AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3362, 20 pp., 7 figures, 1 table March 26, 2002

The First Mesozoic Zoraptera (Insecta)

MICHAEL S. ENGEL[1] AND DAVID A. GRIMALDI[2]

ABSTRACT

The earliest representatives of the polyneopteran insect order Zoraptera are described and figured. Four species, representing both alate and apterous morphs, are preserved in Cretaceous amber from Myanmar (Burma) and are the first fossil records of the order from the Old World and the Mesozoic. ***Zorotypus cretatus,*** new species, is represented by an apterous individual of indeterminate sex whereas ***Z. nascimbenei,*** new species, is represented by an alate female and ***Z. acanthothorax,*** new species, is known from an alate male. ***Xenozorotypus burmiticus,*** new genus and species, is represented by an alate male and possesses distinct plesiomorphies suggesting that it may be sister to all other zorapterans (Recent and extinct). Based on some peculiar apomorphies of the metafemoral and terminalic structure as well as wing venation it is placed in a separate genus. These species, particularly *Z. cretatus*, *Z. acanthothorax*, and *Z. nascimbenei*, are remarkably similar to living zorapterans, which indicates antiquity of the genus *Zorotypus* and the order, the latter perhaps Lowermost Mesozoic in origin. Phylogeny and classification of Polyneoptera is briefly reviewed, and a list of zorapterans and their distributions is updated along with general comments on the evolution of the order.

INTRODUCTION

In a class renowned for its overwhelming diversity of species, the insect order Zoraptera is intriguing because it is one of the smallest orders and the least understood of groups. Zorapterans are minute insects superficially resembling Psocoptera that live gregariously under the bark of decaying logs or within termite nests where they feed principally on fungal hyphae as well as nematodes or minute arthropods (e.g., mites, collembola). Adults occur in two morphs within

[1] Research Associate, Division of Invertebrate Zoology, American Museum of Natural History; Assistant Professor, Department of Ecology and Evolutionary Biology, and Curator, Division of Entomology, Natural History Museum and Biodiversity Research Center, Snow Hall, 1460 Jayhawk Boulevard, University of Kansas, Lawrence, Kansas 66045-7523.

[2] Curator, Division of Invertebrate Zoology, American Museum of Natural History. e-mail: grimaldi@amnh.org

 ISSN 0003-0082

TABLE 1

Distributional Checklist of Zorapteran Species

Updated from Engel (2000) and Engel and Grimaldi (2000), inclusive of records based on unidentified species (32 living species; six fossil species).

Taxon	Distribution
WESTERN HEMISPHERE	
Zorotypus barberi Gurney	Costa Rica (Cocos), Panama, Dominican Republic, Trinidad[a], Venezuela[a], French Guiana[a]
Zorotypus brasiliensis Silvestri	Brazil
Zorotypus cramptoni Gurney	Guatemala
†*Zorotypus goeleti* Engel & Grimaldi	Dominican Republic [Miocene]
Zorotypus gurneyi Choe	Panama, Costa Rica[b]
Zorotypus hamiltoni New	Colombia
Zorotypus hubbardi Caudell	Southcentral–southeastern United States
Zorotypus huxleyi Bolivar y Pieltain & Coronado	Brazil, Peru
Zorotypus juninensis Engel	Peru
Zorotypus leleupi Weidner	Galapagos Islands
Zorotypus longicercatus Caudell	Jamaica
Zorotypus manni Caudell	Bolivia, Peru
Zorotypus mexicanus Bolivar y Pieltain	Mexico
Zorotypus neotropicus Silvestri	Costa Rica
†*Zorotypus palaeus* Poinar	Dominican Republic [Miocene]
Zorotypus shannoni Gurney	Brazil
Zorotypus snyderi Caudell	Jamaica, United States (Florida)
Zorotypus weidneri New	Brazil
EASTERN HEMISPHERE AND OCEANIA	
†*Xenozorotypus burmiticus* Engel & Grimaldi	Myanmar [Cretaceous]
†*Zorotypus acanthothorax* Engel & Grimaldi	Myanmar [Cretaceous]
Zorotypus buxtoni Karny	Samoa
Zorotypus caudelli Karny	Indonesia (Sumatra), Malay Peninsula[c]
Zorotypus ceylonicus Silvestri	Sri Lanka
Zorotypus congensis Ryn-Tournel	Zaire
†*Zorotypus cretatus* Engel & Grimaldi	Myanmar [Cretaceous]
Zorotypus delamarei Paulian	Madagascar
Zorotypus guineensis Silvestri	Guinea, Ghana, Ivory Coast
Zorotypus javanicus Silvestri	Indonesia (Java)
Zorotypus lawrencei New	Christmas Island
Zorotypus medoensis Hwang	Tibet
†*Zorotypus nascimbenei* Engel & Grimaldi	Myanmar [Cretaceous]
Zorotypus newi (Chao & Chen)	Taiwan
Zorotypus philippinensis Gurney	Philippines
Zorotypus silvestrii Karny	Indonesia (Mentawai)
Zorotypus sinensis Hwang	Tibet
Zorotypus swezeyi Caudell	Hawaii
Zorotypus vinsoni Paulian	Mauritius
Zorotypus zimmermani Gurney	Fiji
RECORDS OF UNIDENTIFIED OR UNDESCRIBED SPECIES	
Zorotypus machadoi (nomen nudum)	Angola (Delamare-Debouetteville, 1951)
Zorotypus sp.	Cuba (Gurney, 1938; Zayas, 1974)
Zorotypus sp.	Guyana (Beebe, 1925)
Zorotypus sp.	Vietnam (Denis, 1932, 1949)
"Zorotypus" sp.	Iran (Mossadegh, 1995)[d]

TABLE 1
Continued

† Fossil taxa.

[a] Aberlenc (1995), Engel (2000), and Kukalová-Peck and Peck (1993), report specimens probably of *Z. barberi* from French Guiana, Trinidad, and Venezuela, respectively.

[b] This species was recently recorded form Guanacaste Province, Costa Rica (Engel, 2001b).

[c] This species was only recently recorded from the mainland Malay Peninsula (New, 2000) but, as noted by Dr. New, this population may represent a separate species difficult to distinguish from true *Z. caudelli*.

[d] This enigmatic record of a *Zorotypus* sp. living in a managed honey bee (*Apis mellifera* L.) colony is dubious (see Discussion). Zorapterans can be easily misidentified with Psocoptera and it is perhaps possible that this was a bark-louse, species of which are known to occur in desert regions (unlike all presently known zorapterans).

each species—eyed, winged forms and eyeless, apterous forms.

Despite their low specific diversity and tiny stature in physical size, zorapterans have puzzled entomologists for decades and fueled considerable debate. The Zoraptera have been placed in a bewildering array of phylogenetic positions among insect orders. At one time or another Zoraptera has been considered sister to Isoptera (Boudreaux, 1979; Caudell, 1918; Crampton, 1920; Weidner, 1969, 1970), Isoptera + Blattaria (Silvestri, 1913), Paraneoptera (Hennig, 1953, 1969, 1981; Kristensen, 1975), Embiidina (Minet and Bourgoin, 1986; Engel and Grimaldi, 2000; Grimaldi, 2001), Holometabola (Rasnitsyn, 1998), Dermaptera (Carpenter and Wheeler, 1999), Dermaptera + Dictyoptera (Kukalová-Peck and Peck, 1993); basal within Thysanoptera (Karny, 1922) or Psocoptera (Karny, 1932); or unresolved within either basal Neoptera (Kristensen, 1991) or Orthoptera, Phasmida, and Embiidina (Kukalová-Peck, 1991). Despite this apparent confusion, Zoraptera have been demonstrated to belong to the Polyneoptera (Boudreaux, 1979; Carpenter and Wheeler, 1999; Wheeler et al., 2001), although polyneopteran monophyly is certainly not definitive. Among polyneopteran orders a sister-group relationship with the Embiidina (= Embioptera fide Shipley, 1904) is the most strongly supported hypothesis (Engel and Grimaldi, 2000). Embiidina and Zoraptera share the following synapomorphies: enlarged metafemora and associated musculature; tarsomeres reduced (two in Zoraptera, three in Embiidina); wings dehiscent, narrow, and paddle-shaped; presence of apterous morphs; reduced cerci; loss of gonostyli; and gregarious, cryptic lifestyle (Engel and Grimaldi, 2000). Both orders have a number of remarkable morphological autapomorphies and diverged perhaps as early as the Lowermost Mesozoic. Among insects each possesses not only peculiar anatomical apomorphies but also unusual aspects of biology and behavior (e.g., Valentine, 1986). The combination of only highly apomorphic survivors and a Mesozoic age has rendered it difficult to identify relationships based on Recent taxa alone. It is for just such taxa that Gauthier et al. (1989) hypothesized that fossils would be most important. Unfortunately, at present the geological record of both Zoraptera and Embiidina is extremely sparse. The Embiidina have only two definitive pre-Cenozoic records, both in Cretaceous amber from Myanmar (Cockerell, 1919; Davis, 1939; Grimaldi et al., 2002; Engel and Grimaldi, unpubl. data), while fossil Zoraptera were until now known from only two species in Miocene amber of the Dominican Republic (Engel and Grimaldi, 2000; Poinar, 1988).

