ACTA GEOLOGICA HISPANICA, v. 35 (2000), nº 1,p. 149-164

A Winged *Zorotypus* in Miocene Amber from the Dominican Republic (Zoraptera: Zorotypidae), with Discussion on Relationships of and within the Order

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ABSTRACT

A new fossil zorapteran is described and figured in Miocene Dominican amber. The specimen is the first winged *Zorotypus* fossil, and is described as *Zorotypus goeleti* n.sp. The species is distinguished from the only other fossil zorapteran, *Z. palaeus* also in Dominican amber, as well as an extant species to which it appears most similar, *Z. snyderi*. The new fossil is significant in the possession of segmented cerci, a plesiomorphic character unique for the order. The classification of the order is briefly summarized and genera proposed by Kukalová-Peck and Peck (1993) and Chao and Chen (2000) are newly synonymized under *Zorotypus*. Phylogenetic affinities within Zoraptera and of the order among other lower Neoptera are briefly discussed. The order is considered to be most closely allied to the webspinners, order Embiidina.

Keywords: Amber. Embiidina. Paleontology. Phylogeny. Polyneoptera. Zoraptera.

INTRODUCTION

The insect order Zoraptera is a small group presently consisting of 32 extant and one extinct species with an essentially pantropical distribution (Table I). The order was one of the last living insect orders to be recognized, having been established in 1913 by the great Italian entomologist Filippo Silvestri. Zoraptera are tiny, polyneopterous insects superficially resembling Psocoptera. Species are gregarious, typically living in termite nests and under the bark of decaying logs, where they feed on fungal mycelia. Adults occur in two morphs within a species - eyed, winged forms (Fig. 1) or eyeless, apterous forms (Fig. 3). Much remains to be discovered of Zoraptera biology. The most detailed biological accounts have been prepared for the western hemisphere species *Zorotypus hubbardi* CAUDELL (1918) (Crampton, 1920; Gurney, 1938; Riegel, 1963; Shetlar, 1978; Rasnitsyn, 1998), *Z. barberi* GURNEY (1938) (Choe, 1992, 1995, 1997), and *Z. gurneyi* CHOE (1989) (Choe, 1992, 1994a,b, 1997). No common name has been widely applied to these insects outside of zorapterans; although several early German ar-

Figure 1. Dorsal habitus of holotype of *Zorotypus goeleti* ENGEL AND GRIMALDI n.sp.

ticles refer to them with the unpleasant and not very descriptive name of "Bodenläuse" (soil lice).

The phylogenetic affinities of the order have been controversial and hypotheses have shifted dramatically since its discovery. Numerous authors have addressed the question of Zoraptera's position, placing it as sister group to Isoptera (Boudreaux, 1979; Caudell, 1918; Crampton, 1920; Weidner, 1969, 1970), sister group to Isoptera + Blattaria (Silvestri, 1913), sister group to Embiidina (Minet and Bourgoin, 1986), basal to Paraneoptera (Hennig, 1953, 1969, 1981; Kristensen, 1975), in a basal polytomy of seven neopterous orders (Kristensen, 1991, 1995), sister group to Holometabola (Rasnitsyn, 1998), basal to Thysanoptera (Karny, 1922), a suborder of Psocoptera (Karny, 1932), intermediate between Isoptera and Psocoptera (Tillyard, 1926), sister group to a Dermaptera + Dictyoptera clade (Kukalová-Peck and Peck, 1993), unresolved with Orthoptera, Phasmida, and Embiidina (Kukalová-Peck, 1991), and near the base of Dictyoptera in the Polyneoptera (Carpenter and Wheeler, 1999). Although Tillyard (1926: p. 125) asserted that Silvestri originally placed Zoraptera in the Apterygota owing to the absence of wings in the series before him, this is incorrect since Silvestri (1913: p. 205) clearly states his belief that Zoraptera is near Isoptera + Blattaria.

Herein we present the description of a second fossil species (Figs. 1-2), also in amber from the Miocene of the Dominican Republic (Iturralde-Vinent and MacPhee, 1996, 1999). Poinar (1988) indicated this amber to be Lower Miocene to Upper Eocene but as discussed by Grimaldi (1995) and stratigraphically presented by Iturralde-Vinent and MacPhee (1996, 1999), there is no basis for such an old age as Eocene or even Lower Oligocene. Unlike *Z. palaeus* POINAR (1988) the species presented below is represented by an alate female. The new species is differentiated from *Z. palaeus* as well as extant members of Zorotypidae. We also present a brief summary of affinities among taxa within the order as well as the position of zorapterans among other hemimetabolous insects.

