	38	15	102
Guadeloupe	39	13	1,628
Dominica	40	12	751
Martinique	41	10	1,128
St. Lucia	42	5	620
St. Vincent	43	6	344
Barbados	44	11	430
Grenada	45	5	344

TABLE 12
(Continued)

Island Group/Island	Data #	# Termite Species	Area (km^2)
Tobago	46	16	300
Trinidad	47	48	4,769
Curaçao	48	2	444

a genuine absence of these termites in the amber forest, and not just an absence of data.

Another study surveyed the diversity in Dominican amber of the other major group of eusocial insects in Dominican amber, the ants (Wilson, 1985). When that study was done, 37 genera were known from Dominican amber, and 36 genera presently on Hispaniola (since then, several additional genera have been discovered in Dominican amber). Even though monophyletic genera are not equivalent units like species, this taxic approach may serve as a rough proxy for species diversity, in which case the number of known ant taxa in the amber is approximately equivalent to that in the living Hispaniola fauna, as is the case for the termites. Of the 37 ant genera in Dominican amber, 22 still exist on Hispaniola and 15 genera no longer occur on the island or in the Caribbean. Interestingly, there has been selective extinction on Hispaniola of ant genera that have specialized feeding and nesting habits, such as large colonies, flightless queens, and that are specialized predators or social parasites (Wilson, 1985). Termites are similar, with humus and soil feeding having been replaced by wood feeding, which is the primitive habit. It is not clear whether the faunal turnovers in the ants and termites are due to exclusion by competitively superior colonizers, to populational effects when an area becomes insular, or to both of these.

Biogeographically, the Dominican amber fauna is essentially a Mesoamerican one, with two exceptions. There are three species of *Coptotermes* in Dominican amber, which is a predominantly Asian and African genus, and in fact *C. priscus* appears to be the most common termite in Dominican amber. Much more dramatic is the presence of *Mastotermes electrodominicus* Krishna and Grimaldi in Dominican amber, whose only living congeneric relative is a species in northern Australia. *Mastotermes electrodominicus* too is not particularly rare in Dominican amber. These examples raise questions about the rates and extents of species turnover in biological communities and whether communities ever truly reach equilibrium.

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REFERENCES

Ahmad, M. 1950. The phylogeny of termite genera based on imago-worker mandibles. Bulletin of the American Museum of Natural History 95(2): 37–86.

Emerson, A.E. 1925. The termites of Kartabo, Bartica District, British Guiana. Zoologica (New York) 6(4): 291–459.

Emerson, A.E. 1955. Geographical origins and dispersions of termite genera. Fieldiana Zoology 37: 465–521.

Emerson, A.E. 1971. Tertiary fossil species of the Rhinotermitidae (Isoptera), phylogeny of genera, and reciprocal phylogeny of associated Flagellata (Protozoa) and the Staphylinidae (Coleoptera). Bulletin of the American Museum of Natural History 146(3): 243–303.

Engel, M.S. 2008. Two new termites in Baltic amber (Isoptera). Journal of the Kansas Entomological Society 81(3): 194–203.

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.

Engel, M.S., and K. Krishna. 2007. Drywood termites in Dominican amber (Isoptera: Kalotermitidae). Beiträge zur Entomologie 57: 263–275.

Fontes, L.R. 1979. *Atlantitermes*, novo gênero de cupim, com duas novas espécies do Brasil (Isoptera, Termitidae, Nasutitermitinae). Revista Brasileira de Entomologia 23(4): 219–227.

Fontes, L.R. 1982. Novos táxons e novas combinações nos cupins nasutos geófagos da região Neotropical (Isoptera, Termitidae, Nasutitermitinae). Revista Brasileira de Entomologia 26(1): 99–108.

Grimaldi, D. 1995. The age of Dominican amber. *In* K.B. Anderson and J.C. Crelling (editors), Amber, resinite, and fossil resins. American Chemical Society Symposium Series 617: 203–217. Washington, DC: ACS.

Grimaldi, D.A., and M.S. Engel. 2005. Evolution of the insects. New York: Cambridge University Press, 755 pp.

Grimaldi, D.A., M.S. Engel, and K. Krishna. 2008. The species of Isoptera (Insecta) from the Early Cretaceous Crato Formation: a revision. American Museum Novitates 3626: 1–30.

Iturralde-Vinent, M.A., and R.D.E. MacPhee. 1996. Age and paleogeographical origin of Dominican amber. Science 273: 1850–1852.

Krishna, K. 1996. New fossil species of termites of the subfamily Nasutitermitinae from Dominican and Mexican amber (Isoptera, Termitidae). American Museum Novitates 3176: 1–13.

Krishna, K., and D. Grimaldi. 1991. A new fossil species from Dominican amber of the living Australian termite genus *Mastotermes* (Isoptera: Mastotermitidae). American Museum Novitates 3021: 1–10.

Langenheim, J.H. 2003. Plant resins: chemistry, evolution, ecology, ethnobotany. Portland, OR: Timber Press, 586 pp.

