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The Species of Isoptera (Insecta) from the Early Cretaceous Crato Formation: A Revision

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ABSTRACT

The termite species from Brazil's Early Cretaceous (Aptian-aged) Crato (Santana) Formation are evaluated on the basis of the degree of character variation seen in modern species, using a series of 56 specimens, scanning electron microscopy of minute structures, and a bivariate plot of the proportional sizes of sclerotized body structures. Of the previously described species only the following are considered valid: *Mariconitermes talicei* Fontes and Vulcano, *Meiatermes araripena* Krishna, *Cratomastotermes wolfschweningeri* Bechly, *Cratokalotermes santanensis* Bechly, and *Cretarhinotermes novaolindense* Bechly. The combination *M. araripena* Krishna (once placed in *Cretatermes*) is restored, and *Cretatermes pereirai* Fontes and Vulcano is proposed as a junior synonym of *M. araripena*. The following new species is described: *Meiatermes hariolus* Grimaldi, new species. The following are considered *nomina dubia* based on superficial and even contradictory diagnoses: *Caatingatermitinae* Martins-Neto et al. (likely synonymous with *Hodotermitinae*); *Araripetermes nativa* Martins-Neto et al. (*nomen incorrectum*, *recte*: *nativus*), *Caatingatermes megacephalus* Martins-Neto et al., and *Nordestinatermes obesa* Martins-Neto et al. (*nomen incorrectum*, *recte*: *obesus*). These are probably all new synonyms of the Cretaceous genus *Meiatermes* Lacasa-Ruiz and Martínez-Delclòs and of *M. araripena* in particular, but this assertion cannot be verified without access to the type specimens. Of the six definitive species of Crato termites, reconstructions are provided for four. All species appear to be basal taxa, either a stem group to Isoptera, to Hodotermitidae sensu lato, or to Kalotermitidae. Despite very partial preservation, *Cretarhinotermes* appears to be within the hodotermitid grade and not a rhinotermitid. Some specimens have yielded detailed preservation of soft internal tissues, including the midgut, which has further phylogenetic implications.

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INTRODUCTION

The termites, or Isoptera, are a lineage of 3,130 living species of highly social, morphologically reduced, wood-eating roaches, which have singular ecological impact in terrestrial tropical ecosystems as consumers of lignocellulose (reviewed in Grimaldi and Engel, 2005). Understanding the origins and evolution of Isoptera requires, in conjunction with the phylogenetics of living termites, an exploration of their fossil record.

Termite fossils have historically been largely confined to the Tertiary. Indeed, the first Cretaceous termites were those in Burmese amber described by Cockerell (1916, 1917), but this amber was mistakenly believed to be of Miocene origin until only recently (Zherikhin and Ross, 2000; Grimaldi et al., 2002). Aside from Cockerell's long misdated taxa, the first fossil understood to be of Cretaceous age was *Cretatermes carpenteri* Emerson (1967) from Labrador, Canada. Subsequent to Emerson (1967) there was a slow but relatively steady increase in the number of Cretaceous Isoptera until the rate of discovery rose slightly during the 1990s. Interestingly, Emerson's fossil was discovered and described at about the same time as (but with considerably less attention than) the first Cretaceous ant, *Sphecomyrma freyi* Wilson and Brown. Ants are the other major eusocial group of insects, also ecologically dominant and virtually ubiquitous, and their history of discovery and description has paralleled that of the termites, as summarized in Engel and Grimaldi (2005).

Among the 13 Cretaceous deposits with termites, Brazil's Crato Formation has yielded more specimens than any other Mesozoic paleofauna, probably a result of the prolific nature of this deposit, which is even exploited commercially. The significance of this termite fauna is further heightened by the fact that it is also one of the oldest, only 10–20 million years younger in age than those from Las Hoyas and Montsec, Spain, and the few specimens from Baissa (Transbaikalia) and in Lebanese amber (Engel et al., 2007a). As such, the termites, like all Crato Formation fossils, have garnered significant attention (e.g., Krishna, 1990; Fontes and Vulcano, 1998; Martins-Neto et al., 2006; Bechly, 2007). Herein we provide an

overview of the fauna, with new and revised species, and the first comprehensive reconstructions of the best-known taxa.

The systematics of the Crato Formation termites has become remarkably confused. Specifically, their taxa are greatly inflated. There are a couple of reasons for this: (1) prior descriptions have largely been isolated ones, using only single collections rather than large series of specimens; and (2) isolated studies cannot account for the extensive variation in isopteran wing venation, which differs within a species and even between opposing wings of the same individual, as documented for both modern (e.g., Emerson, 1933; Coaton, 1949, 1958: 23, 30; Roonwal and Bose, 1988) and extinct taxa (e.g., Emerson, 1933, 1968; Weidner, 1967; Engel et al., 2007a). Misled by such variation, some authors have placed individuals of a single species into different genera and even different subfamilies (e.g., Martins-Neto et al., 2006). Some authors have also attempted to split taxa based on trivial or ill-defined metrics. For example, abdominal intersegmental membranes are exceedingly elastic in termites, so variation in abdominal length among individuals largely varies with preservation. Thus, relying solely or largely on variation in the length or width of the abdomen (or total body length which, obviously, incorporates such abdominal variations) (i.e., Martins-Neto et al., 2006) is extremely inaccurate. This is particularly significant in the basal termite families—to which the Crato species belong—whose body size, venation, and other features are more intraspecifically variable than in Kalotermitidae, and far more so than in the “higher” termites, the Rhinotermitidae and Termitidae (Emerson, 1942, 1968, 1969).

Based on what is known of intra- and interspecific variation in modern termites, here we have applied these conservative standards to the largest series of specimens yet studied from the Crato Formation. This perspective allows a more comprehensive and refined evaluation of the new and previously described termite species from this early fauna. The diversity of Cretaceous termites has been tabulated by Engel et al. (2007a), to which can be added the new taxon proposed herein, the three genera and species described by Bechly

(2007), and from which four *nomina dubia* (Martins-Neto, 2006) may be removed. The present paper is the third recent article to describe and revise fossil termites (i.e., Engel et al., 2007a, 2007b), which together provide a framework for current research reconstructing the phylogeny of basal fossil and living Isoptera. Since the phylogenetic work is still in progress, we have not yet formally classified the Crato Formation termite genera into families, but do offer some commentary on placement. Indeed, even though many early termites have been assigned to the extant basal family Hodotermitidae, most Cretaceous Isoptera have features that are plesiomorphic for this family, suggesting that there is probably an extensive grade of basal termites.

The Crato Formation, which is also called the Crato Member of the Santana Formation, is an extensive deposit of organically rich, Aptian-aged limestone outcropping near Nova Olinda in the northeast Brazilian province of Ceará (reviewed by Maisey, 1990). The Santana Formation has yielded diverse vertebrates, whereas the Crato Member is the source of abundant terrestrial arthropods (Grimaldi, 1990). The insect specimens are preserved as three-dimensional but compressed, mineralized replicas, the dark brown cuticle of which is composed of iron hydroxide (goethite); internally, the insect bodies are composed largely of calcite and apatite. Specimens were prepared under a stereoscope by removing limestone matrix from around the body using fine blades and needles; the limestone dust was then removed with slight puffs of compressed air, and then brushed with a 2% solution of acetic acid to further clear the cuticle and setae of limestone matrix. Acid maceration is done carefully under a microscope, generally lasting no longer than 15–20 seconds, and abruptly ended with a gentle wash of water from a pipette. The acid will dislodge fine structures like wing veins and setae if it is allowed to react too long. Prior work (Krishna, 1990) revealed the importance of scanning electron microscopy for visualizing fine details like tibial spurs and tarsomeres. For this study we used acid-prepared material that had been thoroughly dried; the uncoated specimens were examined in a Zeiss Evo60 scanning

electron microscope at 20 kV. We have found that segmentation of tarsi and particularly the cerci (which are highly significant in termite phylogeny) are extremely difficult to discern using light microscopy, even with the high resolution of a Leitz Wetzlar stereoscope at 144 ×. Thus, previous reports of cercal segmentation in Crato termites based just on light microscopy (i.e., Martins-Neto et al., 2006; Fontes and Vulcano, 1998: 267) must be interpreted cautiously. Format and terminology for the descriptions follows those widely employed elsewhere in isopteran systematics (e.g., Emerson, 1933, 1967, 1968; Krishna, 1990; Engel et al., 2007a). Standard metrics are provided in table 1.

Acronyms for the institutions with the studied collections are as follows:

AMNH	American Museum of Natural History (Department of Invertebrate Zoology), New York, USA;
ROM	Royal Ontario Museum (Department of Palaeontology), Toronto, Canada;
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany;
ZMHB	Zoological Museum of Humboldt University (Institute for Palaeontology), Berlin, Germany.

SYSTEMATIC PALAEONTOLOGY

CLASS INSECTA LINNAEUS, 1758

ORDER ISOPTERA BRULLÉ, 1832

Genus *Mariconitermes* Fontes and Vulcano

Mariconitermes Fontes and Vulcano, 1998: 269.
Type species: *M. talicei* Fontes and Vulcano, 1998: 270. By original designation.

DIAGNOSIS (REVISED): Imago: Easily distinguished from other Crato Formation termites by the broad, rounded head, the characteristic, trapezoidal-shaped pronotum, and the large size (12–15 mm body length). Only *Cratomastotermes wolfschwenningeri* (below) is larger than *M. talicei*, by approximately 3–4 mm, but *Cratomastotermes* has a distinctive, extremely broad pronotum. Tarsi pentamerous, pretarsus with arolium; cercus with three segments, length of apical cercomere more than twice that of basal ones; wing with extensive reticulations and well-developed radial field having five large branches.

TABLE 1
Measurements of Crato Formation termites (in millimeters)

	Head		Eye	Pronotum		Forewing		Body
	Length	Width	Length	Length	Width	Length	Width	Length
<i>Mariconitermes talicei</i> Fontes and Vulcano								
AMNH-2	3.3	3.1	—	—	—	—	—	—
ROM 1767	3.0	3.1	0.9	1.7	2.6	13.0	3.6	12.5
ROM 1749	3.4	3.0	0.7	1.6	2.7	13.8	3.8	—
ZMHB MBI.2062	—	2.3	—	—	2.3	12.0	—	9.2
SMNS 66194	—	2.5	—	1.4	2.6	12.1	—	—
SMNS 66193	—	3.1	0.7	1.3	2.7	13.3	4.0	—
<i>Cratomastotermes wolfschweningeri</i> Bechly								
AMNH-1	4.4	4.0	0.9	2.5	5.0	15.0	4.9	16.6
ROM 1746	4.8	3.9	1.4	—	—	16.0	5.2	16.5
ROM 1755	—	—	—	—	—	15.5	—	15.5
ROM 1756	—	—	—	—	—	15.5	—	14.5
SMNS 66186	—	4.0	—	—	4.7	16.3	—	—
SMNS 66188	—	3.6	—	—	4.5	16.4	—	—
SMNS 66189	—	3.4	—	—	4.4	14.3	—	—
SMNS 66187	—	3.9	—	—	5.0	14.6	—	—
<i>Meiatermes araripena</i> Krishna								
AMNH-12	2.2	1.9	—	—	—	10.0	2.8	—
AMNH-15	2.0	—	—	—	—	9.8	2.7	8.0
AMNH-14	2.1	—	—	1.1	1.8	8.3	2.6	7.5
AMNH-21	2.0	1.9	—	—	1.8	—	3.1	7.1
AMNH-11	—	—	—	—	—	—	2.9	—
ROM 1774	2.2	1.9	—	—	—	—	2.8	—
AMNH-25	2.0	1.8	—	1.0	2.0	9.9	2.8	7.3
AMNH-10	—	—	—	—	—	9.6	2.8	—
ZMHB MBI.2061	—	2.0	—	—	2.0	9.6	—	8.1
SMNS 66192	—	1.4	—	—	1.5	8.8	—	—
SMNS 66191	—	1.9	—	—	1.9	9.5	—	—
<i>Meiatermes hariolus</i> , sp. nov.								
AMNH – 22	—	2.0	—	—	—	10.0	3.0	6.5
SMNS 66190	—	1.9	—	—	1.6	9.8	—	—
<i>Cratokalotermes santanensis</i> Bechly								
ROM-1764	1.6	1.6	0.4	0.4	0.8	6.8	2.1	5.6
SMNS 66195	1.6	1.7	0.3	0.4	1.2	8.1	2.5	7.0

DESCRIPTION: Head: Robust, rounded, posterior border apparently gently rounded, lateral borders convex, gently rounded. Right mandible apparently with two marginal teeth, second larger than first and separated from first by distance greater than its length; subsidiary tooth not evident (preservation poor, so not definitively absent); apical tooth longer than either marginal tooth. Left mandible with long apical tooth and at least one sharply pointed marginal tooth (remainder of mandibular margin poorly preserved so pres-

ence of a second marginal tooth cannot be determined with confidence, but apparently with a putative base for second marginal tooth). Antenna moniliform, with ≥ 32 antennal segments (left antenna of AMNH-SAI2 with 31 segments, right one with 32); first article (scape) slightly longer than combined lengths of second and third articles. Compound eye circular to semicircular, moderate-sized, separated from posterior border of head by more than $1.5 \times$ length of eye. Y-shaped coronal ecdysial line present. Ocelli

and fontanelle apparently absent. Thorax: Pronotum flat and subtrapezoidal, anterior margin about as wide as head, posteriorly narrower than head; anterior margin relatively straight, with anterolateral corners pronounced and acute; lateral margins relatively straight to slightly concave, converging posteriorly, posterolateral corners gently rounded, posterior margin relatively straight. All tarsi completely pentamerous; tibial spur formula possibly 3-3-3, tibial macrosetae ("spines") unapparent; arolium small (evident in some specimens). Forewing relatively long and broad; membrane with extensive network of coarse, raised reticulations throughout, especially on apical half of wing. Forewing scale quite large, with humeral (anterior) margin gently but distinctly arched, basal suture slightly convex, claval fissure (CuP) meeting basal suture before posterior margin, all veins originating within wing scale, slight reticulations within scale between posterior vein stems. Vein Sc simple, terminating on costal margin near one-third wing length; radial field relatively broad, gradually and gently expanding to encompass wing apex; R_1 simple, terminating on costal margin just beyond wing midlength; R_2 simple for most of its length, either simple or with a single branch near costal margin shortly before termination along costal margin, termination near apical third of wing length; R_s branching near wing midlength, branches with some secondary branches; course and branching of M not completely evident in preserved material, apparently terminating slightly posterior to wing apex and with a few branches in at least apical half of wing; course and branching of CuA not evident in preserved material. Abdomen: Abdominal styli not evident, possibly absent. Cerci short, trimerous, segments relatively elongate; distal segment approximately twice the length of either proximal segment, cylindrical in form.