SYSTEMATICS

Order: Zoraptera SILVESTRI, 1913
Zoraptera SILVESTRI, 1913: 195.

Diagnosis: Adults minute (around 3 mm), hemimetabolous Neoptera; mouthparts mandibulate; lacinia fused to stipes, lacinia with strong inner, apical tooth, maxillary palpus five-segmented (Figs. 4, 7), distal palpal segment of labial and maxillary palpi larger than preceding palpal segments (Figs. 4, 7); prementum divided, labial palpus three-segmented; antennae nine-segmented, moniliform (Fig. 1); lateropleurite and laterosternite differentiated in alates; six Malpighian tubules (where observed); wings membranous with reduced venation or wings frequently absent, forewings narrow and paddle-shaped due to reduced anal lobe, forewing with radial, median, and cubital veins fused at base; hind wings smaller than forewings; all wings shed by a basal fracture; coxae large; metafemora stoutly expanded, with stiff spines running along ventral surface (Figs. 5, 8); tarsi two-segmented, first minute, second elongate; claws simple; abdomen 11-segmented; two abdominal ganglia (where observed); cerci present, short, unsegmented in living forms (Fig. 9), two-segmented in the fossil *Z. goeleti* (Fig. 6); ovipositor absent; female with 4-6 panoistic ovarioles (where observed); male genitalia asymmetrical.

Comments: Presently consisting of 34 species (Table 1) distributed pantropically, except for *Z. hubbardi*, which extends well into the Nearctic.

Family: Zorotypidae SILVESTRI, 1913
Zorotypidae SILVESTRI, 1913: 196.

*Type genus: Zorotypu*s SILVESTRI, 1913.

Diagnosis: As for the order (see above).

GENUS: ***Zorotypus***SILVESTRI, 1913

Type species: Zorotypus guineensis SILVESTRI, 1913, original designation.

* *Floridazoros* KUKALOVÁ-PECK AND PECK, 1993: 340. Type species: *Zorotypus snyderi* CAUDELL, 1920, monobasic and original designation. New synonymy.

* *Usazoros* KUKALOVÁ-PECK AND PECK, 1993: 340. Type species: *Zorotypus hubbardi* CAUDELL, 1918, monobasic and original designation. New synonymy.

* *Meridozoros* KUKALOVÁ-PECK AND PECK, 1993: 341. Type species: *Zorotypus leleupi* WEIDNER, 1976, monobasic and original designation. New synonymy.

* *Brazilozoros* KUKALOVÁ-PECK AND PECK, 1993: 342. Type species: *Zorotypus brasiliensis* SILVESTRI, 1946, monobasic and original designation. New synonymy.