Herein we describe four additional fossil species of the order, including individuals of both winged and apterous morphs. The present fossils are the first from the Eastern Hemisphere as well as by far the oldest for the order. While three fossils are not atypical for the living genus *Zorotypus*, and are here classified together as the oldest species of their genus; the fourth species, represented by a winged male, is apomorphic in a number of remarkable traits. The combination of these apomorphies along with a few distinctive plesiomorphies for the order indicate that this species is sister to all remaining zorapterans (fossil and living together, see below). A new genus is proposed to accommodate this enigmatic zorapteran. Kukalová-

Peck and Peck (1993) and Chao and Chen (2000) classified the Recent species of the order into seven monotypic genera and a paraphyletic genus *Zorotypus* retaining all remaining species. Engel and Grimaldi (2000) recently proposed a revised diagnosis for the order, family, and genus and recognized only the single, nominal genus, *Zorotypus*. Owing to the homogeneity of living and Tertiary species of the order and the low specific diversity, there is, at present, no justifiable reason to recognize multiple genera of Recent zorapterans. The currently recognized 32 living and six fossil species are summarized in table 1 along with their geographical distributions.

MATERIALS AND METHODS

Burmese amber has historically been of interest (e.g., for its fossils, as a gem), although the only collection of fossils in Burmese amber was in the Natural History Museum, London (hereafter NHML). Recent study of that material indicates it contains some arthropods unique to the Cretaceous (Zherikhin and Ross, 2000; Rasnitsyn and Ross, 2000) and thus, the amber is much older than the commonly presumed Miocene or Eocene ages (e.g., Poinar [1992], following earlier authors, proposed an Eocene age). Even more recent is the development of a larger collection of Burmese amber fossils at the AMNH (Grimaldi et al., 2002), from which the specimens we describe here were derived. Grimaldi et al. (2002) document numerous taxa and records, some providing further, definitive evidence of a Cretaceous age of Burmese amber. Systematics of various insects correlated with those from well-dated amber deposits indicates that Burmese amber may actually be as old as the Turonian or Cenomanian. The AMNH and NHML collections derive from amber mines near Myitkyina, Kachin State, in northern Myanmar.

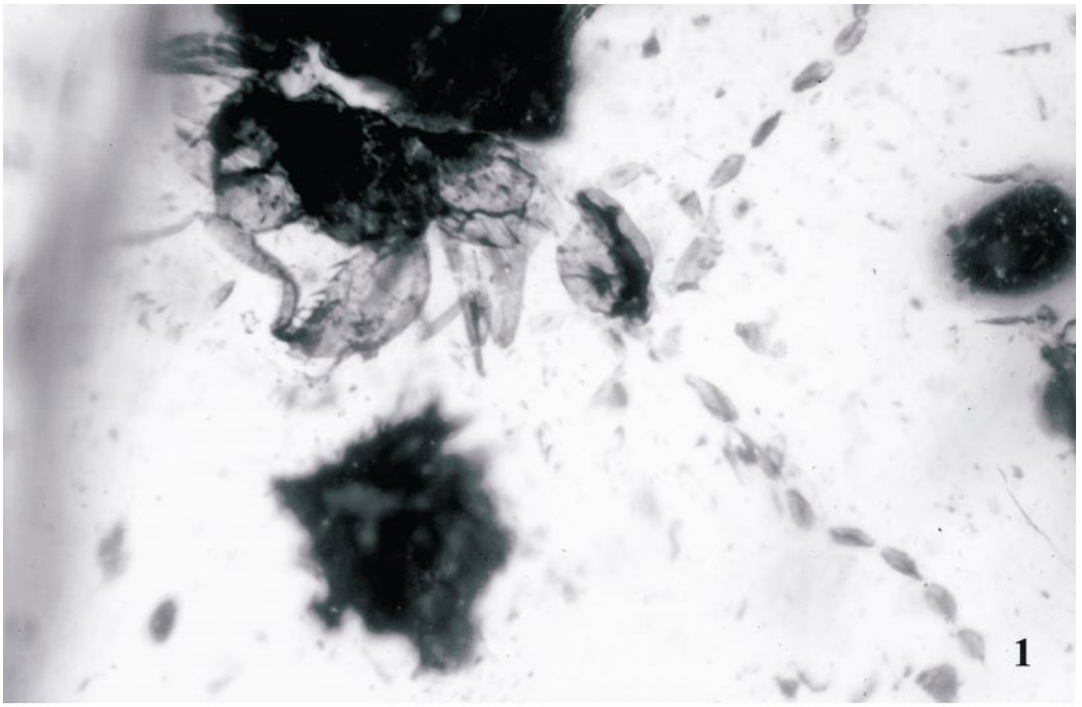
Specimens were embedded in epoxy prior to trimming and polishing, as described by Nascimbene and Silverstein (2000). Specimens were examined using a Leitz stereomicroscope at 48–160×, and a Zeiss compound scope at 160–400× magnification. Format for the descriptions follows that employed by Engel (2000) and Engel and Grimaldi (2000) with wing venational identities essentially after Crampton (1921) with some modifications. In order to simplify communication we have attempted to homologize metafemoral spines across the species in question by numbering the spines from apex to base (e.g., *sp1, sp2*), except that the isolated, proximal spine is referred to as *spB*, since some modern species possess spines in the intervening region. Spines indicated by negative symbols are located on the anterior border of the ventral surface (e.g., *sp-3*), otherwise all spines are positioned on the posterior border. In addition, we have used the term *jugate setae* for distinctive, elongate setae along the posterior margin of the forewing (present in two fossil species, described below). The function of these setae is unknown and they are not recorded for living zorapterans. The fact that in one species these setae are hooked at their apices suggests that they might have played a role in coupling the wings during flight such as hamuli do in the Hymenoptera (although in the opposite direction, i.e., positioned on the leading edge of the hind wing and linking to the posterior margin of the forewing). Measurements should be considered approximate since the optimal visual angle could not always be obtained.