COMMENTS: Fontes and Vulcano (1998) indicated that the holotype of *M. talicei* had apparently five cercal segments, although SEM revealed that only three segments are present in the two AMNH specimens where cerci are exposed (fig. 2C, D) (Fontes and Vulcano may have assumed that the basal-most article was actually three separate

articles). The presence of three cercomeres was cited by Bechly (2007), though none of the SMNS specimens have the cerci preserved. In some primitive termite species the number of cercal segments sometimes varies by one or two (e.g., *Archotermopsis wroughtoni* Desneux with 5–7 articles: Emerson, 1933), but this is uncommon and does not appear to be the situation for *M. talicei*. Scanning electron microscopy has revealed that the apical cercal segment can have some annulations, making it appear as if it were divided into several articles (fig. 2C). The apical cercal segment of *M. talicei* is also characteristically elongate relative to the preceding articles (present across all of the specimens, including the holotype). Cercal segmentation has particular phylogenetic significance (Engel, Grimaldi, and Krishna, in prep.), so it is important to scrutinize this feature in fossils.

Mariconitermes talicei Fontes and Vulcano Figures 1–4

Mariconitermes talicei Fontes and Vulcano, 1998: 270. By original designation. Bechly, 2007: 259.

DIAGNOSIS: As for the genus (see above).

HOLOTYPE: No. 5006 in the private collection of M. A. Vulcano, São Paulo, Brazil. Paratype no. 5007, *ibid*.

DESCRIPTION: Imago: The above description characterizes the genus and species (ICZN, 1999: Art. 13.4). To the generic account can be added the metrics provided in table 1.

MATERIAL EXAMINED: Six imagoes: AMNH Sa-I2, Sa-I5, ROM 1767, ROM 1749 (possibly ROM 1754, but poorly preserved), SMNS 66193, SMNS 66194 (SMNS 66198 labelled as ?*Mariconitermes* but is far smaller (forewing length 9.3 mm, vs. 12–14 mm, and too poorly preserved for definitive identification), ZMHB MBI.2062 [possibly ZMHB MBI.2209 and 2063, but poorly preserved]). Early Cretaceous (Aptian), Crato Formation, Brazil, Araripe Basin.

Genus *Cratomastotermes* Bechly

Cratomastotermes Bechly, 2007: 253. Type species: *M. wolfschweningeri* Bechly. By original designation. Monotypic.

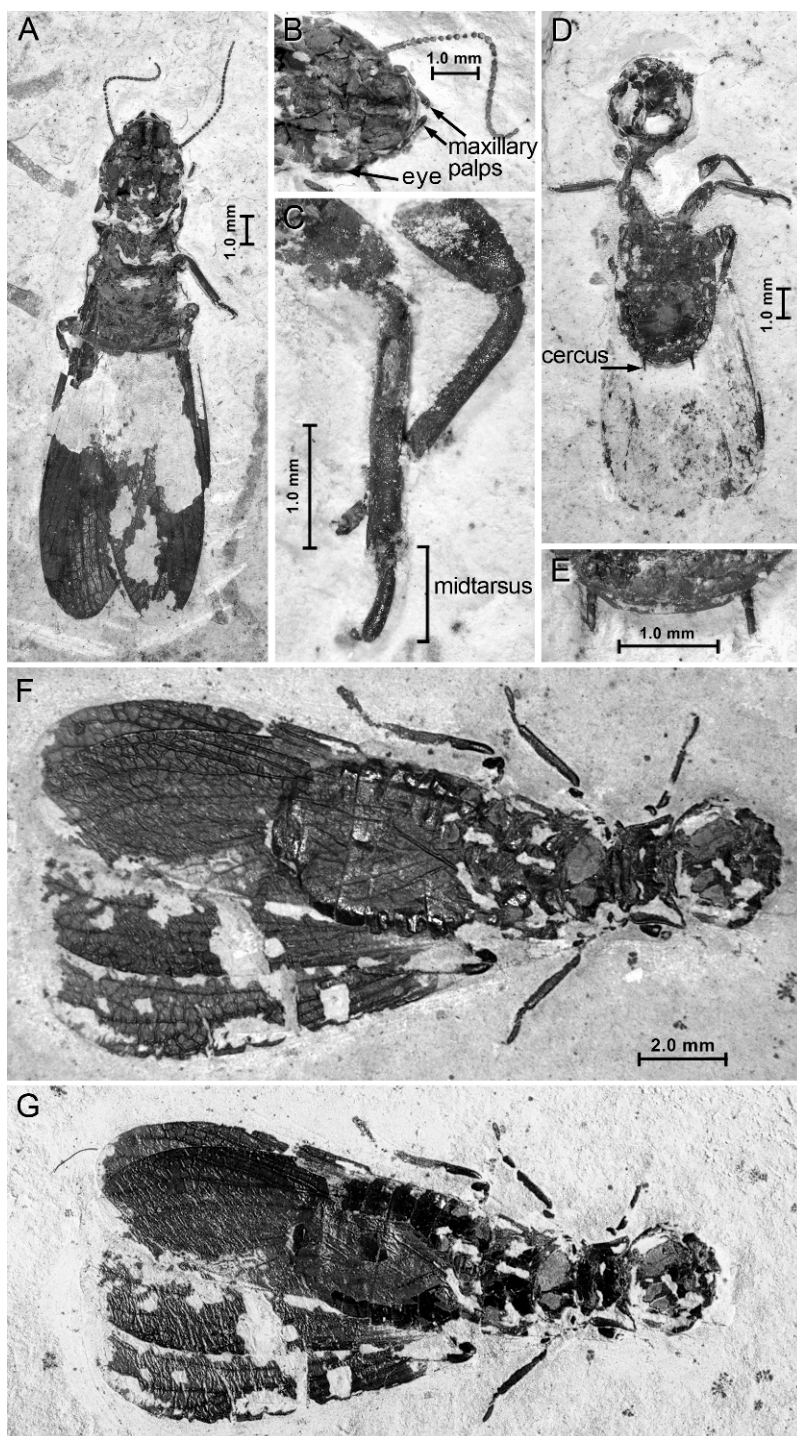


Fig. 1. *Mariconitermes talicei* Fontes and Vulcano. Photomicrographs of well-preserved specimens, with select details. A. AMNHSaI-2. B. AMNHSaI-2 head. C. AMNHSaI-5 legs. D. AMNHSaI-5. E. AMNHSaI-5 cerci. F. SMNS 66192. G. SMNS 66193.

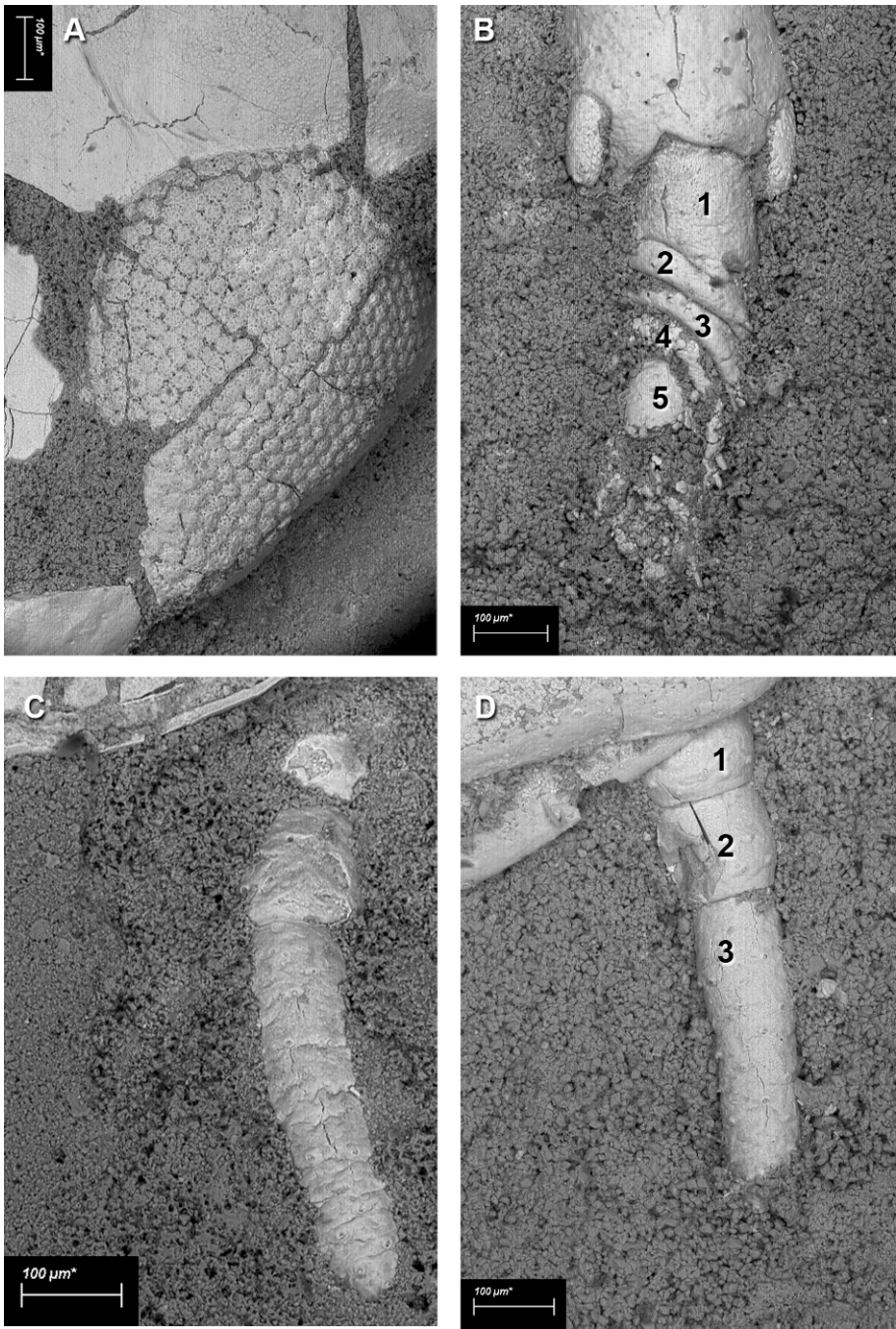
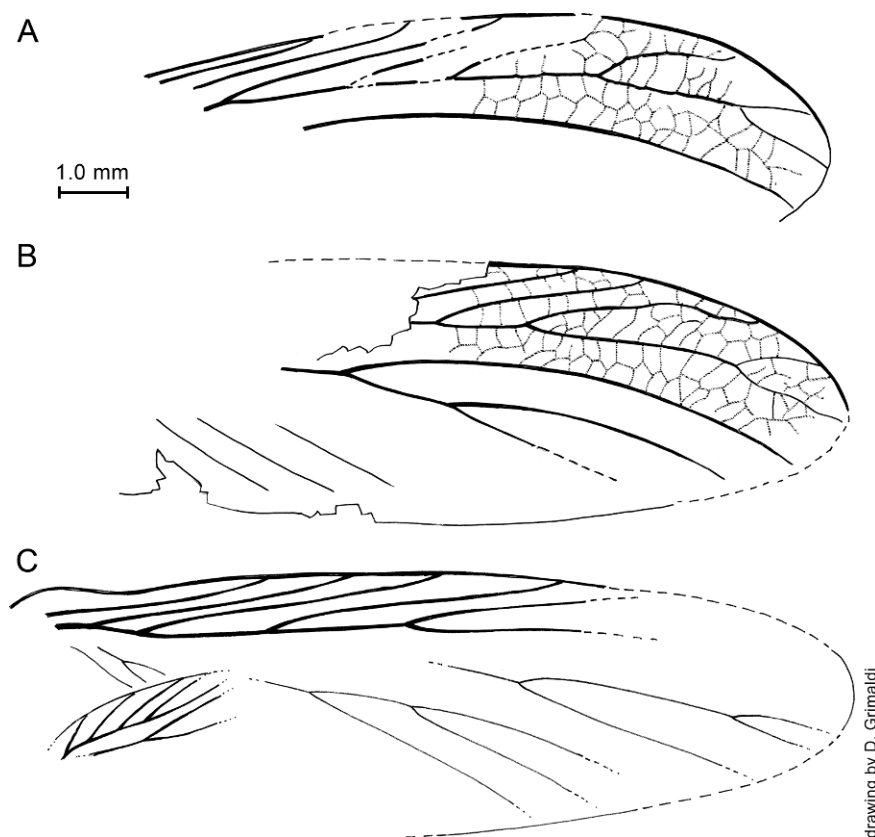


Fig. 2. *Mariconitermes talicei*, scanning electron micrographs of select details. A. Right eye and inner border, showing absence of ocellus. B. Mid left tarsus and tibial apex of AMNHSaI-5. C. Right cercus, AMNHSaI-3, showing fine annulations. D. Right cercus, AMNHSaI-5.



drawing by D. Grimaldi

Fig. 3. *Mariconitermes talicei*, variation in wing venation. **A.** SMNS 66193, left forewing. **B.** SMNS 66193 right forewing. **C.** SMNS 66194, right forewing (reticulations omitted, with anal margin of left forewing shown as preserved). All to the same scale.

DIAGNOSIS (REVISED): The largest and most robust of the Crato Formation termites: pronotum distinctly broader than head, length of pronotum approximately one-half the width, with strongly concave anterior margin and convex posterior margin; head not rounded, with large clypeus; tarsi pentamerous; wing with extensive, well-developed reticulation, like crossveins.