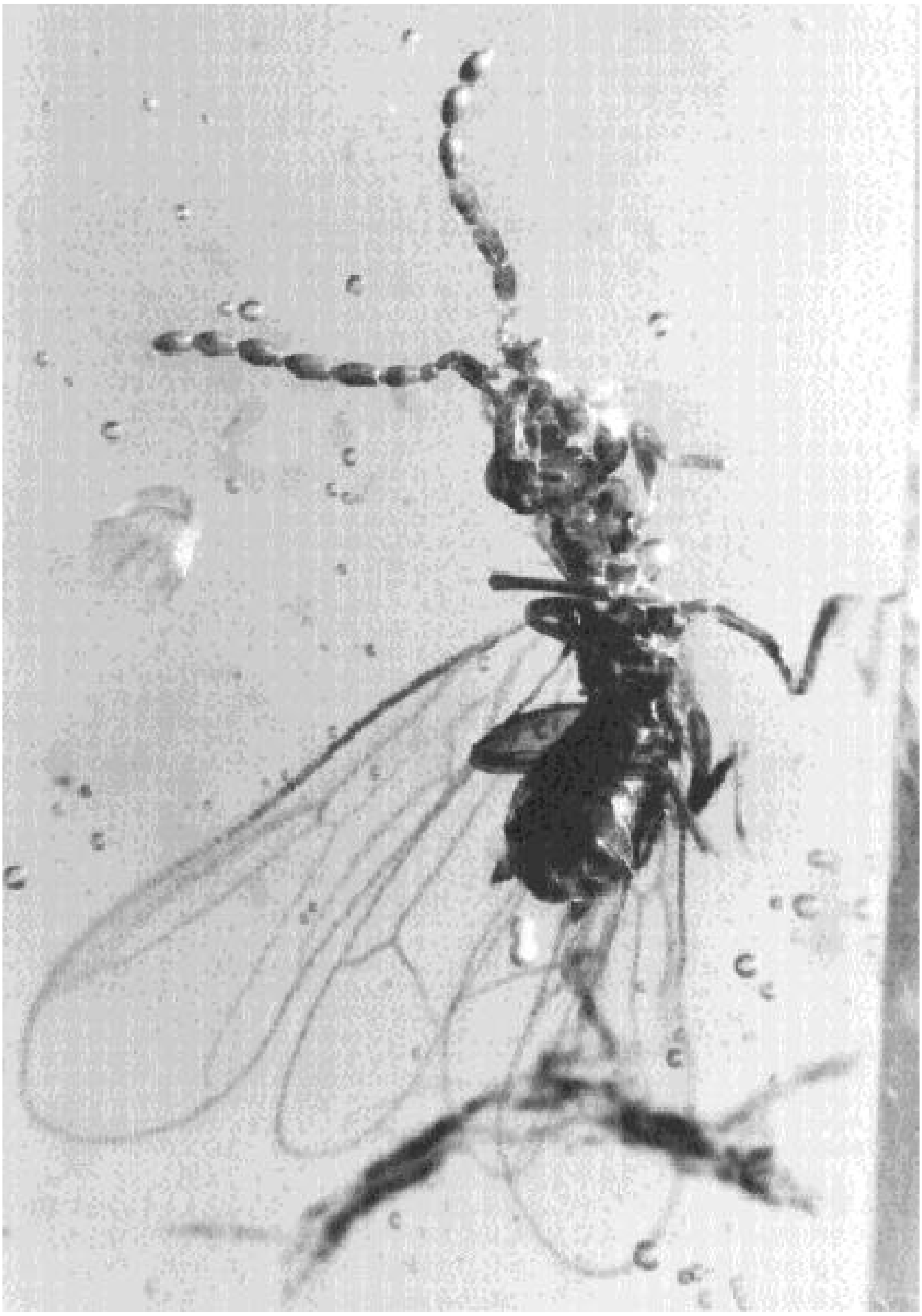


Figure 2. Photomicrograph of holotype of *Zorotypus goeleti* ENGEL AND GRIMALDI n.sp.