SYSTEMATIC PALEONTOLOGY

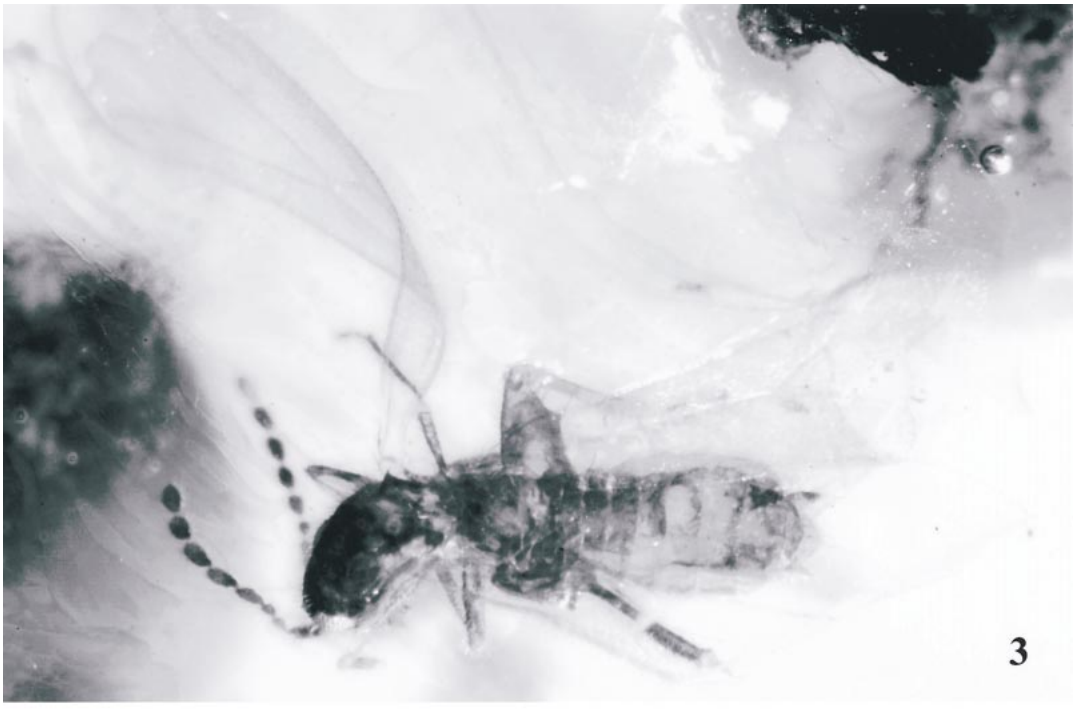
***Zorotypus cretatus*, new species**

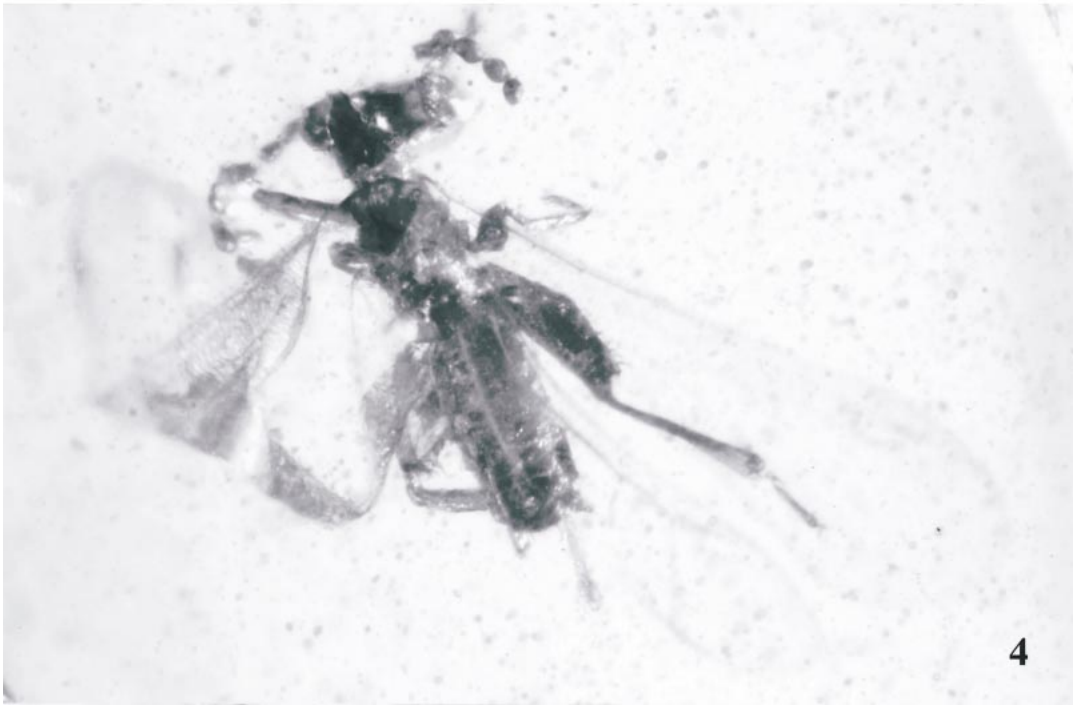
Figures 1, 7

DIAGNOSIS: This species is based on a poorly preserved specimen and therefore only a relatively meager description is presented. However, observable features allow for a meaningful diagnosis and separation from other species, particularly in the structure of the thorax and legs. From *Zorotypus nascimbenei* (described below), the present species differs by the smaller pronotum that lacks the shallow, anterior depression typical of the former species; the greatly expanded metafemur that does not taper toward the apex, with a width that is more than one-half its length; the metafemur with two auxiliary, stout, medial spines (*sp6a* and *sp6b*), the intermediary of which is strongly directed apically; and with *sp2* greatly elongate.



Figs. 1–2. Photomicrographs of Burmese amber Zoraptera. **1.** *Zorotypus cretatus*, new species (AMNH Bu-044). **2.** *Zorotypus nascimbenei*, new species (AMNH Bu-341).





Figs. 3–4. Photomicrographs of Burmese amber Zoraptera. **3.** *Zorotypus acanthothorax*, new species (AMNH Bu-966). **4.** *Xenozorotypus burmiticus*, new genus and species (AMNH Bu-182).

DESCRIPTION: **Apterous and Blind Morph.** Total body length (preserved, excluding antennae) 1.15 mm; head length 0.32 mm; metafemur width (maximal) 0.21 mm. Integument reddish-brown, apparently smooth. Head subtriangular. Compound eyes, ocelli, and wings absent. Head with sparse, minute setae; antennae crushed and broken; preserved flagellomeres bead-shaped. Labial palpus (right side preserved) as described for living *Zorotypus* species (e.g., see Engel, 2000). Pronotum apparently discoid, rectangular; mesoscutum rectangular, approximately as long as wide, not narrowed; metanotum transverse, about twice as wide as long. Procoxa relatively short; metafemur greatly expanded, more so than in Recent *Zorotypus*, maximal width equivalent to more than one-half length; eight stout and strongly sclerotized spines along posterior border of metafemoral ventral surface; *spB* not apparent; two additional, large stout spines (*sp6a, sp6b*) present at midpoint, *sp6a* strongly inclined toward metafemoral apex; *sp1-sp5* shorter than medial spines (*sp6, sp6a, sp6b*) except *sp2* elongate, nearly as long as *sp6*; spines regularly spaced except for slightly wider margin between *sp1* and *sp2*; metatibia slightly longer than metafemur, slender but slightly dilated toward apex, with single, short spine at about three-quarters length from metatibia base and another spine near apex; basalmost metatarsomere minute, distal metatarsomere elongate, slightly less than one-half length of metatibia; claws simple. Abdomen mostly crushed.

HOLOTYPE: Sex indeterminate; Myanmar: Cretaceous, Kachin: Tanai Village (on Ledo Rd. 105 km NW Myitkyna), coll. Leeward Capitol Corp., 1999, AMNH Bu-044; in amber collection, Division of Invertebrate Zoology, AMNH. Observation of microscopic details of the specimen was compromised by thickness of amber between zorapteran and surface. Preparation closer to the specimen was not possible because of many other inclusions in the piece: one adult Blattaria, one nymphal Auchenorrhyncha, one Psocoptera, 10 staphylinid beetles, and one millipede.

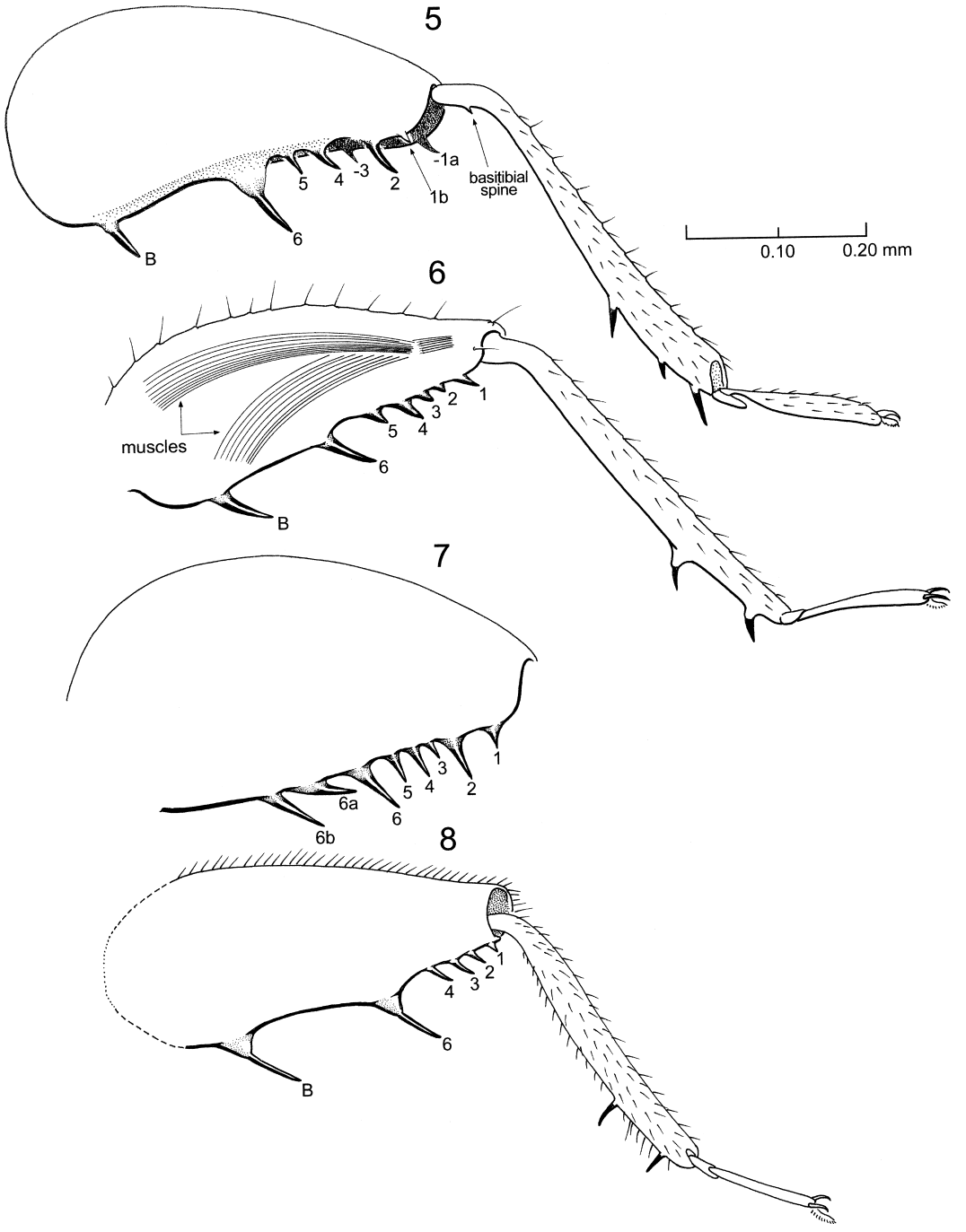
ETYMOLOGY: The specific epithet is derived from Cretaceous and is a reference to the age of the species.