DESCRIPTION: Imago: Head robust, rounded, significantly longer than wide, lateral borders convex, gently rounded; clypeus and postclypeus large. Compound eye circular to semicircular, moderate-sized, separated from posterior border of head by distance slightly less than diameter of eye. Ocelli and fontanelle apparently absent. Y-shaped coronal ecdysial line not visible, if at all present. Pronotum

very broad, transverse, subrectangular, distinctly wider than head; length about one-half the width; anterior margin gently concave and wrapping around posterior portion of head; anterolateral corners pronounced, acute and rounded, slightly angled along border of head; lateral margins relatively straight and parallel; posterolateral corners rounded, posterior margin gently convex. Tibiae stout, width approximately $3 \times$ the width of tarsi; tibial macrosetae ("spines") not preserved/exposed. All tarsi completely pentamerous, tarsomeres 2–4 compact; tibial spur formula with 1-2-2 visible, but probably more; arolium small. Wings relatively long and broad, membrane (where evident) with well-developed reticulations throughout, which connect like crossveins to longitudinal veins; basal scale of

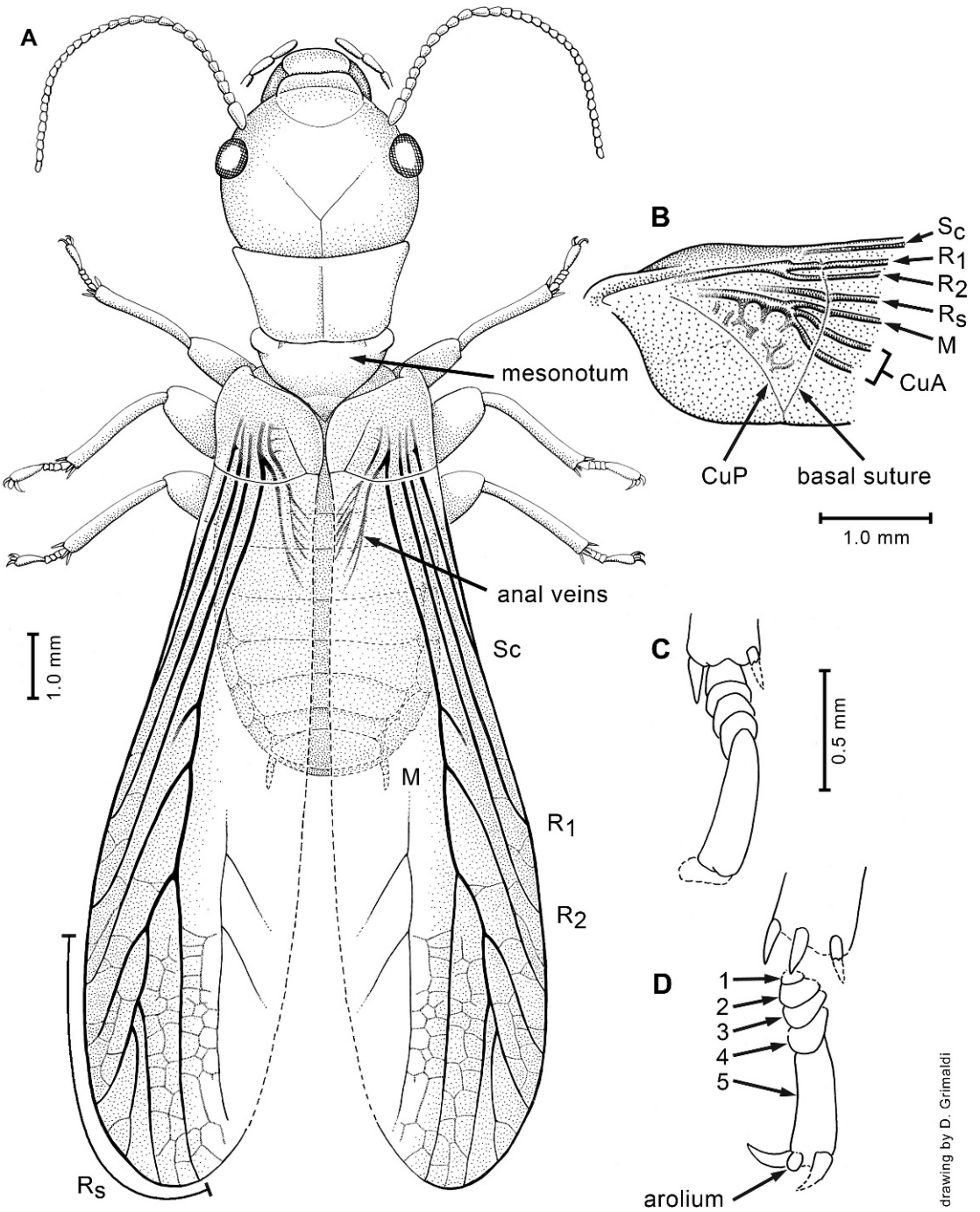


Fig. 4. *Mariconitermes talicei*. **A.** Reconstruction of habitus based on a series of specimens (hind wings not shown). **B.** Base of forewing of AMNHSaI-4. **C–D:** Details of tarsi. **C.** AMNHSaI-5. **D.** AMNHSaI-2.

drawing by D. Grimaldi

forewing possibly large, with humeral (anterior) margin arched; bases of fore- and hind wings well separated from each other, but overlap of basal scales difficult to discern; venation of forewing largely obscured (best seen in SMNS 66186, holotype), with at least four major Rs branches, last branch with series of five lightly sclerotized, parallel, inferior branches that connect to M. Apex of Rs field encompassing wing apex in fore- and hind wings. Hind wing with distinctive merging of Rs veins with inferior Rs vein near apex. Cerci and abdominal styli not evident (latter presumably absent, but terminal structures observable only in a single specimen).

COMMENTS: The body proportions of this termite suggest that *Cratomastotermes* is extremely basal in the Isoptera. In particular, the size of the pronotum is enormous, matched in size only by that of the recently described *Garmitermes succineus* in mid-Eocene Baltic amber (Engel et al., 2007b), and the pronota of both are similar in size to that in the most basal living termite, *Mastotermes darwiniensis* Froggat. Specifically, the ratio of the width of the head to the width of the pronotum in *Cratomastotermes* is 0.80 : 1, in *Garmitermes* it is 0.65 : 1, and in the one living species of *Mastotermes* and three extinct ones it is 0.7–0.9 (Krishna and Grimaldi, 1991: table 1). Because *Garmitermes succineus* is so well preserved, its phylogenetic position near the Mastotermitidae is well established. Also, all three genera are among the largest termites known. Unfortunately, phylogenetically important details of *Cratomastotermes* are not preserved, such as ocelli, bases of the wings, details of the forecoxae, and cercal segmentation. In the original description of the species (Bechly, 2007), the tarsomere number was unknown, but a “well-developed anal fan” was reported, which is a primitive, dictyopteran feature retained only in *Mastotermes*. Study of the SMNS material by the senior author revealed no anal fan, though the portion of the hind wing that is preserved is slightly broader than the forewing. Hopefully, continued excavations of Crato Formation insects will yield complete specimens of this fascinating species.

Cratomastotermes wolfschwenningeri Bechly
Figures 5–7

Cratomastotermes wolfschwenningeri Bechly, 2007: 254. By original designation.

DIAGNOSIS: As for the genus.

DESCRIPTION: Imago: The above diagnosis characterizes the genus and species (ICZN, 1999: Art. 13.4). To the generic diagnosis can be added the metrics provided in table 1.

HOLOTYPE: Imago: SMNS 66186, Paratypes SMNS 66187, 66188. Early Cretaceous (Aptian), Crato Formation, Brazil, Araripe Basin.

Other material examined: AMNH Sa-II, ROM 1746, 1755, 1756, SMNS 66189.

Genus *Meiatermes* Lacasa-Ruiz and
Martínez-Delclòs

Meiatermes Lacasa-Ruiz and Martínez-Delclòs, 1986: 56. Type species: *M. bertrani* Lacasa-Ruiz and Martínez-Delclòs, 1986, Early Cretaceous, Montsec, Spain. By original designation.
Nordestinatermes Martins-Neto et al., 2006: 129; Bechly, 2007: 256. NEW SYNONYMY.

DIAGNOSIS (REVISED): Imago: Head robust, rounded, posterior border apparently gently rounded, lateral borders convex, gently rounded. Antenna moniliform, with more than 23 segments, first article (scape) slightly longer than combined lengths of second and third articles or second through fourth articles. Compound eye semicircular, of moderate size, separated from posterior border of head by more than compound eye length. Ocelli and fontanelle absent. Y-shaped coronal ecdysial cleavage line present. Pronotum flat and transverse, slightly wider than head, anterior margin gently concave, with anterolateral corners acutely rounded, lateral margins gently convex and converging in posterior halves, posterolateral corners broadly rounded, posterior margin medially relatively straight (in *bertrani*) or weakly concave (in *araripena*). All tarsi completely pentamerous; tibial spur formula at least 2-2-2 (but probably at least 3-3-3 because of insufficient preservation), tibiae with subapical macroseta (“spines”); arolium minute. Forewing relatively long and broad, membrane with coarse reticulations throughout; scale quite large, with humeral (anterior) margin gently but

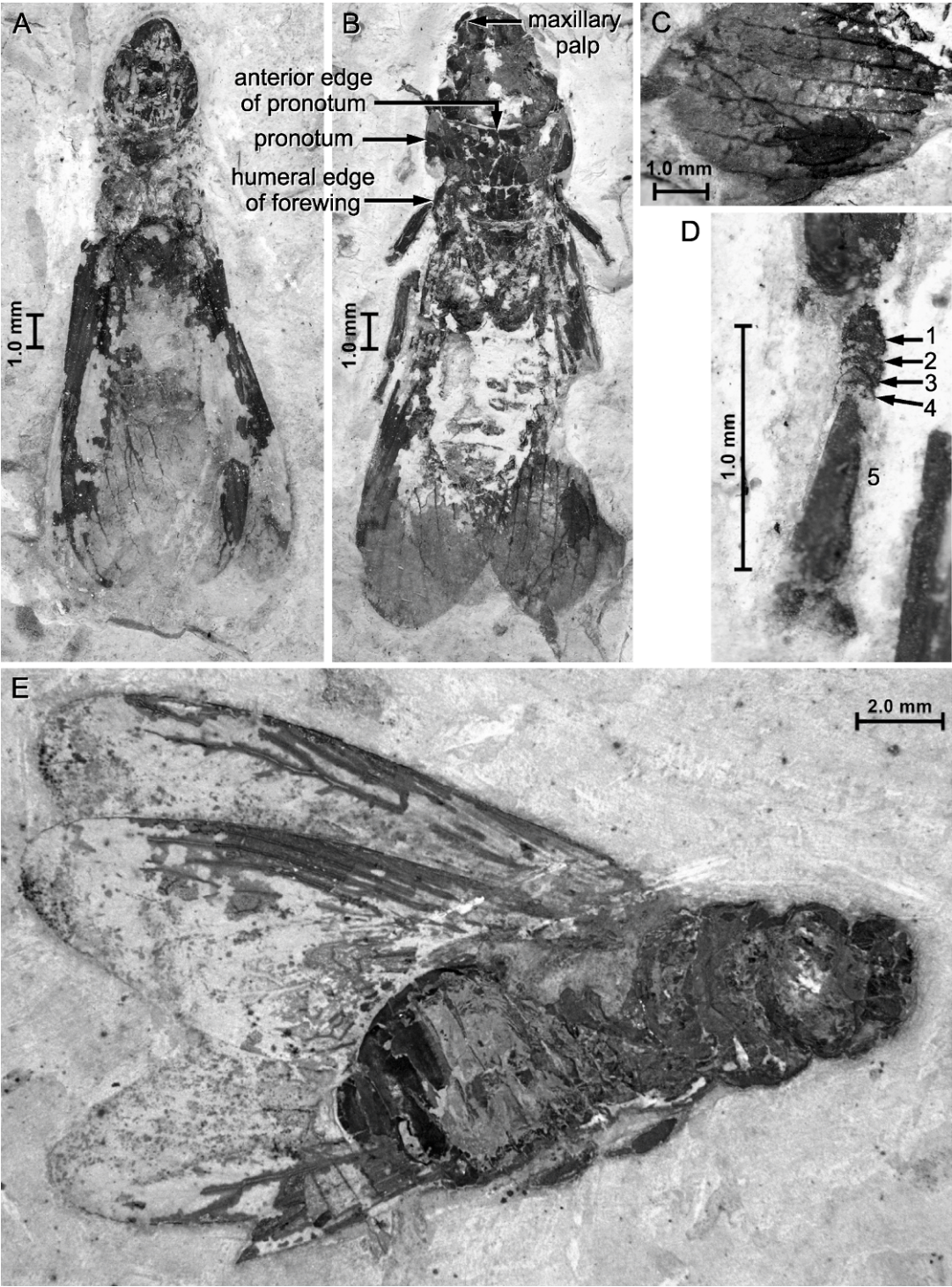


Fig. 5. *Cratomastotermes wolfschwenningeri* Bechly, photomicrographs. **A.** ROM 1746. **B.** AMNHSaI-1. **C.** Detail of wing apex, AMNHSaI-1. **D.** Detail of hind tarsus, AMNHSaI-1. **E.** Holotype, SMNS 66186.

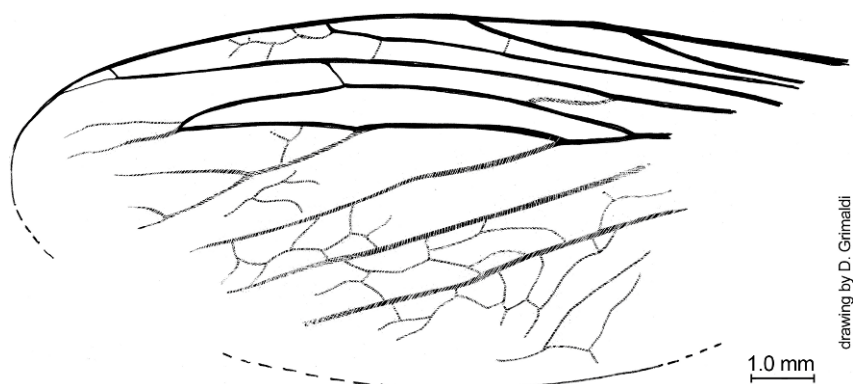


Fig. 6. *Cratomastotermes wolfschweningeri*, venation of left hind wing of SMNS 66186.

distinctly arched (not figured by Lacasa-Ruiz and Martínez-Delclòs, 1986, but present [personal obs.]), basal suture weakly and gently convex, claval fissure (CuP) apparently meeting posterior margin before basal suture, all veins originating within wing scale; Sc simple, terminating on costal margin near one-third (*araripena*) to one-half the wing length (*bertrani*, but some individuals closer to one-third); radial field relatively broad, width relatively consistent until about wing midpoint (*araripena*) or apical third (*bertrani*) then expanding to encompass wing apex; R_1 simple (*araripena*) or with a single branch (*bertrani*), terminating on costal margin prior to wing midlength (*araripena*) or just beyond (*bertrani*); R_2 present or absent, when present then simple along its length; Rs branching near wing midlength, branches with some secondary branches and with at least a couple of inferior branches encompassing wing apex; M branching near or just beyond wing midlength, with two primary branches, sometimes with secondary branches, terminating slightly posterior to wing apex; CuA with numerous branches along posterior margin of wing, some with secondary branches, terminating in apical half to third of wing length.