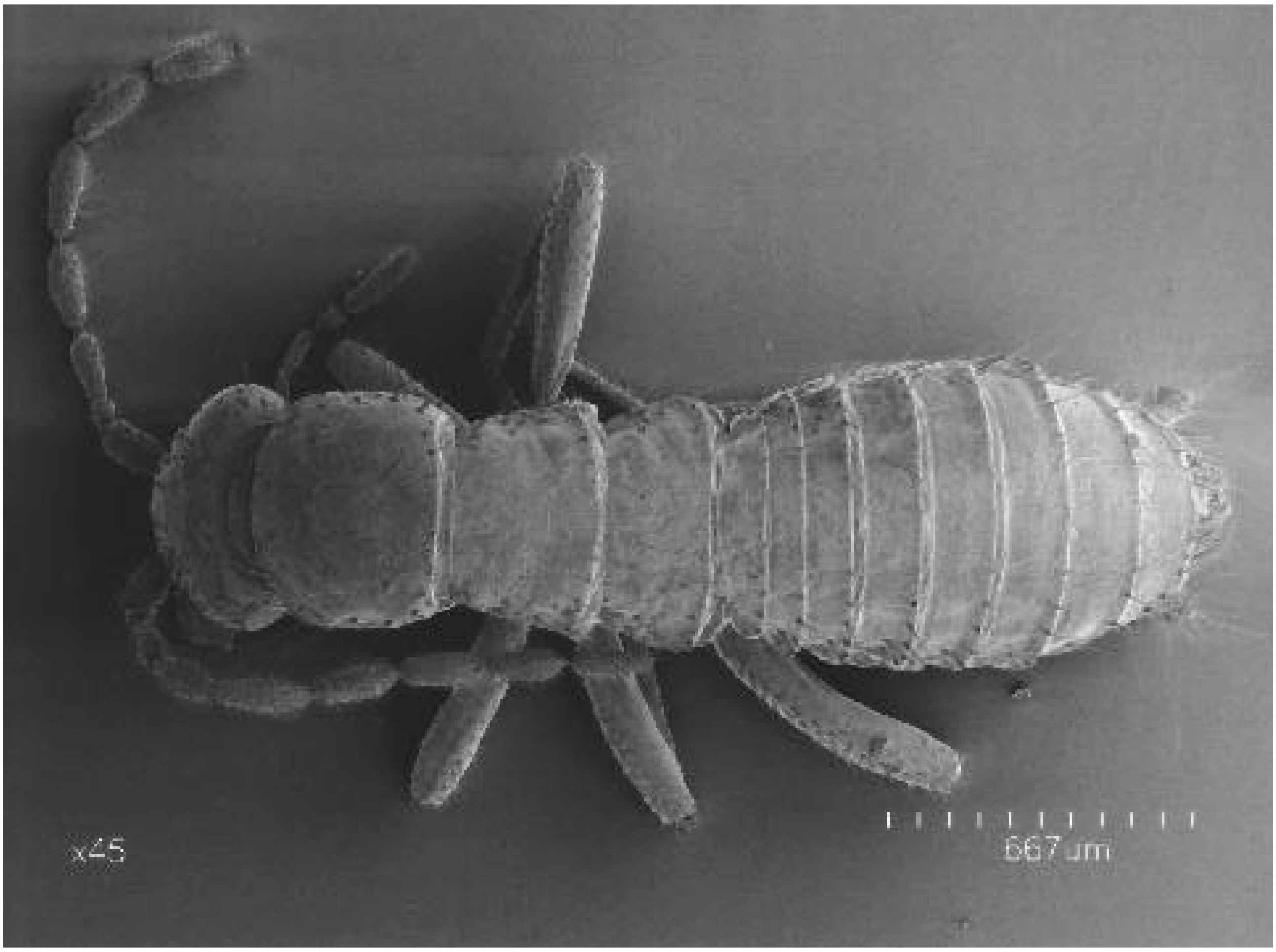


Figure 3. Scanning electron micrograph of *Zorotypus juninensis* ENGEL, dorsal habitus (from Engel, 2000).

* *Centrozoros* KUKALOVÁ-PECK AND PECK, 1993: 342. Type species: Zorotypus gurneyi CHOE, 1989, monobasic and original designation. New synonymy.