Zorotypus nascimbenei, new species
Figures 2, 6, 9

DIAGNOSIS: This species is noteworthy for the reduced antennomere count, absence of mesonotal spines (present in *Z. acanthothorax*), and presence of strong lateral setae on the abdominal terga. All species of the order (where known) have nine-segmented antennae while *Z. nascimbenei* and *Z. acanthothorax* have eight segments. Overall, the combination of a relatively large pronotum with a shallow depression in the apical margin and elongate, stiff, lateral setae; absence of mesonotal spines; spination of the metafemur and metatibia; distinctly elongate first antennomere; abdominal setation; and the presence of an evenly spaced series of seven jugate setae on the posterior margin of the forewings separate this species from all others. See also diagnoses for *Z. cretatus* (above) and *Z. acanthothorax* (below).

DESCRIPTION: **Alate Female.** Total body length (exclusive of antennae) 1.48 mm; antennal length 0.92 mm; forewing length 1.68 mm; hind wing length 1.32 mm; head width 0.32 mm; pronotal length 0.31 mm; pronotal width 0.28 mm; mesonotal length 0.21 mm; mesonotal width 0.26 mm; metanotal length 0.15 mm; metanotal width 0.26 mm; metafemoral width (maximal) 0.18 mm (approximate; viewed at slight angle); metafemoral length 0.50 mm; metatibial length 0.42 mm; metatarsomere II length 0.22 mm; abdominal length 0.54; cercus length 0.08 mm.

Integument generally light reddish-brown and smooth. Head subtriangular, posterior border slightly broader than pronotum. Antenna with eight segments (nine in all other *Zorotypus*, except *Z. acanthothorax* and in *Z. cretatus* where this is unobservable); first antennomere elongate, 4. 5× longer than wide, almost as long as combined lengths of next three segments; second antennomere straight, not gently curved outward, approximately equal in size to third segment; fourth segment longer than third segment, fourth through eighth segments roughly equal in length. Maxillary palpal segments 2, 3, and 5 elongate, segment 4 about as long as wide (segment 1 not visible); segment 2 about as long as segment 3; segment 5 longer than proximal segments, not swollen on ventral



Figs. 5–8. Hind leg characters of Burmese amber Zoraptera; all of the right hind leg; not all to the same scale. **5.** *Xenozorotypus burmiticus*, new genus and species (AMNH Bu-182). **6.** *Zorotypus nascimbenei*, new species (AMNH Bu-341). **7.** *Zorotypus cretatus*, new species (AMNH Bu-044). **8.** *Zorotypus acanthothorax*, new species (AMNH Bu-966).

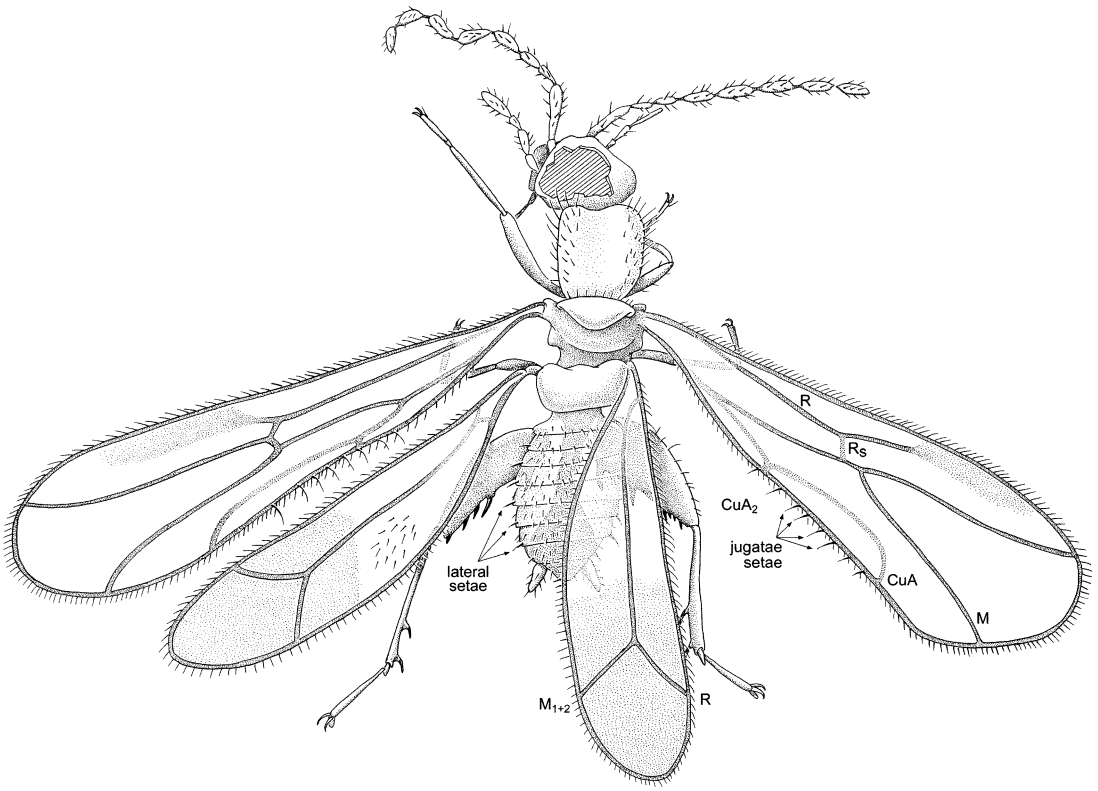


Fig. 9. Dorsal habitus of holotype female of *Zorotypus nascimbenei*, new species (AMNH Bu-341).

surface. Pronotum large, as long as wide, without crescentic ridges along anterior third; posterior and anterior widths equivalent (i.e., not constricted); anterior margin with shallow, medioapical depression; longest setae on anterolateral margins; mesonotum and metanotum each broader than long; mesonotum about as long as metanotum; mesonotum and metanotum with sparse, minute setae. Metafemur expanded, maximal width slightly less than one-half total metafemoral length, gently tapering toward apex; seven stout and strongly sclerotized spines along posterior border of metafemoral ventral surface, spines slightly angled toward metafemoral apex; *spB* present, as large as *sp6* (spine at midpoint of metafemur); *sp1*-*sp5* distinctly shorter than *sp6*; *sp4* and *sp1* slightly longer than other spines of apical series (*sp1*-*sp5*); *sp1*-*sp5* regularly spaced, separated by length of an individual spine or less; *sp6* slightly more distantly separated from apical series, separated by twice *sp5* length; metatibia slightly longer than metafemur, slender but slightly dilated toward apex, with single, short spine at about three-quarters length from metatibia base and another spine near apex; basalmost metatarsomere minute, distal metatarsomere elongate, slightly less than one-half length of metatibia; claws simple. Abdominal terga with scattered, minute setae, without distinct, transverse rows of setae along posterior margin; terga laterally with stiff, erect, posterolaterally directed setae; sterna with sparse, minute setae. Cerci ovoid except tapering toward apex; unsegmented; with scattered setae, none longer than cercus, without apical spinelike seta.