COMMENTS: We have here returned *araripena* Krishna to *Meiatermes*. Fontes and Vulcano (1998, 2004) transferred the species to *Cretatermes*, and Martins-Neto et al. (2006) classified the species in their new genus *Nordestinatermes*, but these transfers are unfounded. Venation of the monotypic genus

Cretatermes (*carpenteri* Emerson, 1967: Late Cretaceous, Labrador) is significantly reduced, with merely two branches to CuA terminating before or at the wing midlength. The pattern and numerous branches in *M. araripena* are nearly identical to that of *M. bertrani* Lacasa-Ruiz and Martínez-Delclòs from the Early Cretaceous of Spain, and in this respect it is important to note that these two large limestone Lagerstätte were not far removed from each other when they were deposited in the Early Cretaceous. Differences between *M. araripena* and *M. hariolus*, n.sp., are significant, namely, the former having three (vs. five) cercal segments, but there are no obvious venational differences. The apparent lack of abdominal styli in *M. araripena* could simply be due to the biased preservation of females (in modern species alates of this sex lack styli), and the preservation of a unique male for *M. hariolus*. Given the similar venation of these two species, and the incomplete nature of the two specimens of *M. hariolus*, it is probably prudent to avoid classifying them in different genera.

Meiatermes araripena Krishna, reinstated combination

Figures 8–11, 19, 20

Meiatermes araripena Krishna, 1990: 76.

Cretatermes araripena (Krishna); Fontes and Vulcano, 1998: 246.

Cretatermes pereirai Fontes and Vulcano, 1998: 265. NEW SYNONYMY.

Nordestinatermes araripena (Krishna); Martins-Neto et al., 2006: 130.

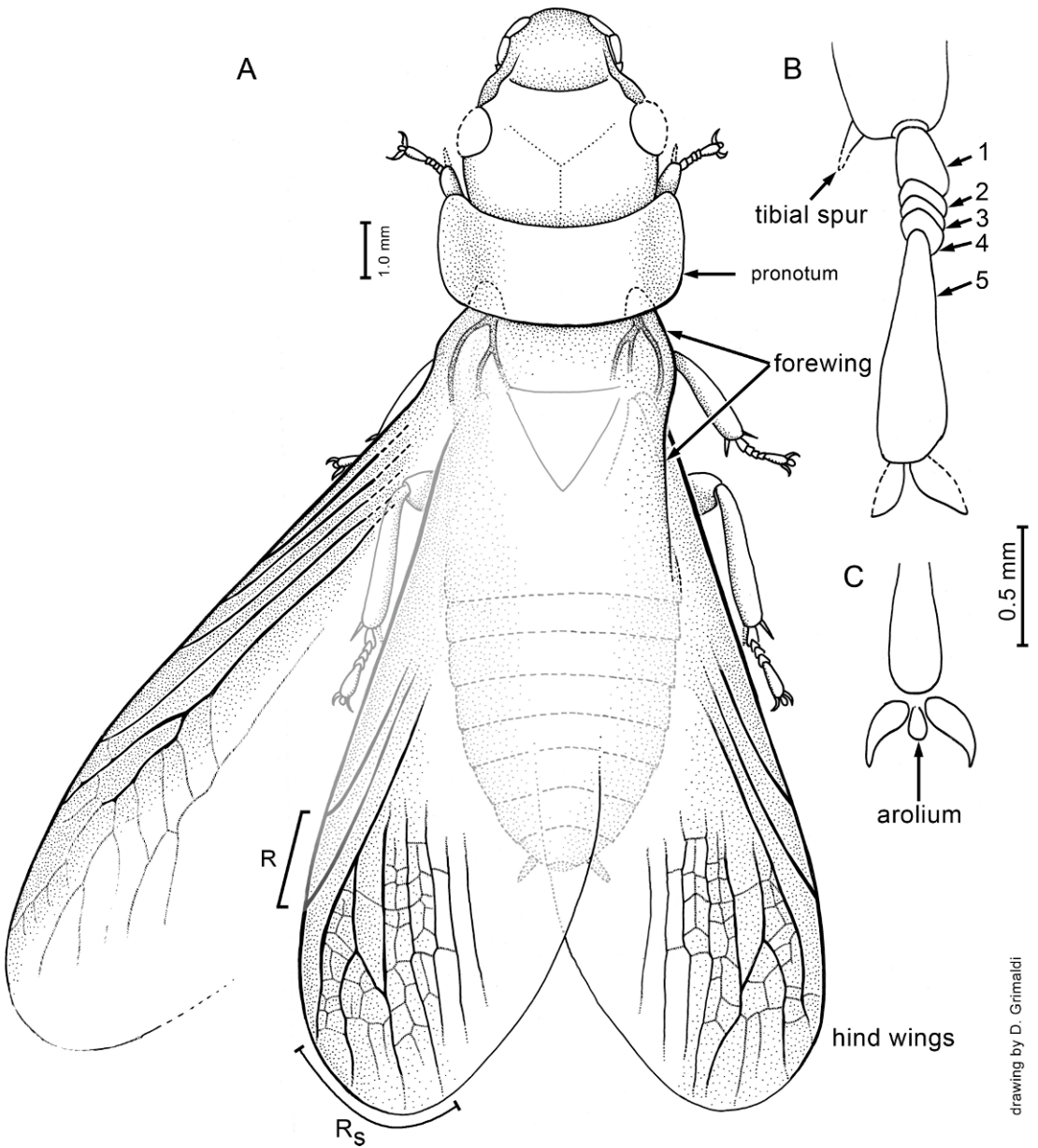


Fig. 7. *Cratomastotermes wolfschwenningeri*. **A**. Reconstruction. Presence of the Y-shaped epicranial ecdysial line and cerci are conjectural, based on their consistent presence in basal termites. **B**. Distal portion of left hind leg of AMNHSaI-1. **C**. Pretarsus and portion of distal tarsomere of left foreleg of same.

DIAGNOSIS: Distinguished from *M. bertrani* by *M. araripena* having the pronotal hind margin with a slight median concavity, and by its radial field encompassing less of the apical margin of the wing. Distinguished from *M. hariolus*, n.sp., as diagnosed below.

DESCRIPTION: Imago: Besides venational features discussed above, other features are the following: Abdominal styli not evident, possibly absent. Cerci short, trimerous (contra Krishna, 1990), basal segment transverse, length of second one slightly shorter than its

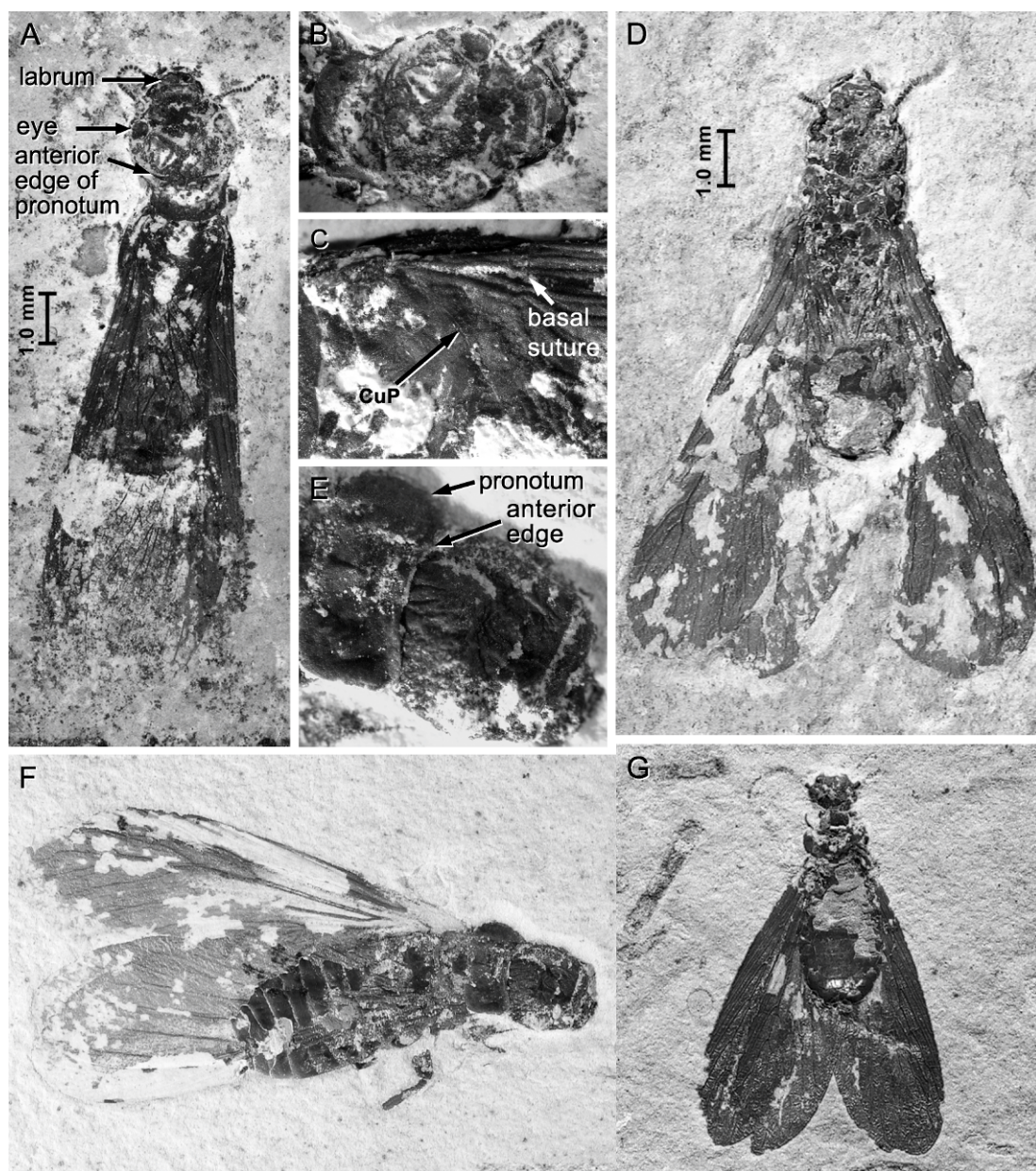


Fig. 8. *Meiatermes araripena* Krishna. Photomicrographs of well-preserved specimens. A. AMNHSAI-1749. B. AMNHSAI-1749 head. C. AMNHSAI-1749 wing base. D. ROM 1746. E. ZMHB 2061 head. F. ZMHB 2061. G. SMNS 66192.

width; distal cercal segment distinctly longer than preceding segments, $2.5 \times$ the length of second segment, conical in form. Metrics provided in table 1. Otherwise, as described for the genus.

MATERIAL EXAMINED: Holotype imago, AMNH 43902, two paratype imagoes (AMNH 43901–43903), and 28 additional, newly studied imagoes (AMNH Sa-I7, 8, 11, 12, 14, 15, 16, 21, 25, 27, 28, 29, 30; ROM