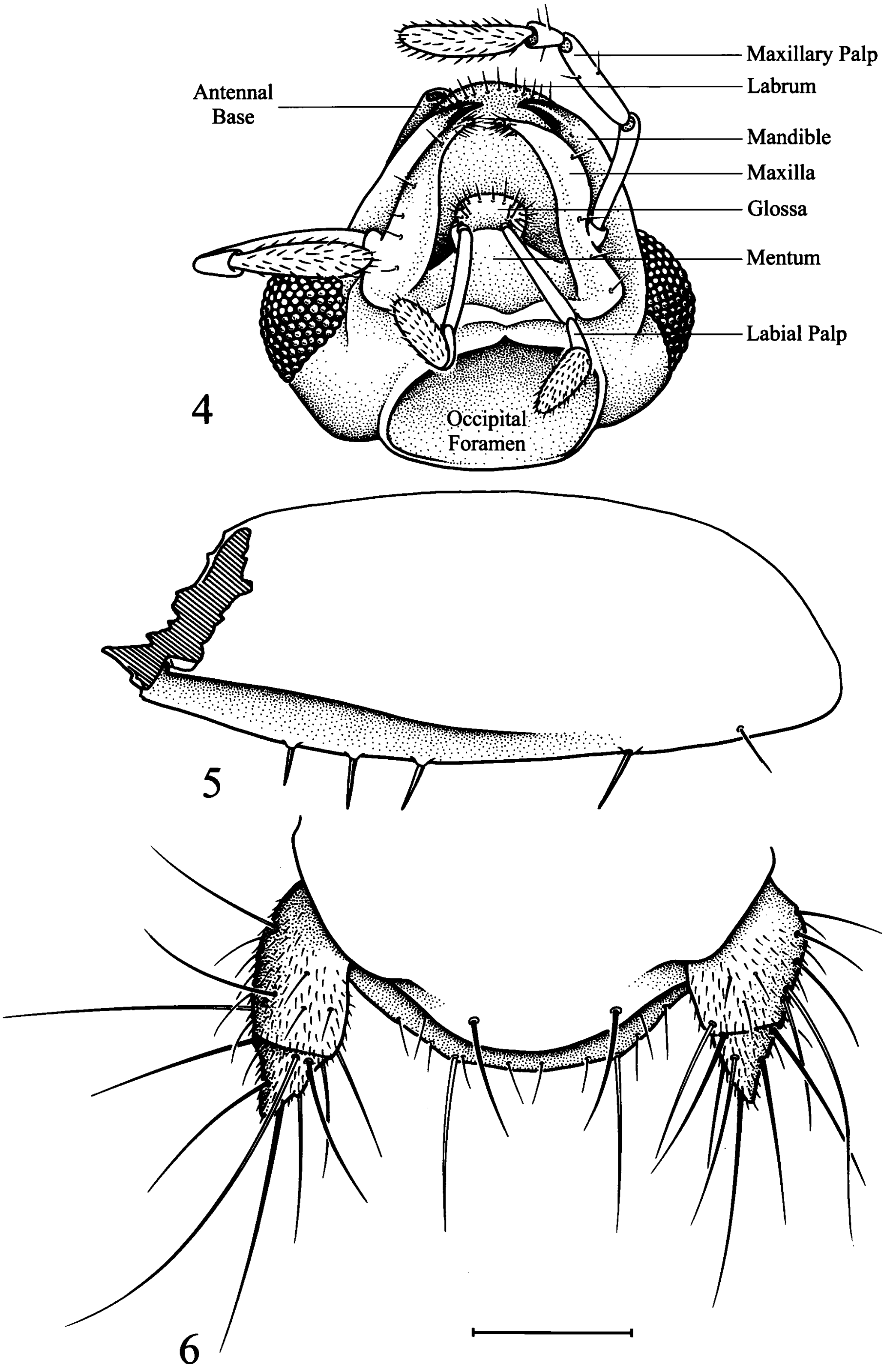
* *Latinozoros* KUKALOVÁ-PECK AND PECK, 1993: 342. Type species: *Zorotypus barberi* GURNEY, 1938, monobasic and original designation. New synonymy.

* *Formosozoros* CHAO AND CHEN, 2000: 24. Type species: *Formosozoros newi* CHAO AND CHEN, 2000, monobasic and original designation. New synonymy.

Diagnosis: As for the family (see above).

Comments: We have taken a conservative stance with zorapteran classification. The generic characters proposed by Kukalová-Peck and Peck (1993) are either continuous across taxa or variable within a given species. For example, the breadth of the petiole in the forewing varies continuously across species, with no discrete separation between "broad" and "narrow". Similar continuous variation occurs for their characters "breadth of C-R+RA area", "length of ScP", "length of MP+Cu", "length of MP+CuA", "length of "CuA_{1+2}", "height of CuA_{1+2} curve", and "length of CuA_{3+4}" (terms in accordance with Kukalová-Peck's wing vein terminology). The degree to which the pterostigma is developed is continuous both across taxa and individuals of a single species. The venational homologies proposed by these authors are dubious.

The classification of Kukalová-Peck and Peck (1993) is based solely on wing venation and owing to the great variability in these characters, the classification is probably unstable; additionally so given that most species are known on the basis of apterous individuals only. Thus, owing to the extreme morphological homogeneity among



Figures 4-6. Characters of *Zorotypus goeleti* ENGEL AND GRIMALDI n.sp. 4. Ventral surface of head. 5. Metafemur. 6. Abdominal apex detailing cercal structure and setae. Scale bar = 1 mm.

the species and the low specific diversity of the order, the recognition of multiple genera is unneeded, particularly since *Zorotypus s.str.* is rendered paraphyletic. Until a system can be developed and taxa diagnosed on a variety of character systems, including metafemoral spination, genitalia, wing venation, structure of the cerci, chaetotaxy of the vertex, etc. (e.g., see below "Internal Affinities..."), it is most prudent not to present a new, formal classification. All of the specific combinations proposed by Kukalová-Peck and Peck (1993) are, therefore, here returned to *Zorotypus*.