MacArthur, R.H., and E.O. Wilson. 1967. The theory of island biogeography. Princeton, NJ: Princeton University Press, 203 pp.

Martins-Neto, R.-G., and M. Pesenti. 2006. The first fossil Termitidae (Isoptera) from the Oligocene of South America: the Entre-Córregos Formation of the Aiuruoca Basin, Minas Gerais, Brazil. Journal of the Entomological Research Society 8: 63–68.

Mathews, A.G.A. 1977. Studies on termites from the Mato Grosso State, Brazil. Rio de Janeiro: Academia Brasileira de Ciências, 267 pp.

Müller, F. 1873. Beiträge zur Kenntniss [sic] der Termiten. Jenaische Zeitschrift für Medizin und Naturwissenschaft 7(3): 333–358, 451–463.

Nel, A., and J.-C. Paicheler. 1993. Les Isoptera fossils: état actuel des connaissances, implications paléoécologiques et paléoclimatogiques (Insecta, Dictyoptera). *In* A. Nel, X. Martínez-Delclòs and J.-C. Paicheler (editors), Essai de révision des Aeschinioidea (Insecta, Odonata, Anisoptera) / Les Isoptera fossiles (Insecta, Dictyoptera): 103–179. Paris: CNRS Editions [Cahiers de Paléontologie], 179 pp.

Roisin, Y., R.H. Scheffrahn, and J. Křeček. 1996. Generic revision of the smaller nasute termites of the Greater Antilles (Isoptera, Termitidae, Nasutitermitinae). Annals of the Entomological Society of America 89(6): 775–787.

Sands, W.A. 1972. The soldierless termites of Africa (Isoptera: Termitidae). Bulletin of the British Museum (Natural History) Entomology (suppl.) 18: 1–244.

Scheffrahn, R.H., J.P.E.C. Darlington, M.S. Collins, J. Křeček, and N.-Y. Su. 1994. Termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of the West Indies. Sociobiology 24(2): 213–238.

Scheffrahn, R.H., S.C. Jones, J. Křeček, J.A. Chase, J.R. Mangold, and N.-Y. Su. 2003. Taxonomy, distribution, and notes on the termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of Puerto Rico and the U.S. Virgin Islands. Annals of the Entomological Society of America 96(3): 181–201.

Scheffrahn, R.H., and J. Křeček. 1993. *Parvitermes subtilis*, a new subterranean termite (Isoptera: Termitidae) from Cuba and the Dominican Republic. Florida Entomologist 76(4): 603–607.

Scheffrahn, R.H., J. Křeček, J.A. Chase, B. Maharajh, and J.R. Mangold. 2006. Taxonomy, biogeography, and notes on termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of the Bahamas and Turks and Caicos Islands. Annals of the Entomological Society of America 99(3): 463–486.

Scheffrahn, R.H., and Y. Roisin. 1995. Antillean Nasutitermitinae (Isoptera: Termitidae): *Parvitermes collinsae*, a new subterranean termite from Hispaniola and redescription of *P. pallidiceps* and *P. wolcotti*. Florida Entomologist 78(4): 585–600.

Scheffrahn, R.H., Y. Roisin, and N.-Y. Su. 1998. Greater Antillean Nasutitermitinae (Isoptera: Termitidae): *Parvitermes dominicanae*, a new subterranean termite from Hispaniola. Florida Entomologist 81(2): 179–187.

Schlemmermeyer, T., and E.M. Cancello. 2000. New fossil termite species: *Dolichorhinotermes domin-*

icanus from Dominican amber (Isoptera, Rhinotermitidae, Rhinotermitinae). Papéis Avulsos de Zoologia (São Paulo) 41(20): 303–311.

Silvestri, F. 1923. Descriptiones termitum in Aanglorum Guiana repertorum. Zoologica (New York) 3(16): 306–332.

Snyder, T.E. 1949. Catalog of termites (Isoptera) of the world. Smithsonian Miscellaneous Collections 112: 1–490.

Snyder, T.E. 1956. Termites of the West Indies, the Bahamas and Bermuda. Journal of Agriculture of the University of Puerto Rico 40(3): 189–202.

Thorne, B.L., D.A. Grimaldi, and K. Krishna. 2000. Early fossil history of the termites. *In* T. Abe, D.E. Bignell and M. Higashi (editors), Termites: evolution, sociality, symbioses, ecology: 77–93. Dordrecht, the Netherlands: Kluwer Academic Publishers, xxii + 466 pp.

Williamson, M. 1981. Island populations. Oxford: Oxford University Press, xi + 286 pp.

Williamson, M. 1990. Relationships of species number to area, distance, and other variables. *In* A.A. Myers and P.S. Giller (editors), Analytical biogeography: an integrated approach to the study of animal and plant distributions: 91–115. New York: Chapman and Hall, xiii + 578 pp.

Wilson, E.O. 1985. Invasion and extinction in the West Indian ant fauna: evidence from the Dominican amber. Science 229: 265–267.

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