Wing venation faint with most veins represented by fuscous lines, membrane generally hyaline with scattered minute setae except infuscation forming pterostigma in forewing and slight infuscation in distal half of hind wing; marginal setae on both fore and hind wings numerous and short, slightly lon-

ger than those setae of membrane; posterior margin of forewing with series of seven, regularly spaced, elongate (i.e., 2–3 times longer than other marginal setae), stiff setae (i.e., jugate setae) in middle third. Forewing with pterostigma faint but present as an infuscated, elongate area along anterior margin, proximally bordered by R_1, disappearing well before Rs; C+Sc relatively strong on margin to wing apex; R_1 short, disappearing into pterostigma base, not reaching wing margin; Rs separating from radial stem near midpoint of wing, fusing with M in right wing for a distance subequal to first free abscissa of Rs, in left wing Rs not fusing with M and instead separated by short rs-m crossvein that is slightly shorter than first abscissa of Rs; Rs reaching anterior wing margin near wing apex; M reaching posterior wing margin near wing apex although slightly proximal relative to termination of Rs; CuA present, CuA_1 reaching posterior wing margin at distal quarter of wing, CuA_2 present as a short stub in basal third of wing. Hind wing with M+R running in anterior half, both R and M reaching respective wing margins; Cu present near wing base as a short stub.

HOLOTYPE: Alate female; Myanmar: Cretaceous, Kachin: Tanai Village (on Ledo Rd. 105 km NW Myitkyna), coll. Leeward Capitol Corp., 2000, AMNH Bu-341; in amber collection, Division of Invertebrate Zoology, AMNH. Preserved in a piece with one psychodid fly, three immature Collembola, and one undetermined larva emerging from an egg.

ETYMOLOGY: The specific epithet is a patronymic honoring Mr. Paul C. Nascimbene, who located two of the three zorapterans reported in this study.

Zorotypus acanthothorax, new species

Figures 3, 8, 10

DIAGNOSIS: This species is quite similar to *Z. nascimbenei* (see above) and both have a reduced number of antennomeres (8) and series of jugate setae on the posterior margin of the forewing. *Zorotypus acanthothorax* can most readily be distinguished from all fossil and living zorapterans by the presence of large, anterolateral spines on the mesonotum that extend out over the bases of the forewings. Additionally, the absence of stiff, lateral setae on the tergal margins; the more numerous jugate setae (some of which are hooked at their apices); much shorter antennae (nearly one-half length of those in *Z. nascimbenei*); shortened metatibia (distinctly shorter than metafemur; the metatibia is longer than the metafemur in *Z. nascimbenei*); setation of the cerci; and metafemoral spination serve to distinguish this species from all others.

Since *Z. nascimbenei* is known from a female and *Z. acanthothorax* is known from a male, differences between them might be interpreted as sexual characteristics of a single species. While this indeed could be the case, the striking differences in significant, nongenitalic features (e.g., mesonotal spines, length of metatibia, length of antennae) suggest that the two are not conspecific.

DESCRIPTION: **Alate male.** Total body length (exclusive of antennae) 1.51 mm; antennal length 0.53 mm; forewing length 1.67 mm; hind wing length 1.52 mm; pronotal length 0.24 mm; mesonotal length 0.18 mm; metanotal length 0.18 mm; metafemoral width (maximal) 0.18 mm; metatibial length 0.38 mm; metatarsomere II length 0.22 mm; abdominal length 0.71; cercus length 0.09 mm.

Integument generally light reddish-brown and smooth. Head subtriangular, posterior border slightly broader than pronotum. Antenna with eight segments (nine in all other *Zorotypus* except *Z. nascimbenei* and in *Z. cretatus* where this is unobservable); first antennomere elongate, 3× longer than wide, slightly longer than combined lengths of next two segments; second antennomere straight, not gently curved outward, approximately equal in size to third segment; fourth segment nearly twice length of third segment, fourth through eighth segments roughly equal in length; antenna relatively short. Gena very narrow; malar space elongate. Pronotum large, as long as wide, without crescentic ridges along anterior third; posterior and anterior widths equivalent (i.e., not constricted); anterior margin straight; setae scattered, of approximately uniform length; mesonotum about as long as wide, with pair of strong, thornlike spines on anterolateral corners and projecting laterally; metanotum

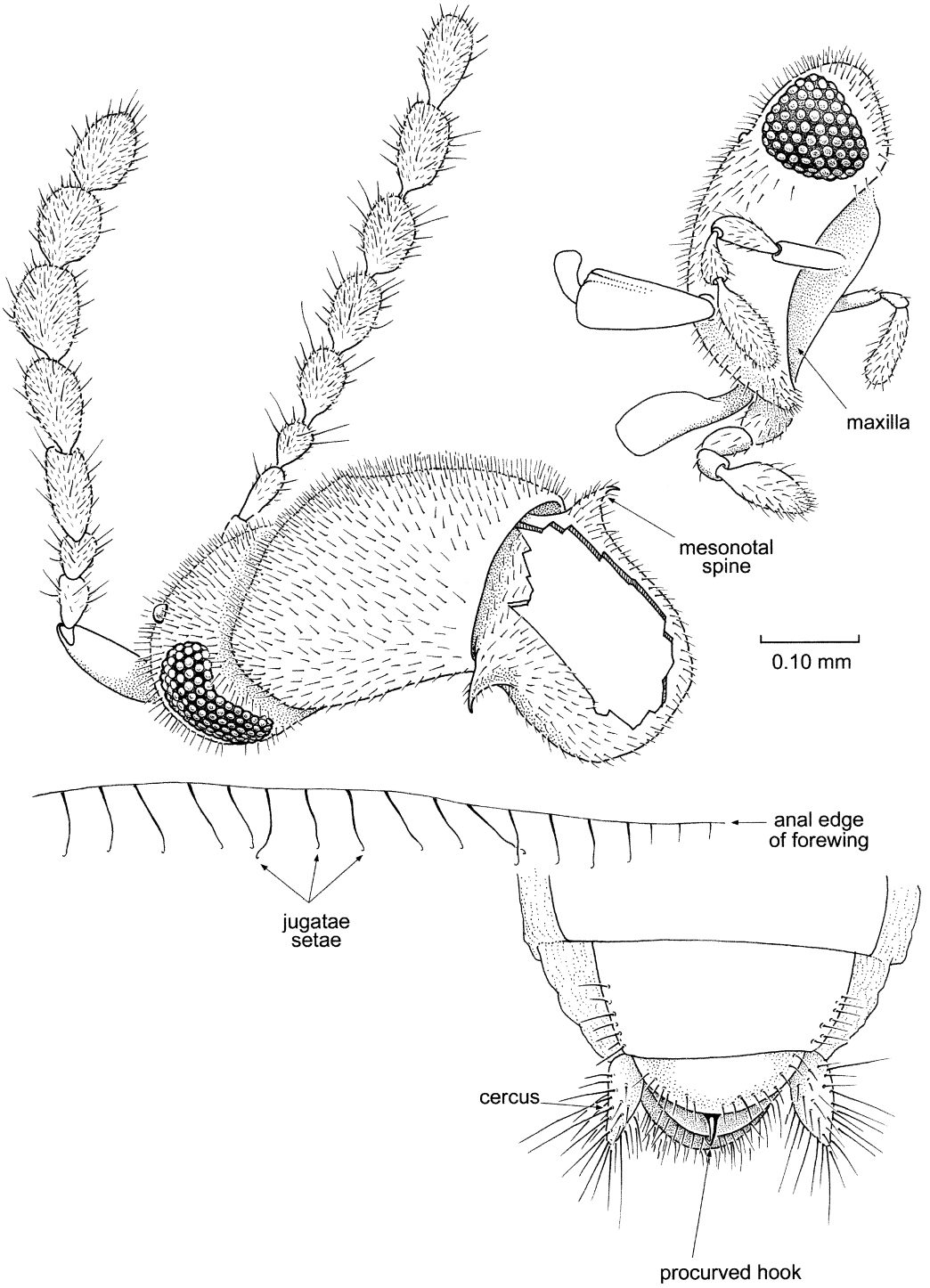


Fig. 10. *Zorotypus acanthothorax*, new species (AMNH Bu-966).

broader than long; mesonotum longer than metanotum; thorax with scattered, short setae. Metafemur expanded, maximal width slightly less than one-half total metafemoral length, gently tapering toward apex; six stout and strongly sclerotized spines along posterior border of metafemoral ventral surface, anterior border without spines and separated from posterior border by exceedingly shallow depression, spines slightly angled toward metafemoral apex; *spB* present, about as large as *sp6* (spine at midpoint of metafemur); *spB* and *sp6* situated on tubercles; *sp5* absent; *sp1–sp4* distinctly shorter than *sp6*; *sp3* slightly longer than other spines of apical series (*sp1–sp4*); *sp4* slightly shorter than *sp3*, otherwise apical series of spines progressively shorter toward metafemoral apex; *sp1–sp4* regularly spaced, separated by less than length of an individual spine; *sp6* slightly more distantly separated from apical series, separated by nearly twice *sp4* length; metatibia distinctly shorter than metafemur, slender, not dilated toward apex, with single spine at about three-quarters length from metatibia base and another spine near apex, neither spine situated on tubercles; basalmost metatarsomere minute, distal metatarsomere elongate, more than one-half length of metatibia; claws simple. Abdominal terga with scattered, minute setae, without distinct, transverse rows of setae along posterior margin; terga without stiff, erect setae at posterolateral corners; sterna with sparse, minute setae. Cerci ovoid except tapering toward apex; unsegmented; with scattered setae, setae longer than cercus, without apical spine-like seta.