Most recently Chao and Chen (2000) proposed another genus in the family based on a single apomorphic species from Taiwan. All of the characters in their generic description except for two are universal for the order (i.e., found in all zorapterans). The remaining two characters, relatively long first tarsomere and eloncate cerci, while noteworthy and apomorphic are not generically distinctive. The first feature serves to separate the Taiwanese species from all other Asian species but is an isolated apomorphy that certainly renders *Zorotypus* paraphyletic, particularly when the following character is considered with a global view. The elongate cerci are by no means distinctive of the species from Taiwan and are identical in shape and overall structure to those of *Z. longicercatus* CAUDELL from Jamaica. *Zorotypus longicercatus* has the same elongate cerci (perhaps even slightly longer than Chao and Chen's species) that lack a terminal spine. While certainly an important new species and a valuable contribution, the recognition of a monotypic genus is not warranted or advisable and *Formosozoros newi* is transferred to the genus *Zorotypus* [*Zorotypus newi* (CHAO AND CHEN), new combination].

Zorotypus goeleti n.sp.

Figures 1-2, 4-6

Diagnosis: The new fossil would apparently belong to a group of western hemisphere species in which the row of spines on the ventral surface of the metafemur is interrupted (Fig. 5); alternatively this species could be sister to all living species (see discussion of relationships below). *Zorotypus goeleti* can be readily distinguished from the only other fossil zorapteran, *Z. palaeus*, which has a single, uninterrupted row of such spines, more numerous spines closely spaced along the distal third of the metafemur, and a basal-most spine which is not significantly longer than the others. *Zorotypus goeleti* most closely resembles *Z. snyderi* CAUDELL (1920), which differs in having a quadrate pronotum, the basal half of the metafemur more pronouncedly swollen than the distal half, R1 reaching to the wing apex in the forewing, and ovoid cerci. Perhaps the most distinctive feature of the new species is the presence of segmentation in the cerci which readily separates it from all other members of the order.

Description: Alate female.- Body length (exclusive of antennae) 1.98 mm; antennal length 1.25 mm; forewing length 2.43 mm; hind wing length 1.95 mm; head length 0.5 mm, anterior width (just anterior to compound eyes) 0.42 mm, posterior width 0.51 mm (from outer margins of the compound eyes); distance between lateral ocelli 0.26 mm; distance from median ocellus to lateral ocellus 0.18 mm; distance from lateral ocellus to compound eye 0.03 mm; pronotal length 0.38 mm, anterior width 0.4 mm, posterior width 0.29 mm; mesonotal length 0.33 mm, width 0.38 mm; metanotal length 0.21 mm, width 0.37 mm; metafemoral width 0.23 mm, length 0.65 mm; metatibial length 0.71 mm; metatarsomere II length 0.3 mm; abdominal length 0.86 mm; cercus length 0.14 mm. Integument generally light brown to brown and smooth except pterothorax dark brown.

Head: Head subtriangular, portion of head anterior to compound eyes slightly longer than compound eye, of equal width to anterior margin of pronotum; posterior border of head slightly broader than pronotum. Median ocellus set just apical to anterior tangent of compound eyes; distance between lateral ocelli slightly greater than length of first antennomere. Second antennomere weakly curved outward, narrow, width one-half that of first antennomere; combined length of second and third antennomeres slightly less than that of first, about as long as that of fourth; second antennomere about as long as third. Inner margins of compound eyes emarginate above, two facets deep by five facets long, emargination on posterior half of eye. Integument just posterior to compound eyes weakly bulging, creating an exceedingly short posterior collar. Setae of vertex mostly restricted to posterior borders of head, a few fine, scattered setae between lateral ocelli. Epicranial suture exceedingly faint. Gena with a few long setae just below compound eyes. Setal pattern of head depicted in figure 1. Mandible apparently simple without subapical teeth, apex pointed; lacinia with pointed apex, and possibly with subapical tooth (difficult to see); galea with fringed apex as in living species; maxillary palpal segments 2, 3, and 5 elongate, segments 1 and 4 about as long as apical width, segment 2 not widened at apex and about as long as segment 3, segment 3 slightly wider at apex than at base, segment 5 slightly longer than proximal segments, gently swollen on ventral margin, more densely setose than preceding segments; glossa