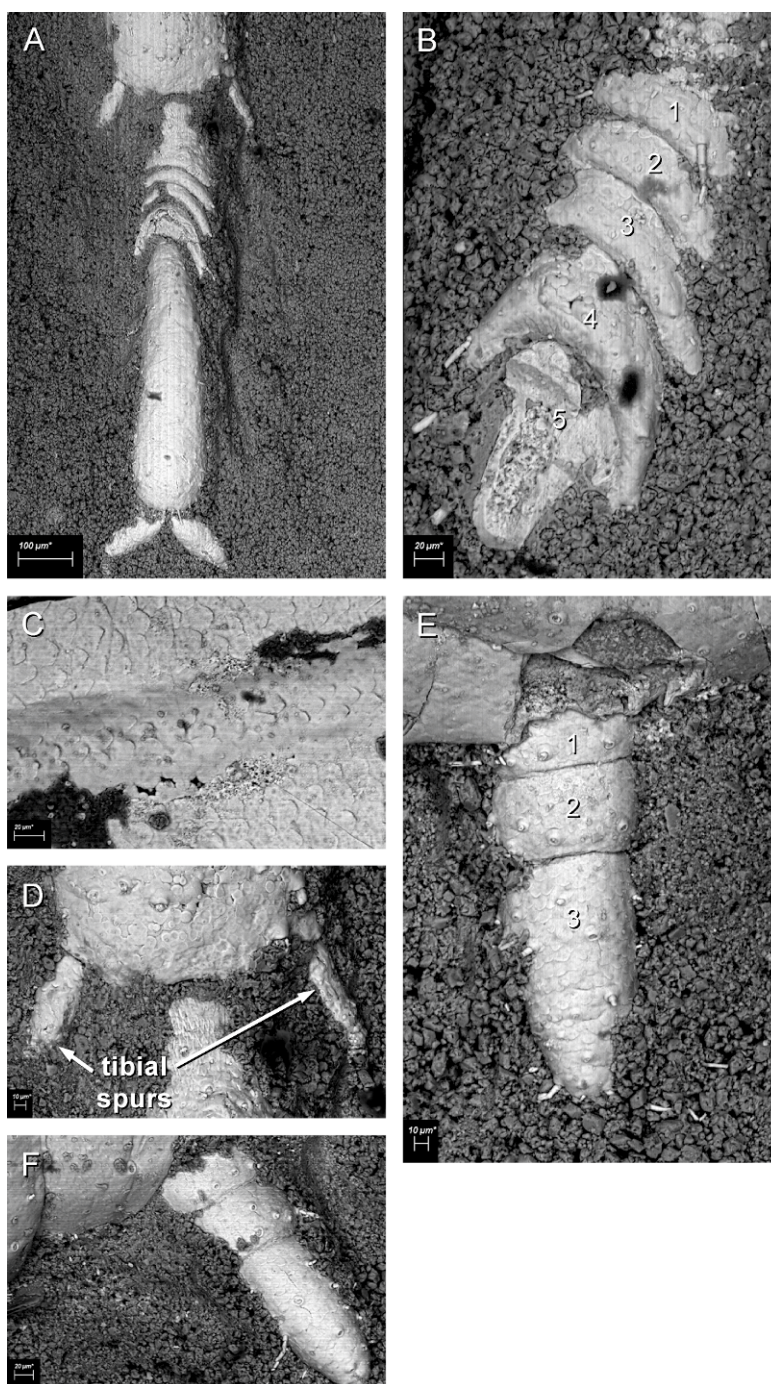
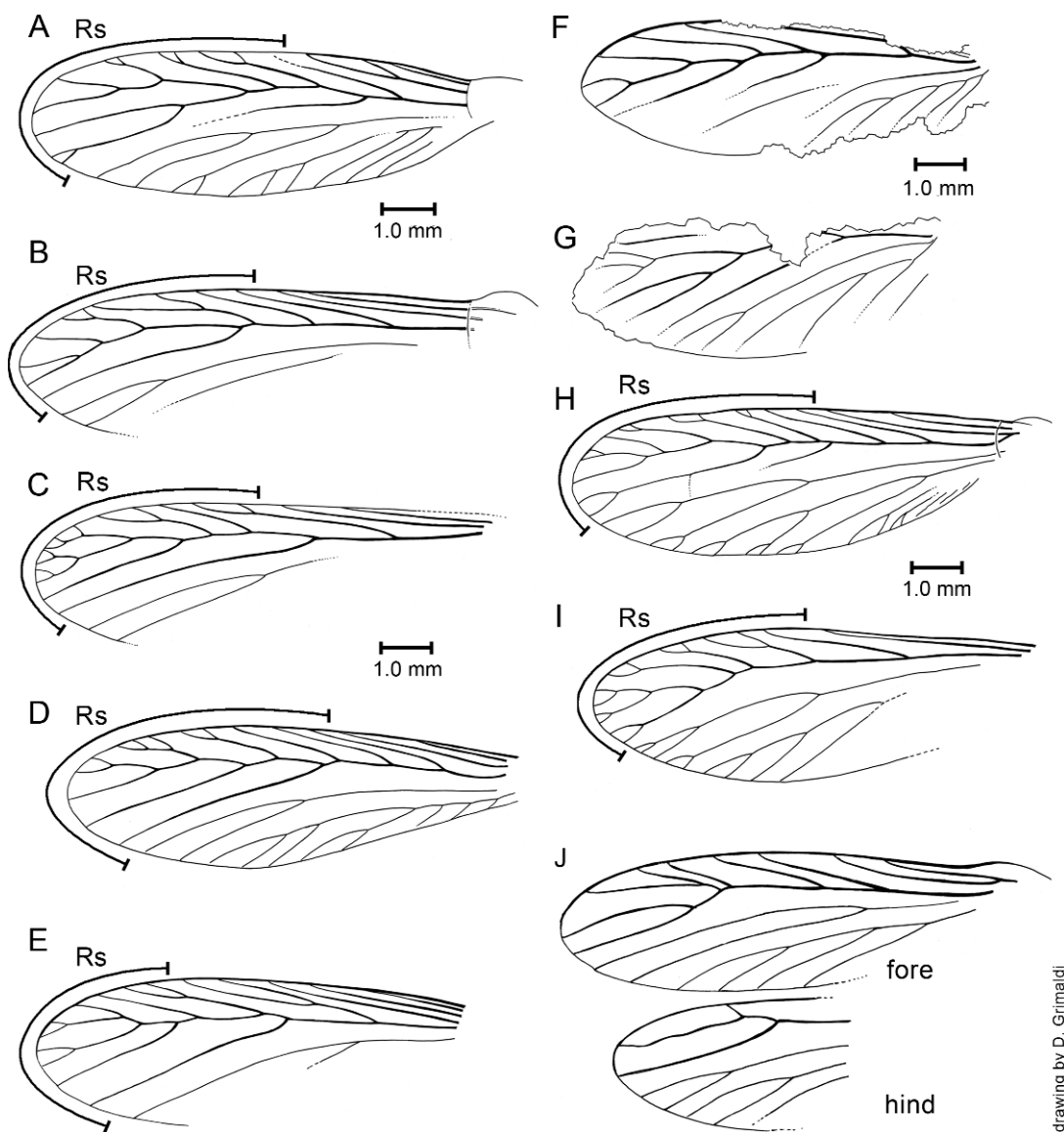


Fig. 9. *Meiatermes araripena*. Scanning electron micrographs of select details of AMNHSaI-13. **A, B, D:** Distal portions of legs. **A.** Mid left tarsus and tibial apex (dorsal view). **B.** Portion of mid right tarsus (most of distal tarsomere is lost). **C.** Detail of wing surface, showing faintly imbricate microsculpture. **D.** Midtibial apical spurs (serrations are not discernable). **E, F:** Cerci (E, right; F, left).



drawing by D. Grimaldi

Fig. 10. Intraspecific variation in wing venation in *Meiatermes araripena*, all to the same scale and arranged in the same orientation to facilitate comparisons. **A.** AMNHSaI-10, left forewing; **B.** AMNHSaI-12, right forewing; **C.** ROM 1762, right forewing; **D.** AMNHSaI-23, left forewing; **E.** AMNHSaI-16, left forewing; **F–G:** AMNHSaI-20 (F, forewing; G, hind wing); **H, I:** AMNHSaI-11 (H, right forewing; I, right hind wing). **J:** SMNS 66192, fore- and hind wings.

1747a, b, 1748a, 1750, 1751a, b, 1759, 1761, 1762, 1765, 1766, 1770, 1774, 1777; SMNS 66191, 66192; ZMHB MBI.2061). All Early Cretaceous (Aptian), Crato Formation, Brazil.

COMMENTS: *Cretatermes perarai* Fontes and Vulcano appears to be a synonym of *M.*

araripena, based on the similar body size, wing length, pronotal shape (i.e., figs. 29 and 30 in Fontes and Vulcano, 1998), number of tarsomeres, and venation. Unfortunately, none of the three specimens were preserved well enough that each one could be measured for

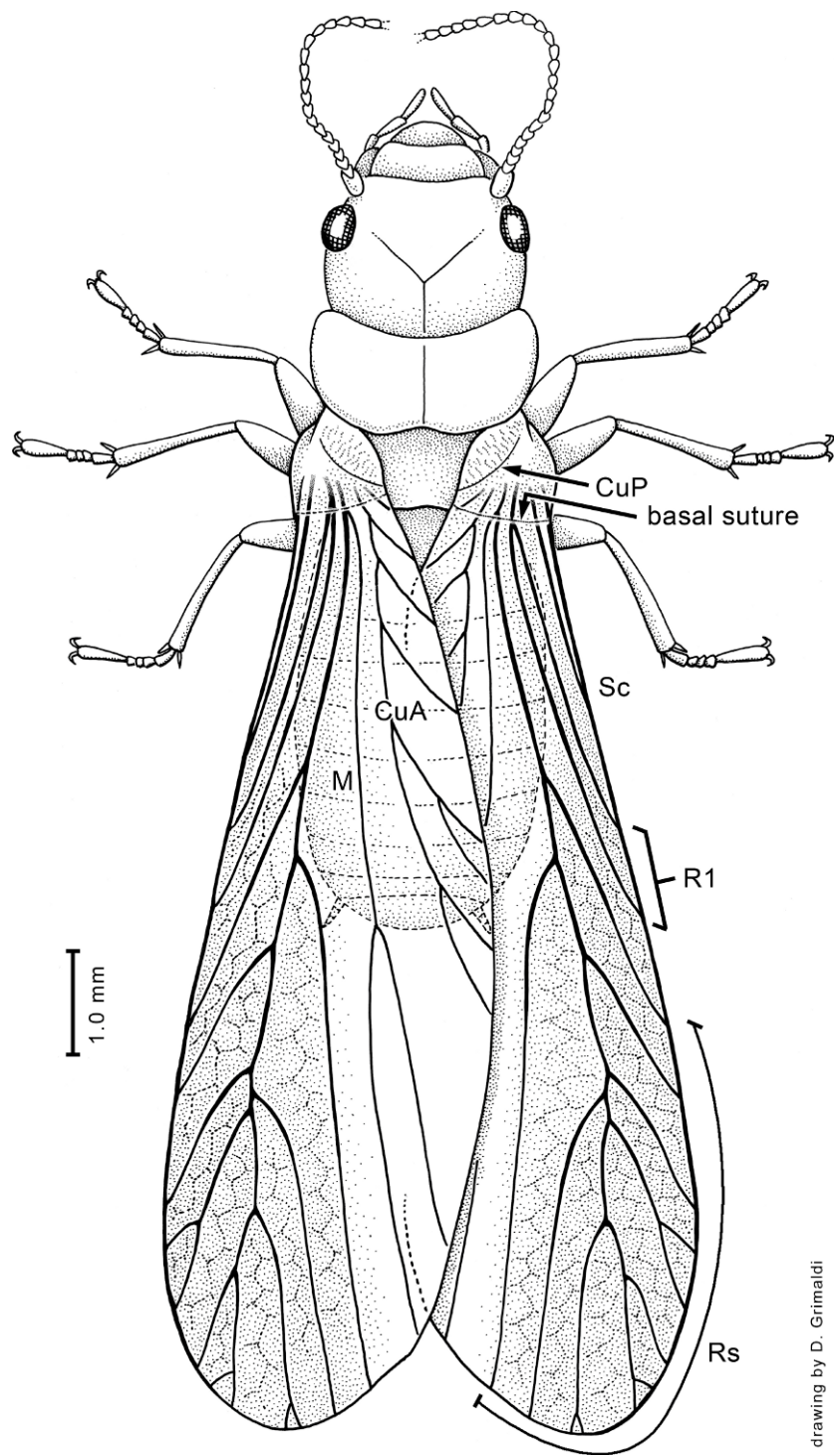


Fig. 11. *Meiatermes araripena*. Reconstructed habitus, as based on a series of specimens. Venation is generalized to accommodate the variation seen in this species (see fig. 10).

head width, pronotal length, and wing length. As discussed below (under *nomina dubia*), we suspect that the three new genera and species proposed by Martins-Neto et al. (2006) are synonyms of *M. araripena*, but unfortunately the descriptions do not allow definitive identification.

Meiatermes hariolus Grimaldi, new species
Figures 12, 13

Nordestinatermes araripena: Bechly, 2007: 255, fig. 11.25c, d.

DIAGNOSIS: The new species can be distinguished from *M. araripena* most readily by the five cercal articles (three in *araripena*, although the distal segment in *araripena* can appear subdivided and be easily misinterpreted as four total). Wing venation with four to five dorsal branches of Rs.

DESCRIPTION: Imago: Body length slightly smaller than *M. araripena* (6.5 mm, vs. 7.5–8.5 mm). Venation without long ventral branch of Rs (arising from near middle of wing in *araripena*, and occasionally absent); four to five (vs. five) dorsal branches of Rs. Abdominal styli present (male?); cerci short, pentamerous, of approximately same length and shape, individual lengths subequal to individual widths. Metrics provided in table 1.

HOLOTYPE: Imago, AMNH Sa-I22; Early Cretaceous (Aptian), Crato Formation, Brazil. Deposited in the Division of Invertebrate Zoology, American Museum of Natural History. Paratype: SMNS 66190. The holotype specimen is ventrally exposed; the pronotum is obscured, though its exposed lateral edges suggest a width equal to that of the head. Forelegs are lost; coxae, trochanters, and femora of mid- and hind legs are preserved; all tarsi are lost. Forewing is well preserved, but veins preserved only as impressions and must be observed with a raking light. Paratype is well preserved, with details of cerci and tarsi observable, and costal portions of fore- and hind wings. Paratype with dorsal surface of head and pronotum largely crushed.

ETYMOLOGY: The specific epithet is Latin for “prophet”.

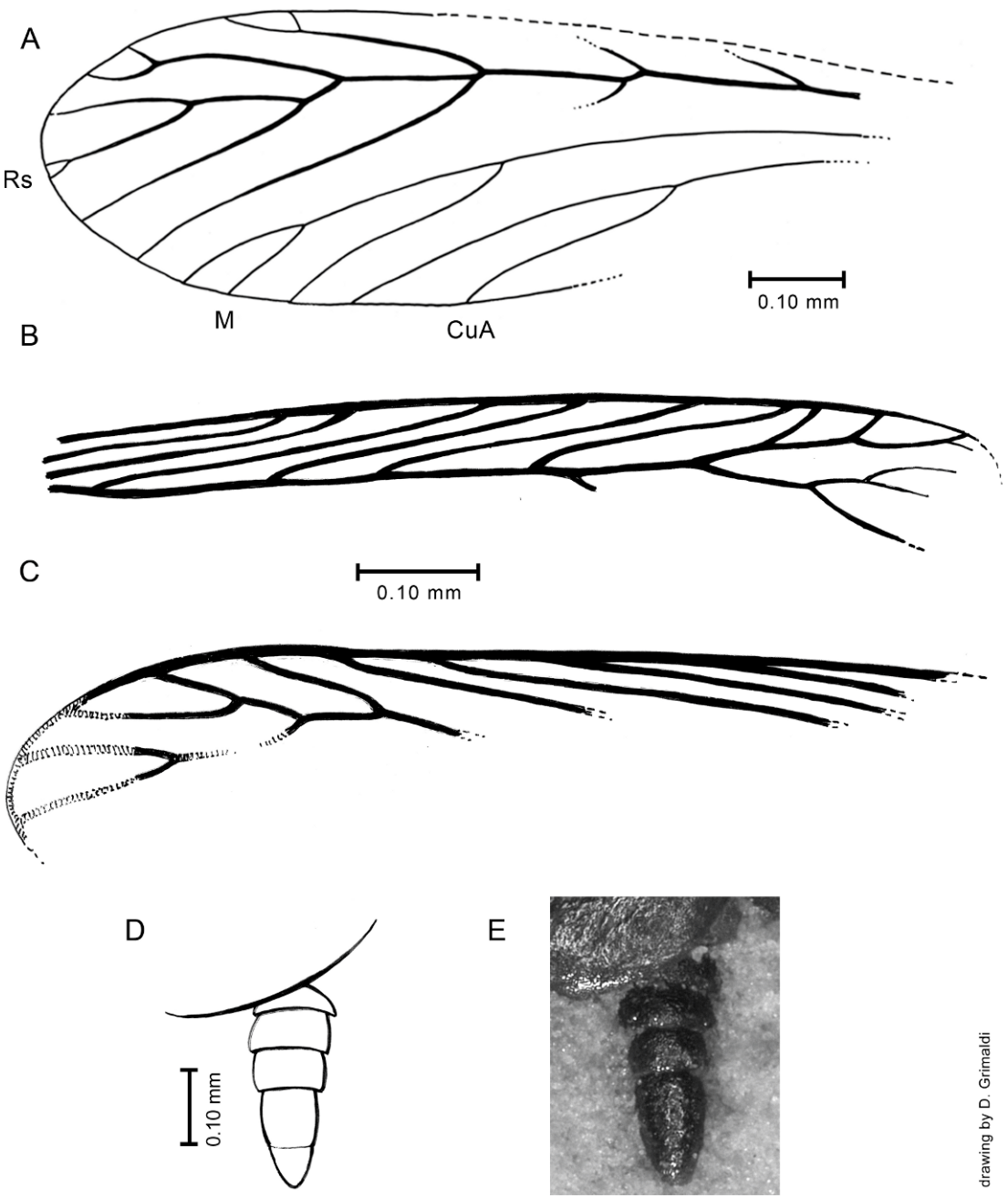
COMMENTS: It is critical when observing the cerci to use an oblique, raking light

positioned at one end, which is directed along the axis of the cercus, in order to observe the faint suture between cercomeres four and five (i.e., fig. 13, cf: fig. 9 E, F). The photomicrograph of the cercus in Bechly (2007: 255: fig. 11.25d) indicates four cercomeres of SMNS 66190, but when this specimen was observed by the senior author using the lighting described above, the faint, distalmost suture was apparent.