Wing venation faint with most veins represented by fuscous lines, membrane generally hyaline with scattered minute setae except infuscation forming pterostigma in forewing; marginal setae on both fore and hind wings numerous and short, slightly longer than those setae of membrane; posterior margin of forewing with series of 15, regularly spaced, elongate (i.e., three or more times longer than other marginal setae), stiff, jugate setae in middle third, jugate setae with minute hooks at apices. Forewing with pterostigma faint but present as an infuscated, elongate area along anterior margin, proximally bordered by R_1, disappearing near Rs; R_1 short, disappearing into pterostigma base, not reaching wing margin; Rs separating from radial stem near midpoint of wing, separated from M by short rs-m crossvein that is distinctly shorter than first abscissa of Rs; Rs reaching anterior wing margin near wing apex; M reaching posterior wing margin near wing apex although slightly proximal relative to termination of Rs; CuA absent. Hind wing venation exceedingly difficult to discern, apparently with M+R running in anterior half, both R and M reaching respective wing margins; Cu not visible.

HOLOTYPE: Alate male; Myanmar: Cretaceous, Kachin: Tanai Village (on Ledo Rd. 105 km NW Myitkyna), coll. Leeward Capitol Corp., 2000, AMNH Bu-966; in amber collection, Division of Invertebrate Zoology, AMNH. Preserved in a piece with one spider and a nematoceran (Diptera).

ETYMOLOGY: The specific epithet is a combination of the Greek words *akantha* (meaning, ''spine'') and *thorax*, and is a reference to the large, anterolateral spines of the mesonotum.

Xenozorotypus, new genus

TYPE SPECIES: *Xenozorotypus burmiticus*, new species.

DIAGNOSIS: As for the family (see Engel and Grimaldi, 2000) with the following modifications: Metafemur with exceptionally deep ventral furrow extending from apex to midpoint (much deeper than in those living species with a ventral depression), spines of metafemur quite stout and strongly sclerotized; medial spine (*sp6*) greatly expanded at base and elongate; metatibia with three exceptionally strong, apical spines, regularly spaced in distal two-thirds; short, basal spine present on ventral surface of metatibia; empodium of meta-pretarsus strong, slightly expanded; hind wing with M_{3+4} present (Cu at wing base not visible). Male with procurved hook on central disc of T10 greatly enlarged, hook one-half cercus length.

ETYMOLOGY: The new genus-group name is a combination of *xenos* (Greek, meaning, ''strange'') and *Zorotypus* (itself a combination in Greek of *zoros*, ''pure,'' and *typos*, ''impression'' or ''figure''), type genus of the family. The name is masculine.

COMMENTS: Although we have advocated (and still do) the reduction of genus-group names within this small insect order (Engel and Grimaldi, 2000), the erection of a monotypic genus for this fossil seems amply justified. Unlike previous generic concepts in the Zoraptera, *Xenozorotypus* does not render *Zorotypus* paraphyletic. The presence of M_{3+4} in the hind wing is a distinctly plesiomorphic feature not found in any other species of the order for which winged morphs are known (living or fossil). The loss of this vein is a synapomorphy of all other Zorotypidae. Furthermore, the apomorphic structure of the metafemur, the presence of the basal metatibial spine, and terminalia of *Xenozorotypus* supports its validity.

Xenozorotypus burmiticus, new species
Figures 4, 5, 11, 12

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Alate Male.** Total body length (exclusive of antennae) 1.87 mm; forewing length 1.94 mm; hind wing length 1.56 mm; pronotal length 0.22 mm; mesonotal length 0.22 mm; metanotal length 0.13 mm; metafemoral width (maximal) 0.18 mm; metafemoral length 0.50 mm; metatibial length 0.48 mm; metatarsomere II length 0.17 mm; abdominal length 0.68; abdominal width 0.27 mm; cercus length 0.09 mm.

Integument generally reddish-brown and smooth. Head crushed, apparently with posterior border broader than pronotum. Antenna nine-segmented (not all segments of right antenna preserved and those apical segments of left antenna badly crushed, however, the remains show nine antennomeres); first antennomere only slightly elongate, apparently only 2. 5× longer than wide, about as long as combined lengths of next two segments; second antennomere gently curved outward, slightly smaller than third segment; third segment subequal to fourth segment. Pronotum large, partly crushed but perhaps slightly longer than posterior width, apparently without crescentic ridges along anterior third; with scattered setae, those of anterolateral margin (where preserved) not elongate relative to those of central disc. Mesonotum slightly longer than metanotum, each slightly broader than long and with scattered setae. Metafemur expanded, maximal width about one-half total metafemoral length, gently tapering toward apex; six stout and strongly sclerotized spines along posterior border of metafemoral ventral surface, two stout spines on anterior border (*sp-1a* and *sp-3*), spines slightly angled toward metafemoral apex; *spB* present, shorter than *sp6*; *sp6* greatly enlarged at base and elongate; *sp1-sp5* distinctly shorter than *sp6*; *sp4* and *sp2* slightly longer than other spines of apical series (*sp1-sp5*), *sp1b* shortest; *sp1-sp5* regularly spaced, separated by length of an individual spine or less although spines may alternate between anterior and posterior borders; along posterior border separation between *sp1b* and *sp2* nearly one-half distance between *sp2* and *sp4*, longer than space between *sp4* and *sp5*; base of *sp6* separated from *sp5* by approximately same distance between *sp5* and *sp4*; exceptionally deep ventral groove running between anterior (*sp-1b* and *sp-3*) and posterior (*sp1b*, *sp2*, *sp4*, and *sp5*) spines of apical series, much deeper than those shallow furrows present in some modern species; metatibia slightly longer than metafemur; metatibia with minute, basal spine present on ventral surface, with single, short spine at about three-quarters length from metatibial base as well as an apical and subapical spine; basalmost metatarsomere minute, distal metatarsomere elongate, slightly less than one-half length of metatibia; claws simple. Abdominal terga with scattered, minute setae, without distinct, transverse rows of setae along posterior margins; ninth tergum with paired rows of stiff, short setae on either side of midline; tenth tergum with strong, elongate, procurved hook, hook about one-half cercus length. Cercus ovoid except tapering toward apex, unsegmented, with scattered setae, none longer than cercus, without apical spinelike seta.

Wing venation faint with most veins represented by fuscous lines, membrane generally hyaline with scattered minute setae except exceedingly faint infuscation forming ill-defined pterostigma in forewing; marginal setae on both fore and hind wings numerous and short, not much longer (if at all) than those setae on membrane. Forewing with ill-defined, elongate pterostigma along anterior margin, proximally appearing slightly be-