Genus *Cratokalotermes* Bechly

Cratokalotermes Bechly, 2007: 260. Type species: *Cratokalotermes santanensis* Bechly, 2007. By original designation.

DIAGNOSIS (REVISED): Imago: Head ovoid, posterior border apparently gently rounded, lateral borders greatly convex. Antenna moniliform (total number of articles unknown), scape apparently short, scarcely longer than following article. Compound eye circular or semicircular, moderate-sized, separated from posterior border of head by slightly more than compound eye length. Ocelli, fontanelle, and Y-shaped coronal ecdysial line absent. Pronotum flat and subtrapezoidal, distinctly narrower than head ($0.6 \times$ head width); anterior margin relatively straight, with anterolateral corners broadly rounded but not pronounced, lateral margins gently curved and slightly converging posteriorly in posterior halves, posterolateral margins broadly rounded, posterior margin relatively straight medially. Forewing relatively long and broad; basal scale relatively large, with apices of basal suture and CuP not converged; CuP relatively straight (not strongly arched); radial field narrow, confined to costal third of wing, terminating prior to the wing apex; R_1 simple, terminating on costal margin near wing base; five superior branches of Rs in forewing, most are simple (fewer branches in hind wing). Area between C and Rs significantly sclerotized. M with basal branch near midlength of forewing, two shorter branches in distal third of wing, which reach to wing apex (similar in hind wing). Seven parallel branches of Cu in forewing (hind wing obscured). Abdomen broad, well sclerotized, apical margin of each tergite with row of minute striae. Cerci short, apex conical, with



drawing by D. Grimaldi

Fig. 12. *Meiatermes hariolus*, n. sp. A. Wing, AMNH SaI-22. B-C. Wings, SMNS 66190. D. Drawing of cercus of SMNS 66190. E. Photomicrograph, same (to same scale).

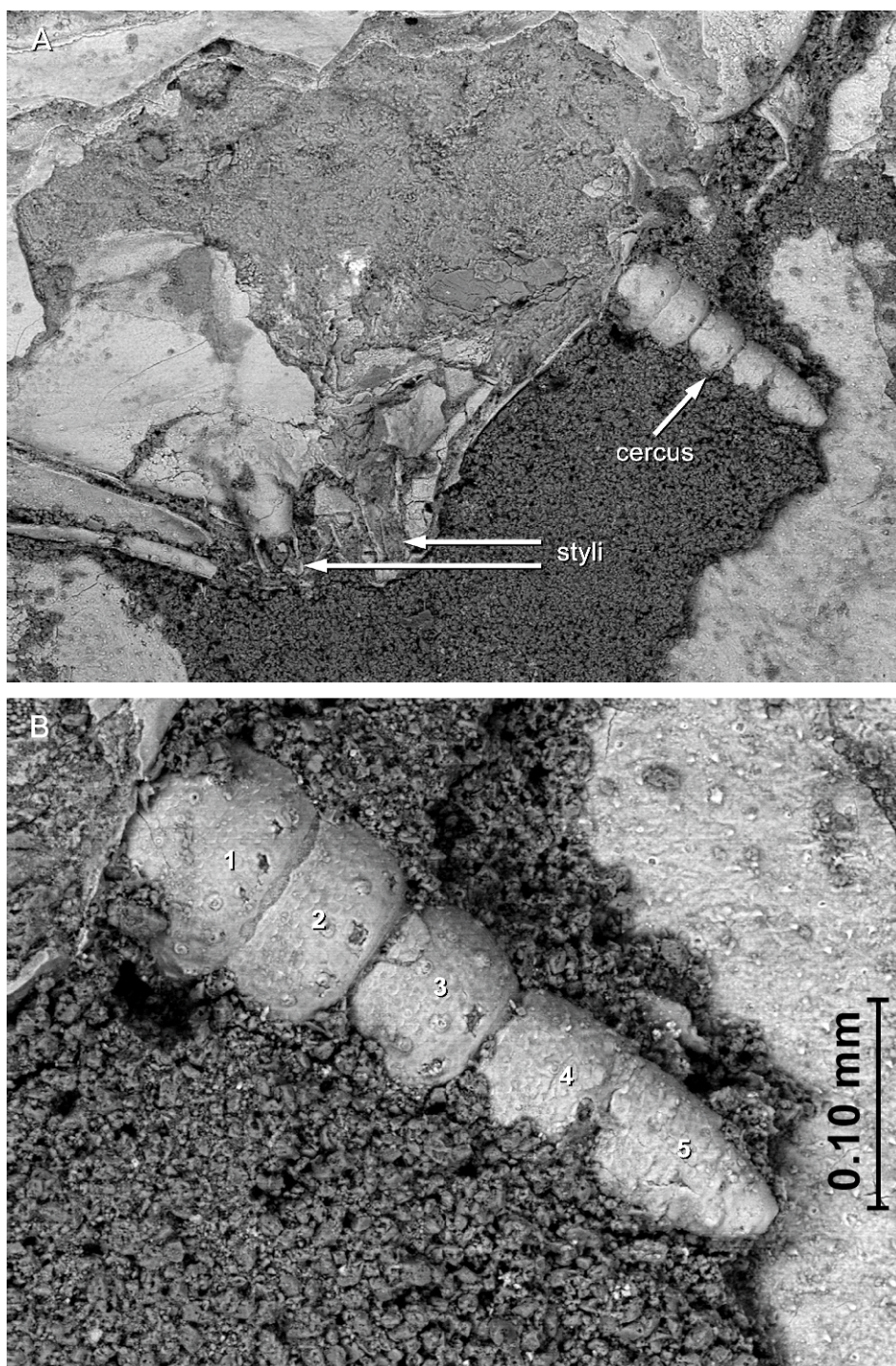


Fig. 13. *Meiatermes hariolus*, n. sp. Scanning electron micrographs of holotype, AMNHSAI-22. **A.** Abdominal apex, showing right cercus and bases of styli (broken off distally). **B.** Detail of right cercus showing the five cercomeres.

two segments; cuticular microsculpture with coarse imbrication.

Cratokalotermes santanensis Bechly

Figures 14–16

Cratokalotermes santanensis Bechly, 2007: 261.

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: Imago: The above diagnosis characterizes the genus and species (ICZN, 1999: Art. 13.4). To the generic diagnosis can be added the metrics provided in table 1.

HOLOTYPE: Imago, SMNS 66195. Other material examined: ROM 1764. Both specimens from Early Cretaceous (Aptian), Crato Formation, Brazil.

COMMENTS: The head, pronotum, and cerci of the ROM specimen are very well preserved; this specimen has just portions of the costal half of the forewing preserved. The SMNS specimen (holotype) has beautifully preserved fore- and hind wings (including the basal scale), as well as the thorax and cerci, but the head and pronotum are not well preserved. The reconstruction (fig. 16) is thus combined from the best-preserved features of both specimens.

Based on the apparent lack of a coronal ecdysial line, the rounded head shape, a two-segmented cercus, and the relatively small pronotum, this species appears to be the most derived in the Crato fauna and from the Early Cretaceous in general. Kalotermitidae and all more recently derived families of Isoptera have only two cercomeres. *Cratokalotermes* shares with living Kalotermitidae the crowded radial field and long cubital field (extends to near the apex of the wing). *Cratokalotermes* differs from living kalotermitids by the wing membrane lacking small nodules/pimples, and by having a larger field of M veins (specifically, the apices of M veins encompass the wing tip, and there is a basal fork of M near the distal third of the wing). These features suggest a possible basal position in Kalotermitidae or else a stem group to this family or the kalotermitid + higher termite lineage. Unfortunately, the two specimens are each missing the legs (i.e., tarsomere number), which compromises an estimate of its phylogenetic position.

Genus *Cretorhinotermes* Bechly

Figure 17

Cretorhinotermes Bechly, 2007: 262. Type species: *C. novaolindense* Bechly, 2007: 262. By original designation. Monotypic.

DIAGNOSIS: Very partial remains with primarily just the apical half of the forewing: Radial field narrow, apparently simple (with few superior branches), Rs comprised of at least 4 long branches, most ventral one of which nearly extends to wing apex. M field large, extending from wing apex to anal margin, with series of at least nine long, parallel branches. Longitudinal veins with extensive, well-developed, and coarse reticulations among them.

COMMENTS: Without doubt, this genus does not belong to the Rhinotermitidae as originally classified (Bechly, 2007), though the M field was probably originally interpreted as Cu. One definitive rhinotermitid exists from the Cretaceous, preserved in 100 myo amber from Myanmar (Krishna and Grimaldi, 2003), and it possesses most of the features of modern Rhinotermitidae: a fontanelle, four tarsomeres, a simple R vein, a simple M, and a pectinate series of Cu veins with very sparse and faint reticulations between them. Unfortunately, the bodies of both Crato specimens are very poorly preserved (details of the head and tarsi are not preserved), and in light of such limited features we can only suggest that this species belongs to a basal grade of termites near Hodotermitidae and Termopsidae s.l.

NOMINA DUBIA

Three new genera and species were proposed by Martins-Neto et al. (2006), all taxa of which must unfortunately be considered *nomina dubia* and possibly synonyms of the most common and variable species, *Meiatermes araripena* Krishna. These taxa are the following:

Caatingatermes megacephalus Martins-Neto et al., 2006: 128.

Araripetermes nativa Martins-Neto et al., 2006: 129. *Nomen incorrectum: recte nativus.*

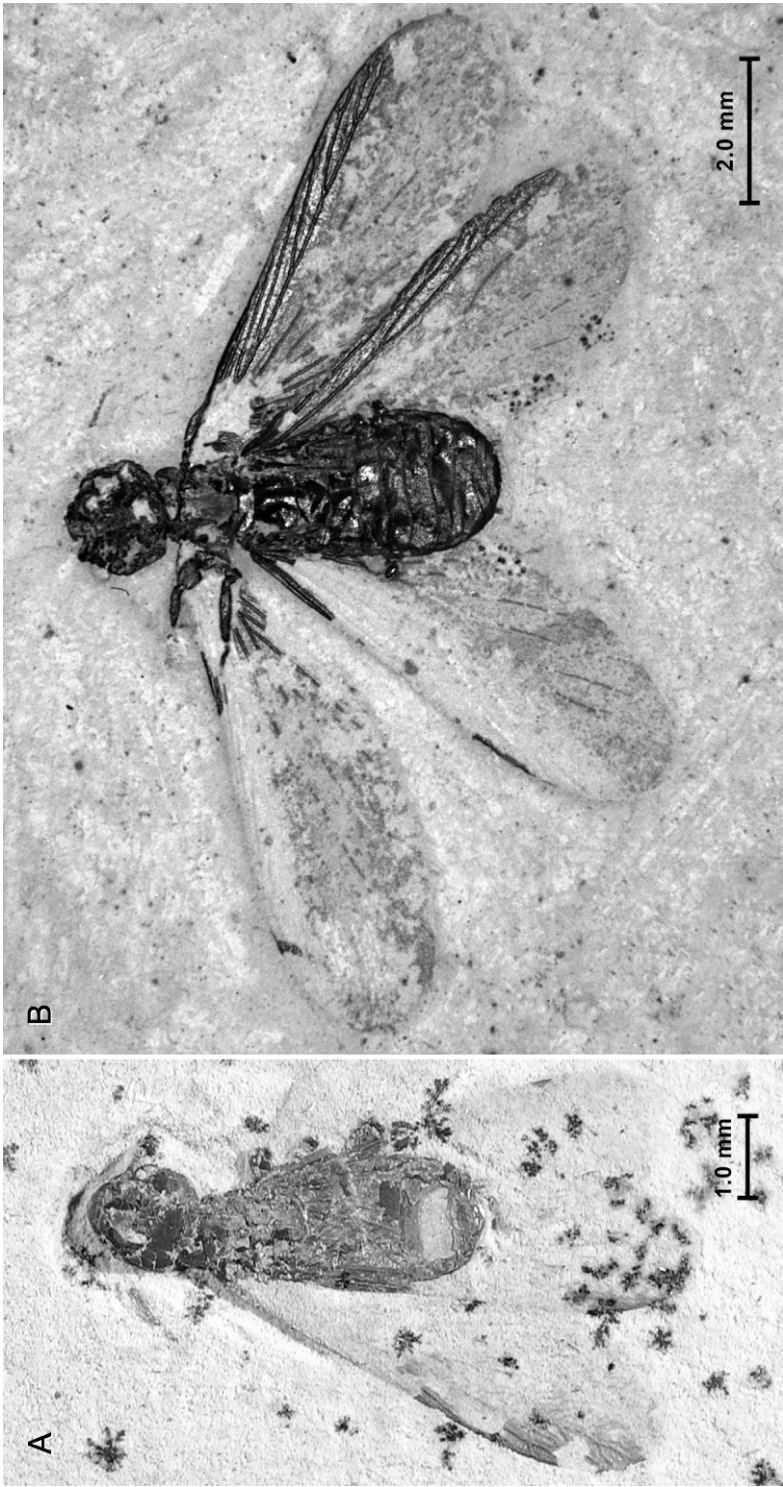


Fig. 14. *Cratokalotermea santanensis* Bechly, photomicrographs. A. ROM 1764. B. Holotype, SMNS 66195.

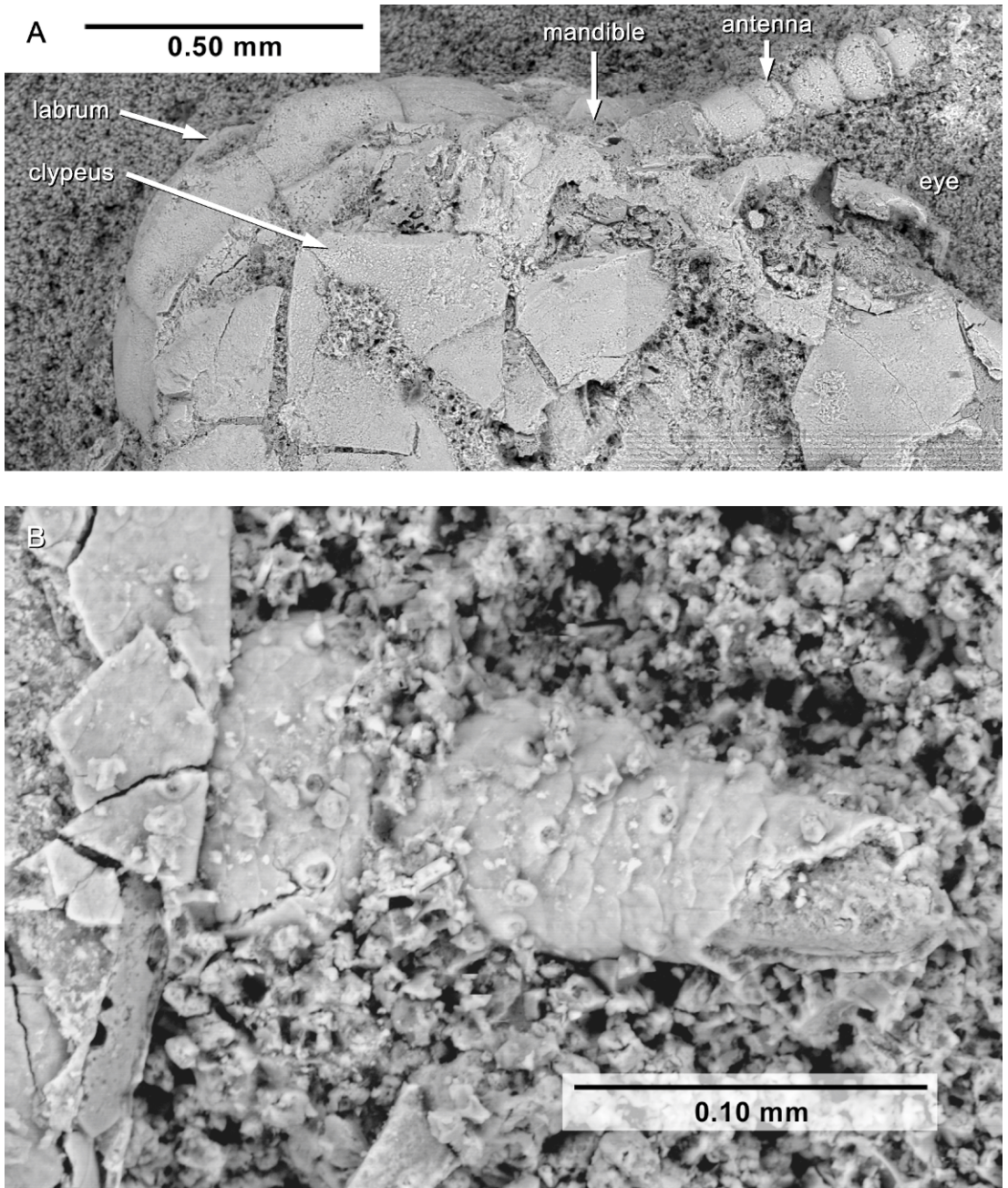


Fig. 15. *Cratokalotermees santanensis*. Scanning electronmicrographs of ROM 1764. **A.** Anterior portion of head (composite of several images). **B.** Detail of right cercus, showing the coarsely imbricate cuticular microsculpture of the distal segment. Cuticle on the tip is lost, but the cercus appears to be two-segmented.

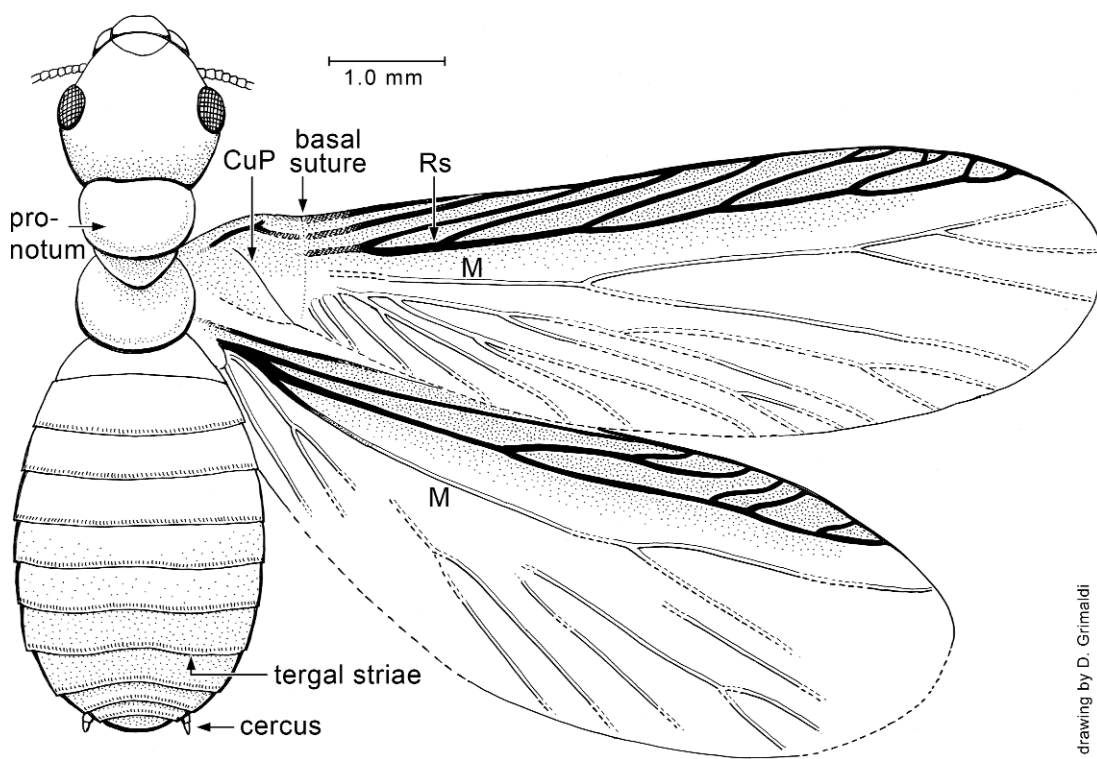


Fig. 16. *Cratokaloterme santanensis*, reconstruction. Venation and abdomen are largely based on the holotype (SMNS 66195); head and pronotum on ROM 1764; the two-segmented cerci are preserved in both specimens.

Nordestinatermes obesa Martins-Neto et al., 2006: 130. *Nomen incorrectum: recte obesus*.

The diagnoses and descriptions of these taxa are brief and superficial, providing very few details of diagnostically important characters for termites. Moreover, there is no mention of specimens examined other than the holotypes, so it must be assumed that the three new species and genera are based entirely on three specimens—even though series are generally required to diagnosis species in isopteran systematics. For example, the four-segmented cerci reported for “*Araripetermes nativa*” could easily have been misinterpreted because of preservational imperfections in this structure (see above, fig. 2C). Venation of “*Araripetermes nativa*” and “*Nordestinatermes obesa*”, if properly illustrated, is too incomplete for diagnostic purposes. Also, there are

gross contradictions within the descriptions. For example, illustrations of the right and left forewing venation of the same (holotype) specimen of “*Araripetermes nativa*” hardly correspond (Martins-Neto et al., 2006: fig. 1d, f), and even the fore- and hind wing venation of the same “*Caatingatermes megacephala*” specimen do not correspond (ibid., fig. 1a, b), but the forewing venation of this species (his fig. 1a, which ignores the obviously incorrect crossveins and large series of radial branches anterior to Rs) falls within the variation seen in *M. araripena* (see fig. 10, specifically 10D, E). Lastly, the few measurements that are provided (if indeed correct) fall within the proportions of the variable species *Meiatermes araripena*. The holotype specimens are in the “Martins-Neto Collection, belonging to the Sociedade Brasileira de Paleoartropodologia,” and were unavailable for loan. The publication of these *nomina dubia* exemplifies the

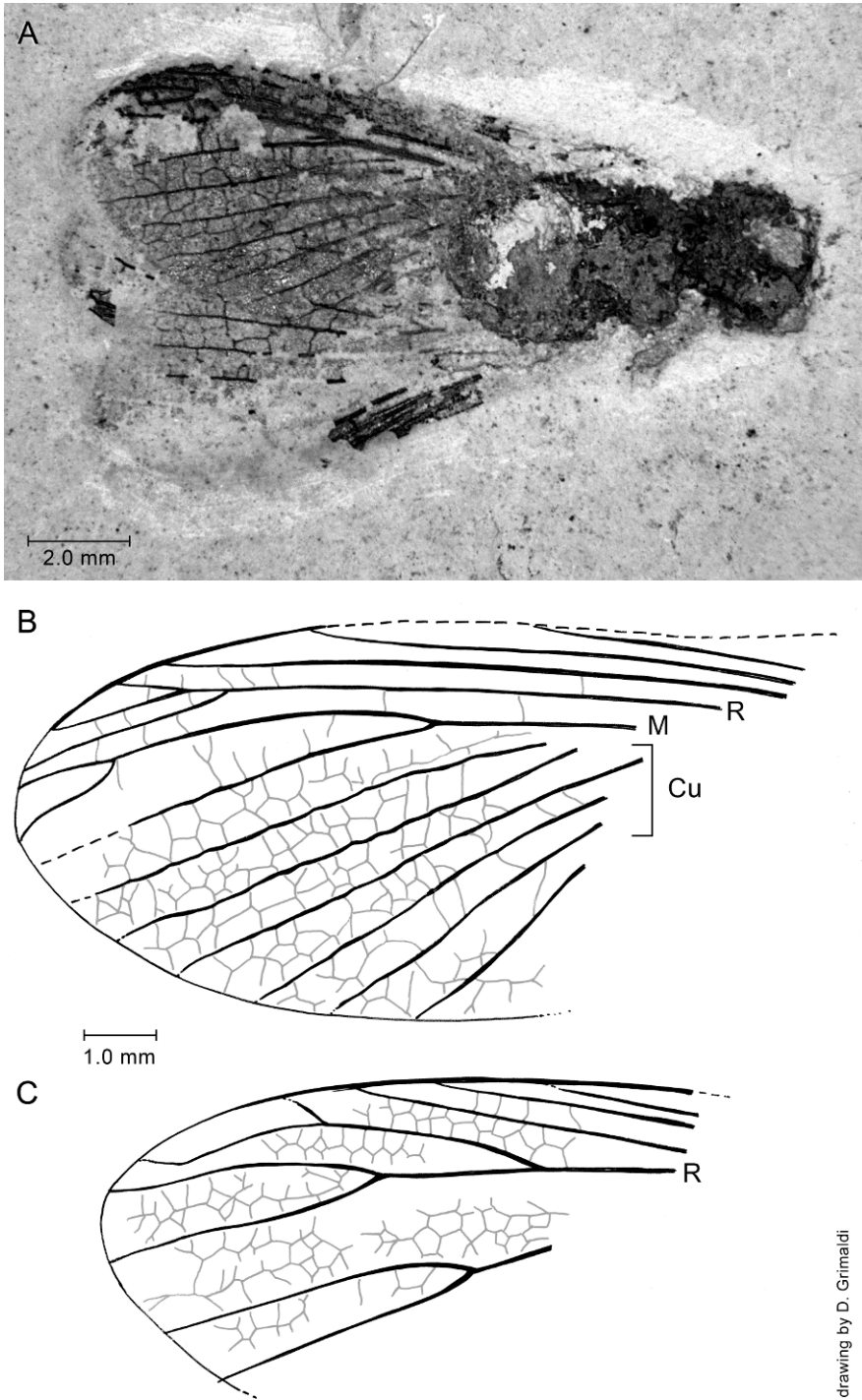


Fig. 17. *Creterhinotermes novaolindense* Bechly. **A.** Photomicrograph of holotype, SMNS 66196. **B.** Venation of preserved section of forewing of holotype. **C.** Venation of preserved section of forewing of paratype, SMNS 66197, oriented to match that of the holotype wing.

drawing by D. Grimaldi

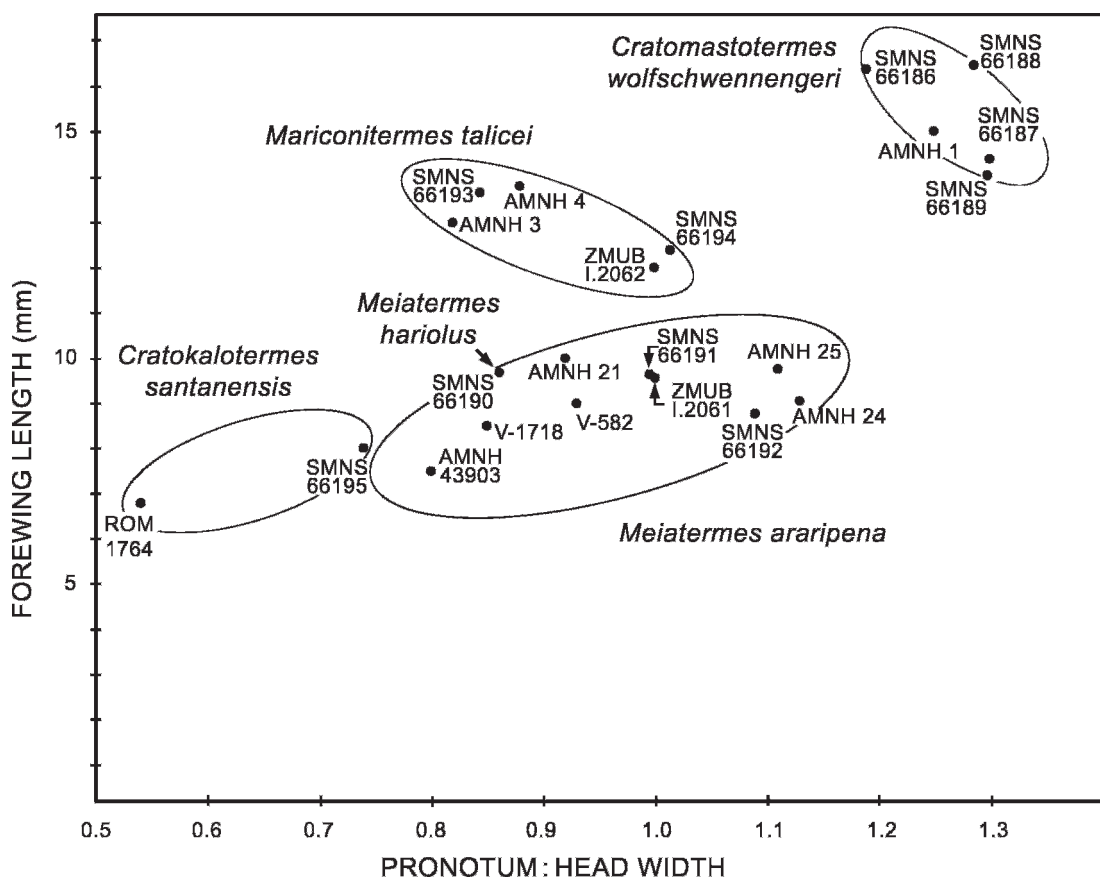


Fig. 18. Plot of select body proportions of Crato Formation termite species: pronotum width/head width vs. forewing length (mm). Only those specimens were included for which forewing length, head width, and pronotum width could all be measured (see table 1).

taxonomic confusion created by journals that are not peer reviewed and which allow types to be kept in private collections.