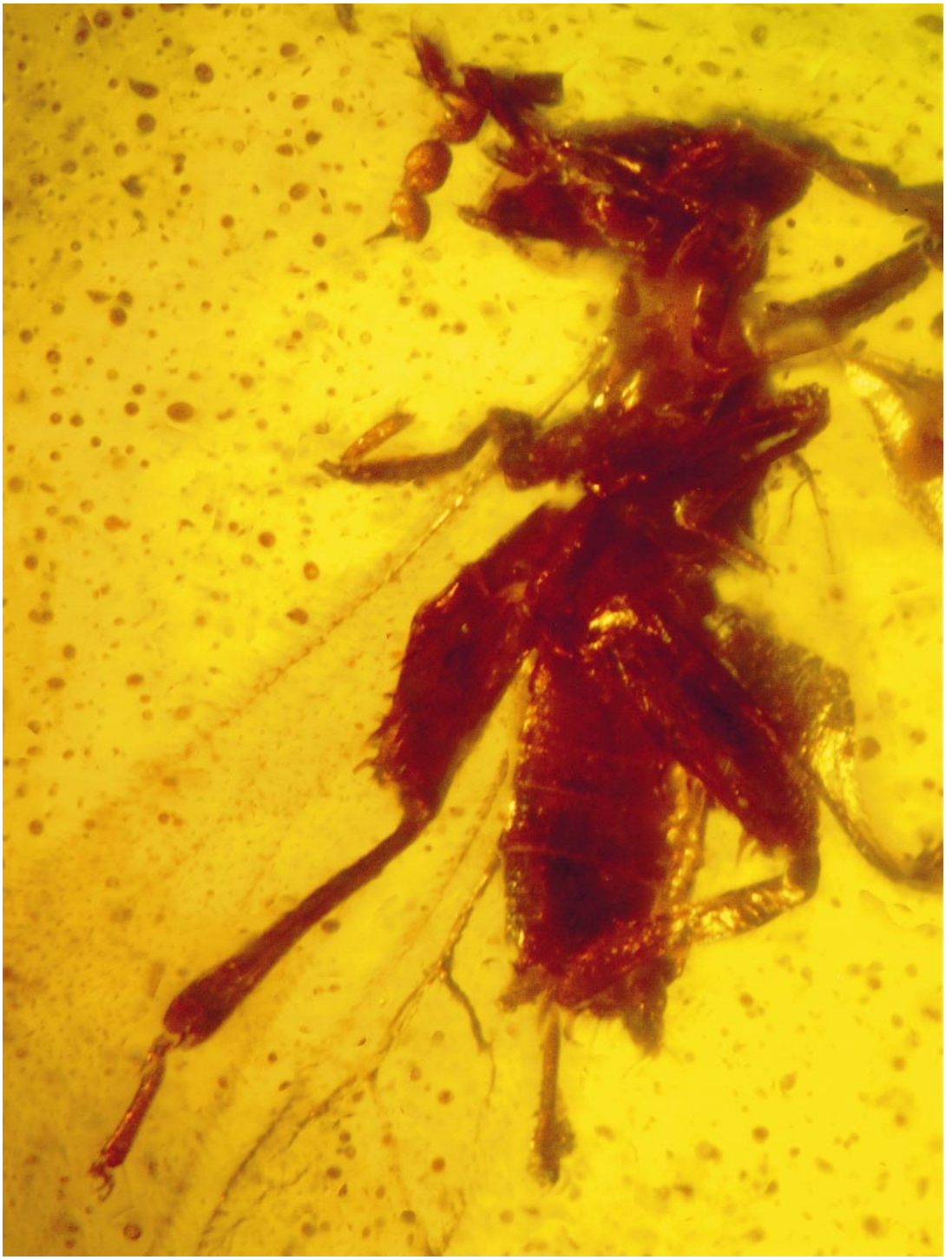


Fig. 11. Color, ventral photomicrograph of holotype male of *Xenozorotypus burmiticus*, new genus and species (AMNH Bu-182).

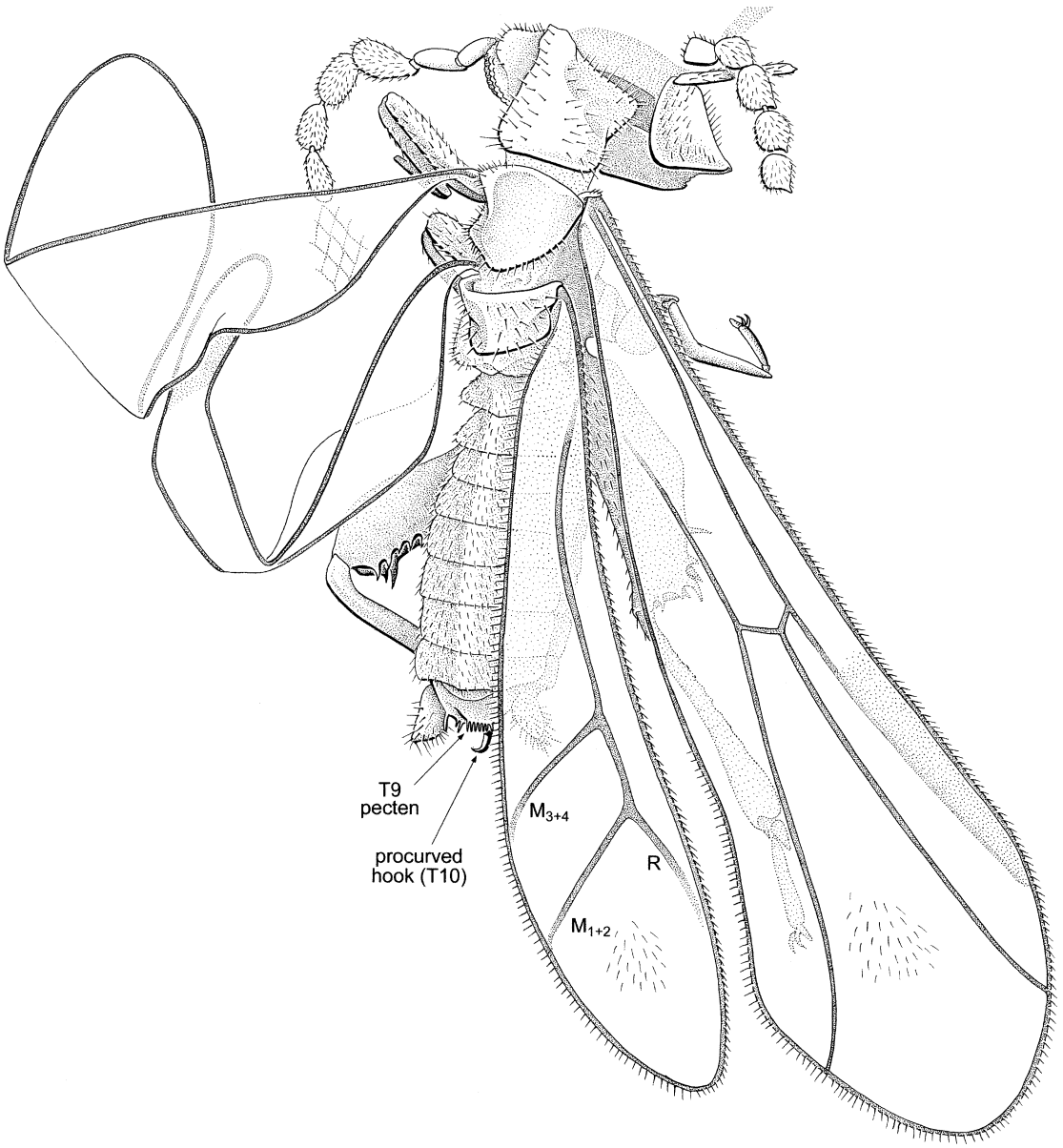


Fig. 12. Dorsal habitus of holotype male of *Xenozorotypus burmiticus*, new genus and species (AMNH Bu-182).

yond origin of Rs, bordered posteriorly by R_1, disappearing well before termination of Rs on wing margin; C+Sc relatively strong on margin to point just beyond Rs termination; R_1 becoming exceedingly faint near pterostigma, apparently reaching wing margin at pterostigmal apex; Rs separating from radial stem near midpoint of wing, connected with M by rs-m crossvein that is longer than first abscissa of Rs, Rs reaching anterior wing margin near wing apex, becoming spectral by wing margin; M reaching posterior wing margin near wing apex at approximately comparable position as termination of Rs; CuA not evident (this region of the wing is quite difficult to see and thus it can-

not be considered as truly absent). Hind wing with M+R running in anterior half; R, M_{1+2}, and M_{3+4} each reaching wing margins; M_{3+4} separating in distal half of wing shortly beyond wing midpoint; $R+M_{1+2}$ shorter than free abscissae of M_{3+4}, M_{1+2}, or R, approximately twice as long as distance between vein and anterior wing margin; distal abscissa of R shorter than abscissae of M_{3+4} and M_{1+2}; Cu not evident at wing base (difficult to see so it cannot be considered as truly absent).

HOLOTYPE: Male; Myanmar: Cretaceous, Kachin: Tanai Village (on Ledo Rd. 105 km NW Myitkyna), coll. Leeward Capitol Corp., 2000, AMNH Bu-182; in amber collection, Division of Invertebrate Zoology, AMNH.

ETYMOLOGY: The specific epithet is derived from Burmite, an older name for Burmese amber.

DISCUSSION

The discovery of *Z. acanthothorax*, *Z. cretatus*, *Z. nascimbenei*, and *X. burmiticus* extends the age of the genus *Zorotypus* and order Zoraptera from the Lower Miocene back to what is probably the late mid-Cretaceous, thereby nearly quadrupling the previous oldest age for the group (a geological leap of approximately 75 million years, if not more). Owing to the scarcity of zorapterans today, it is remarkable that four clearly distinct species should be discovered from a single deposit. Although one species, *X. burmiticus*, is relatively plesiomorphic, the other species are remarkably modern in many traits. This diversity of Burmese zorapterans is slightly more than that observed in modern tropical forests. In areas that have been heavily studied (e.g., Barro Colorado Island, Panamá, or areas in Costa Rica) typically two or three species have been discovered. Particularly, noteworthy is the presence of both alate and apterous morphs indicating that the dimorphic state of modern and Tertiary *Zorotypus* had already become established by the Cretaceous. Alate males are particularly rare and that two such individuals should be discovered is of great significance. It would appear that zorapteran diversity in tropical forests of the Cretaceous was at least comparable to that known from extant forests, and the true diversity and abundance was likely even greater.

Both *Z. acanthothorax* and *Z. nascimbenei* are noteworthy for a reduced number of antennomeres and the presence of jugate setae. While the jugate setae are undoubtedly apomorphic, the reduced number of antennomeres could be a plesiomorphic feature relative to other zorapterans. Outgroup comparison with *Xenozorotypus* and other polyneopteran orders, however, suggests that the reduction in antennomeres is apomorphic. Certainly the reduction to nine flagellomeres is apomorphic for the order while further reduction to eight is apparently apomorphic for these two species. The differences between these two species and other *Zorotypus* might eventually warrant their separation as a distinct group as it is undoubtedly monophyletic. Despite the monophyly of a group consisting of these two species, proposal of a separate genus or subgenus for them is unadvisable until the cladistic affinities of zorapteran species-groups have been established. At present there is little or no evidence to support the monophyly of the remaining *Zorotypus* species apart from this clade and thus a monophyletic group of *Z. acanthothorax* and *Z. nascimbenei* likely renders the rest of the genus paraphyletic. A separate genus or subgenus must rely not only on the supported monophyly of the new group but for *Zorotypus* sensu stricto as well. Thus, since a monophyletic *Zorotypus* s. str. cannot be conclusively established, a classification with multiple subgenera is unwarranted, no matter how strongly a *Z. acanthothorax* + *Z. nascimbenei* clade is supported. Once a cladistic study of all living and fossil *Zorotypus* has been completed in conjunction with a comprehensive, modern revision of the species, then the validity of monophyletic subgenera can be evaluated.

Huang (1980), assuming poor dispersal abilities for zorapterans, took the isolation of many species on oceanic islands to be evidence of great antiquity and considered that continental movements and climate were the principal factors leading to the present distribution of the order. Undoubtedly the order is of ancient origin and our discovery of Cretaceous *Zorotypus* indicates that distributions could have been effected by late Mesozoic

continental movements. However, species endemic to distantly isolated islands such as Hawaii, Mauritius, and Christmas Island do not reflect ancient isolations, but instead are direct evidence of their dispersal (perhaps via driftwood, since they reside in logs). Each of these volcanic islands is of Pliocene–late Miocene geological origin and the present flora and fauna is the result of dispersal with subsequent speciation/radiation on these young landmasses. That zorapterans live in relatively ephemeral, subcortical habitats also argues for their dispersal capabilities and is consistent with the dimorphism within species. During the general life of a zorapteran colony blind, wingless morphs predominate. As the population grows, resources become limited either owing to the natural decomposition of the logs in which they reside or through the consumption of local nutrients by the larger numbers of individuals. Such crowding or nutrient deficiencies trigger the production of fully eyed alates capable of dispersing to new nesting sites; females of these winged morphs probably mate prior to dispersal, thereby accounting for the relatively low abundance of alate males. Once arriving at a new log, individuals shed their wings (as do termites, ants, and some male embiids). Dealated individuals can often be found in young colonies. Experimental evidence lends credence to this scenario since both habitat quality and crowding can lead to the production of alates (Choe, 1992).

Huang (1980) is correct in noting that climate is a factor that adequately describes a large portion of zorapteran distribution. Except for four species, all zorapterans are restricted to a pantropical band between the Tropics of Capricorn and Cancer—very similar to their sister group, the Embiidina. Besides the tropical phylum Onychophora (Grimaldi et al., 2002) and a few other tropical insect taxa preserved in Burmese amber (Rasnitsyn and Ross, 2000), the zorapterans provide additional compelling evidence that Burmese amber was formed in a tropical or subtropical paleoenvironment. Today, only *Z. hubbardi*, *Z. sinensis*, and *Z. medoensis* occur north of this tropical range (but in warm temperate to subtropical regions), while the principally Caribbean *Z. snyderi* does so only marginally (by extending into southern Florida) (table 1). Species do not occur in xeric environments, so the report of a *Zorotypus* from Iran (Mossadegh, 1995) is probably a misidentification with Psocoptera (table 1), although nearly subtropical conditions are approximated by some areas in southwestern Iran along the Persian Gulf. Little emphasis should be paid to absences in distributions, but despite the intensive efforts of Australian insect surveys, no zorapteran is yet known from the mainland of Australia. A single species has been discovered on Christmas Island (New, 1995), politically an Australian territory but geographically and biologically part of Indonesia[3] and a region where zorapterans are already known to occur. If indeed the order does occur in the Australian region, then individuals would be expected in tropical Queensland or New Caledonia, areas that are typical components of old, relict distributions and particularly those affected by continental vicariance.

It is interesting to note that basal neopteran orders generally have far older geological records than those of the Zoraptera and Embiidina. For instance, the Blattodea, Grylloblattaria[4], Orthoptera, and Plecoptera each extend into the Paleozoic. The Phasmida are typically believed to be similarly distributed through time, back to the earliest Triassic (e.g., Sharov, 1968; Carpenter, 1992); however, Tilgner (2001) has thrown suspicion on the identity of the described Mesozoic and Paleozoic phasmids. The Dermaptera are well known by the Jurassic, but retain primitive characteristics. The suborder Archidermaptera, known from the Upper Jurassic and Lower Cretaceous of Asia, is notable for the plesiomorphic retention of venation (albeit

[3] Christmas Island is a small tropical island located 362 km S of the western end of Java. The island was ceded to Australia in 1958, but recently rejected secession in an unofficial 1994 referendum.

[4] Although dozens of compression fossils (mostly Permian or early Mesozoic) have been assigned to the order Grylloblattaria, these are exceedingly dubious and more accurately represent a polyphyletic assemblage of orthopteroid insects related to any number of modern orders. Grylloblattaria today are *apterous* and with several distinctive apomorphies, none of which are preserved in any of the fossils assigned to this order. Moreover, most of these fossils are preserved as wings only! Thus, hypotheses of changes in diversity and habitat that have been established for Grylloblattaria based on these fossils should be viewed with considerable skepticism.

already quite reduced) in the tegmina, segmented cerci, and pentamerous tarsi. Dermaptera, sharing the unsegmented cerci, reduced tarsi, and loss of tegminal venation typical of modern species are also known from the Lower Cretaceous (e.g., Popham, 1990) and the order perhaps originated in the earliest Jurassic or Triassic. The geological distributions of these related orders overall suggests that there is a considerable gap in the fossil record of Zoraptera and their sister group, Embiidina, particularly if derived zorapterans and webspinners already occur in the Cretaceous. The orders Zoraptera and Embidiina are perhaps of early Jurassic or Triassic origin. It is unfortunately unlikely that a pre-Cretaceous record of the Zoraptera will be added anytime soon since preservation of these small, delicate insects is most probable in amber (particularly since they are associated with trees). No pre-Cretaceous amber with insect inclusions is yet known and all such older ambers are extremely mature and fragmented, frequently represented by mere microscopic traces (Grimaldi, 1996). Baltic amber, which was produced in a warm temperate or even subtropical environment (Larsson, 1978; Engel, 2001a), has been excavated in huge amounts and the inclusions studied for three centuries, but no zorapteran has ever been discovered. It is not coincidental that the only fossil zorapterans are preserved in ambers that were formed under definitively warm-tropical paleoclimates, i.e., Dominican and Burmese ambers. The paleoenvironment during the formation of Dominican amber was wet, lowland, tropical, broadleaf forest—very similar to modern forests in Central and South America (Grimaldi, 1996). As discussed above, Burmese amber was likely produced under similarly tropical conditions.

ACKNOWLEDGMENTS

We are indebted to Paul C. Nascimbene (AMNH), whose dedicated assistance made discovery and study of these zorapterans and many other Burmese amber fossils possible. Paul was supported by NSF grant DBI-9987372 to DAG. We are further thankful to James S. Ashe for access to the automontage digital imaging system used to capture the image of *X. burmiticus* depicted in figure 11 (supported by NSF PEET Grant DEB-9978110 to J. S. Ashe); and to Tam C. Nguyen for assistance with the computer layout of the plates. MSE is grateful to Dr. Mossadegh (Shahid Chamram University, Iran) for a copy of his article on a putative *Zorotypus* in Iran. Lastly, Antonio Arillo, Charles D. Michener, Molly G. Rightmyer, and an anonymous reviewer kindly read an earlier version of the manuscript and provided valuable comments. This is contribution Nr. 3265 of the Division of Entomology, Natural History Museum and Biodiversity Research Center, University of Kansas.

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