SPECIES DISTINCTIONS

Among the five Crato termite species, three are rare, and one, *Meiatermes araripena*, is relatively common (>70% of the specimens). In a bivariate plot of the 22 specimens with head, pronotum, and wings sufficiently preserved to allow measurement, all four of the measured species are easily distinguished (fig. 18). The variability seen in *M. araripena* may be due simply to the much larger series of specimens. The ratio of pronotal to head width in termites shows a distinctive transformation from >1 in the most basal taxa (where

the pronotum is significantly broader than the head), to approximately 1 in intermediate taxa, to significantly <1 in the most derived taxa, the Rhinotermitidae and Termitidae. Another transformation from basal to derived taxa is from larger to smaller body size, respectively. Except for *Cratokalotermes*, all Crato species are large-bodied termites, and four of the species have pronota that are as wide or significantly wider than the head. *Cratomastotermes* is particularly significant in this respect, since it has one of the largest pronota among all termites. These features, plus the primitive state of pentamerous tarsi (unknown for *Cratokalotermes* and *Cretorhinotermes*) and the venation indicate that the Crato species are largely basal in Isoptera. The venation of all species, with the exception of

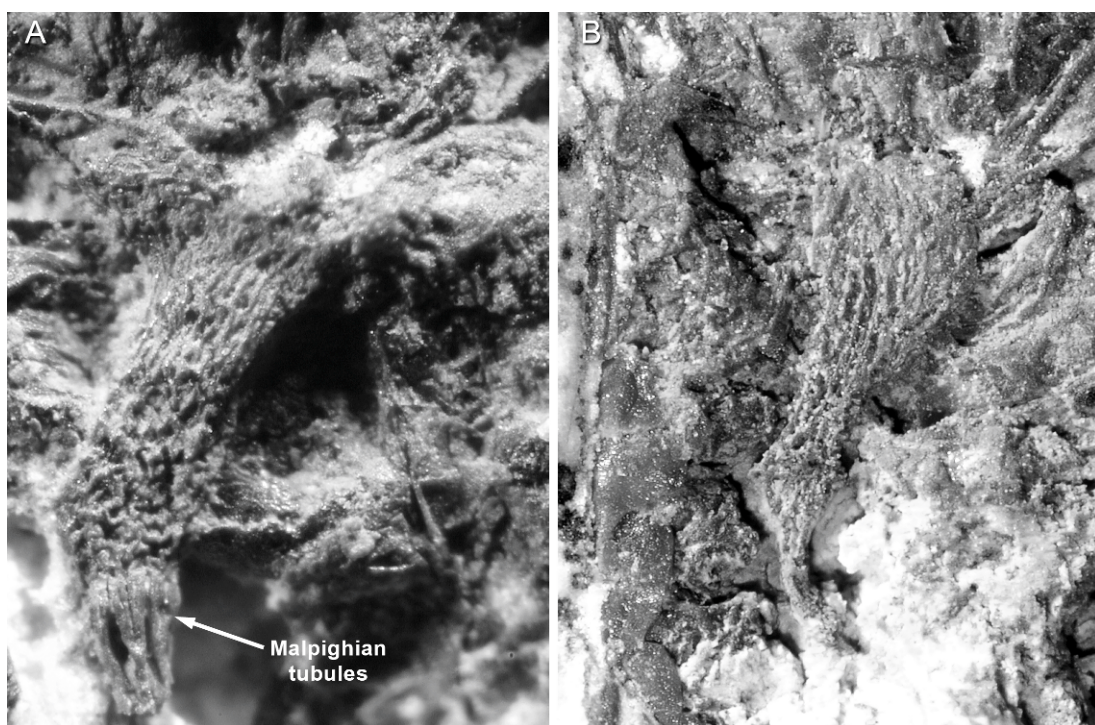


Fig. 19. Photomicrographs of midguts of *Meiatermes araripena*. A. ROM 1762 (cf. fig. 16C–F). B. ROM 1770.

Cretarhinotermes novaolindense, has an extensive field of radial branches, and all species have at least two branches of M, which are, again, largely plesiomorphic features for the termites.

It is presently premature to classify the Crato termites into families since a phylogenetic analysis of fossil and living termites is presently underway. With the exception of *Cratokalotermes*, it is doubtful that these species could be included within the present definitions of modern families, as all the termite fossil species have to date, and indeed preliminary analyses suggest an extensive basal grade of Cretaceous termites from Mastotermitidae and mastotermitid-like species, to stem-group Rhinotermitidae.

PRESERVATION

Various specimens revealed well-preserved, soft internal tissues, of which the midgut was most recognizable by a series of fine, longitudinally parallel folds. These specimens

included SMNS 66188 (paratype of *Cratomastotermes wolfschwenngeri*), SMNS 66197 (paratype of *Cretarhinotermes novaolindense*), and three specimens of *Meiatermes araripena* (ROM 1762, ROM 1770, and AMNH SaI-30: figs. 19, 20A–C, E). This is significant, since the gross structure of the isopteran digestive tract is systematically important. Basal termites, for example, have a large paunch at the anterior end of the hindgut, in which reside masses of symbiotic protists that metabolize lignocellulose; “higher” termites (Termitidae) have extensive, diverse modifications of the paunch and especially the juncture of the midgut and hindgut (Noirot, 1995; Noirot and Noirot-Timothee, 1969). Unfortunately, the paunch was not observable in the Crato fossils. Also in the basal termites, the internal, sclerotized armature within the proventriculus (the “gizzard,” at the posterior end of the crop) is well developed (though variable in fine structure among species), whereas in Termitidae the armature is highly vestigial. In one specimen,

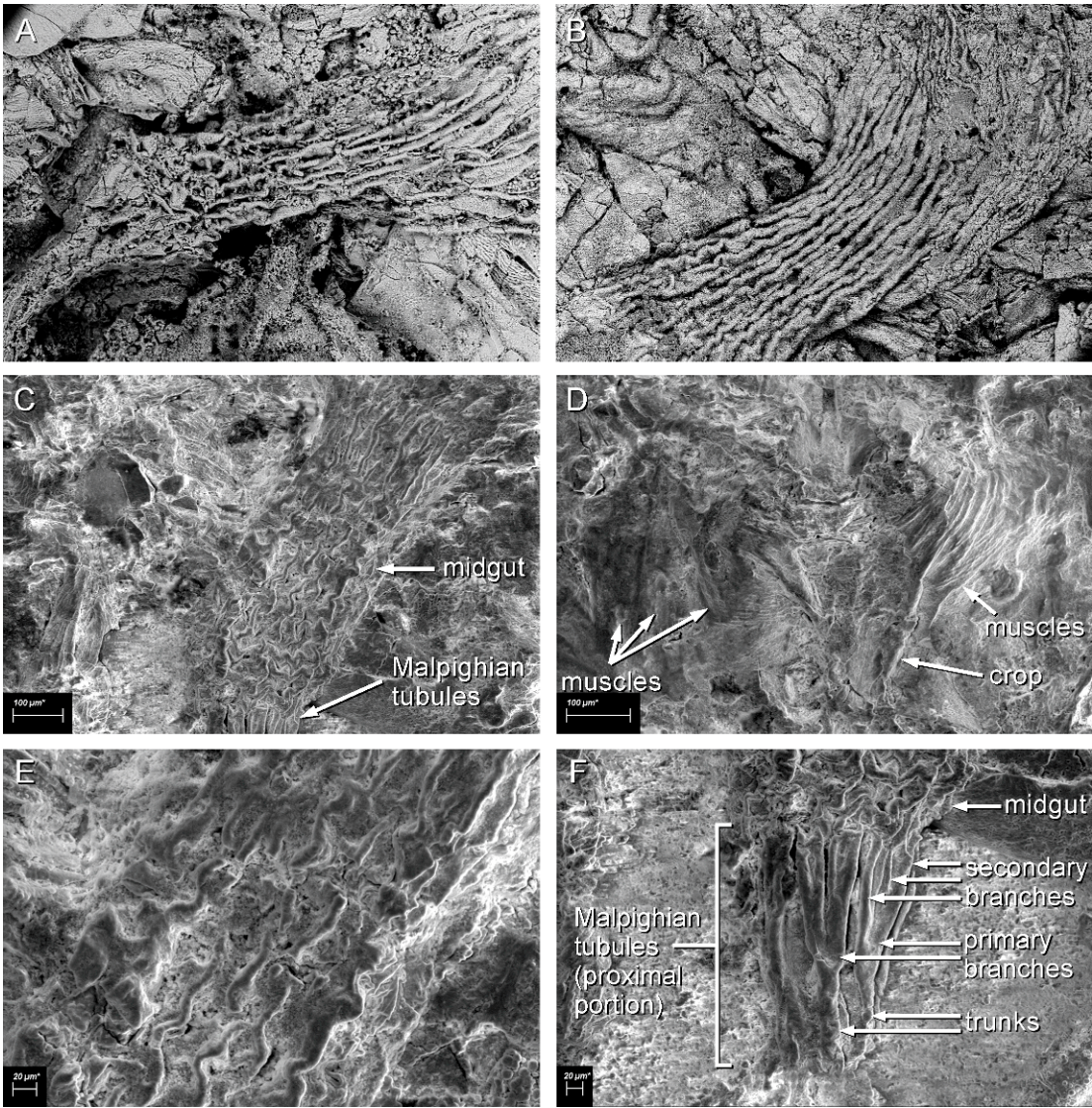


Fig. 20. Scanning electronmicrographs of the details of digestive tract preserved in *Meiotermes araripena*. **A, B:** Midgut (ROM 1770, AMNHSAI-30, respectively). **C–F:** ROM 1762. **C,** Midgut. **D,** Proventriculus. **E,** Detail of midgut shown in fig. C. **F,** Detail of the base of Malpighian tubules, where they connect to the end of the midgut and showing the branched bases.

ROM 1762 (fig. 20D), there is a swelling at the anterior end of the midgut, which is possibly the proventriculus. This structure lies approximately at the anterior end of the abdomen and is strapped with bands of fine muscles as in modern termites (Noirot, 1995), and suggesting a muscular activity used in the grinding action of the proventriculus. It is very likely that, if indeed this is the proven-

tricus, the internal sclerotized denticles would be preserved, but we feel it would be inappropriate to break into the structure just to expose the denticles. Significantly, the apparent proventriculus is located considerably posterior in this specimen. In most termites the crop and proventriculus are located in the thorax, but in at least one Recent hodotermitid species whose gut was

carefully examined (*Anacanthotermes ochraceus* [Noirot and Noirot-Timothee, 1969]), the crop is long and both it and the proventriculus lie in the abdomen.

Even more unexpected was the preservation of the bases of apparent Malpighian tubules in specimen ROM 1762 (fig. 20F). These are preserved at the posterior end of the midgut, at a level of approximately the middle of the abdomen. They have a very interesting structure unique within Isoptera. In *Mastotermes* there are 12–16 Malpighian tubules (Noirot, 1995; Noirot and Noirot-Timothee, 1969), and in the basal termites there are 10 (Termopsinae) to eight (Hodotermitinae, Stolotermitinae, Kalotermitidae, and Rhinotermitidae). The “higher” termites, family Termitidae, have four Malpighian tubules. In ROM 1762, four bundles of tubules are preserved, at least three of which have a thick trunk that splits at the base into four fine tubules and that connect to the gut (fig. 20F). Thus, *Meiatermes araripena* possessed at least 12 Malpighian tubules, but, since the attachment of the tubules in lower termites is radially symmetrical (the other half of them hidden in the fossil), *M. araripena* could have had as many as 24 tubules, which are bundled beyond the bases into eight thick tubes. This number and configuration (i.e., fusion) of the tubules is similar to the condition in roaches (Noirot, 1995), indicating that *M. araripena* may have retained the most plesiomorphic tubule structure known in termites.

ACKNOWLEDGMENTS

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copies of photomicrographs of SMNS specimens. Their assistance and advice greatly facilitated this work and the phylogenetic work in progress. We are additionally grateful to Mr. Tam Nguyen, Senior Scientific Assistant at the AMNH, who did SEM of the Crato specimens; to Dr. Michael Ohl for carrying the loan of Crato termites from the Humboldt Museum to the AMNH, to Dr. Valerie Krishna for careful proofreading, and to Drs. Günter Bechly and Torsten Wappler for reviews.

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