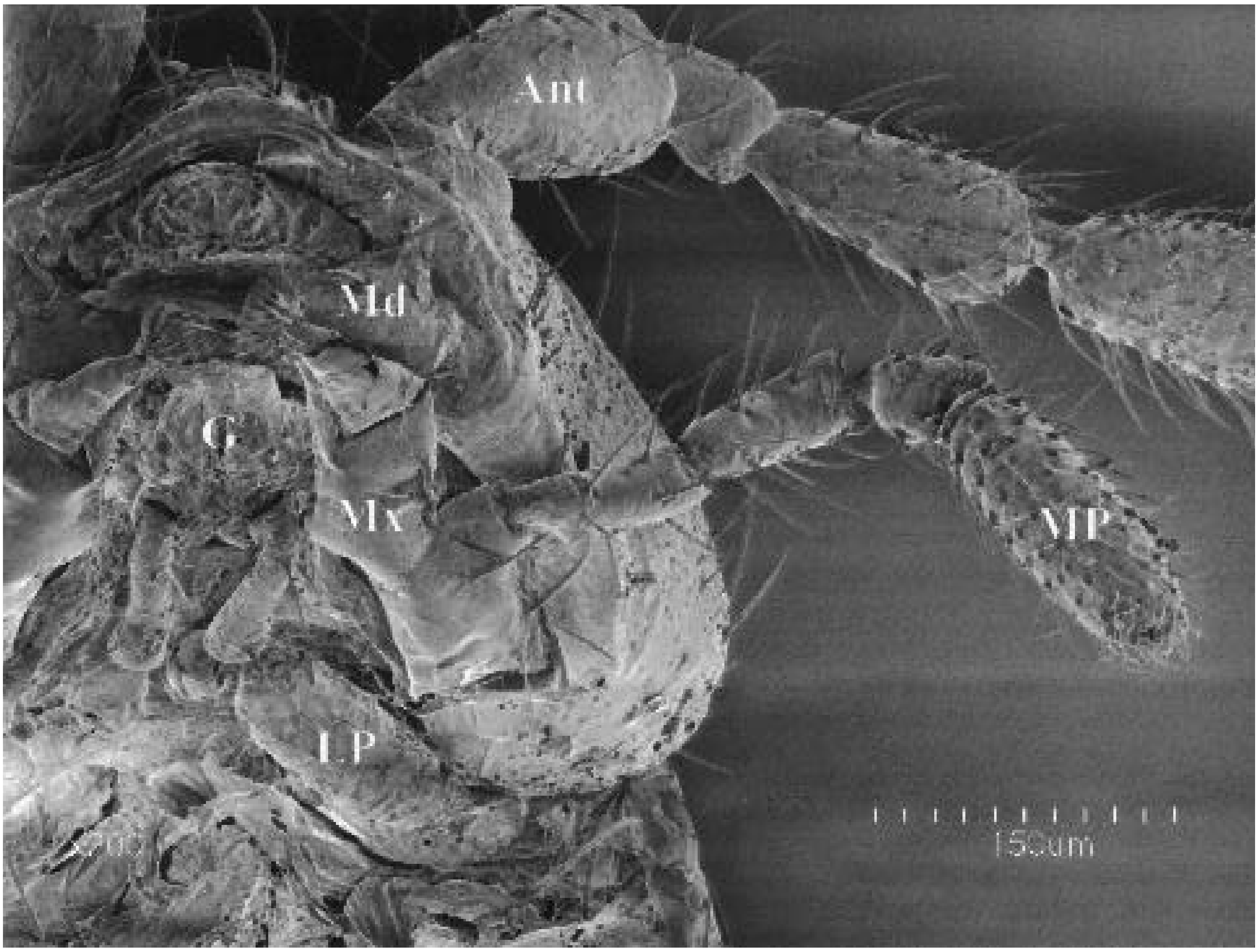
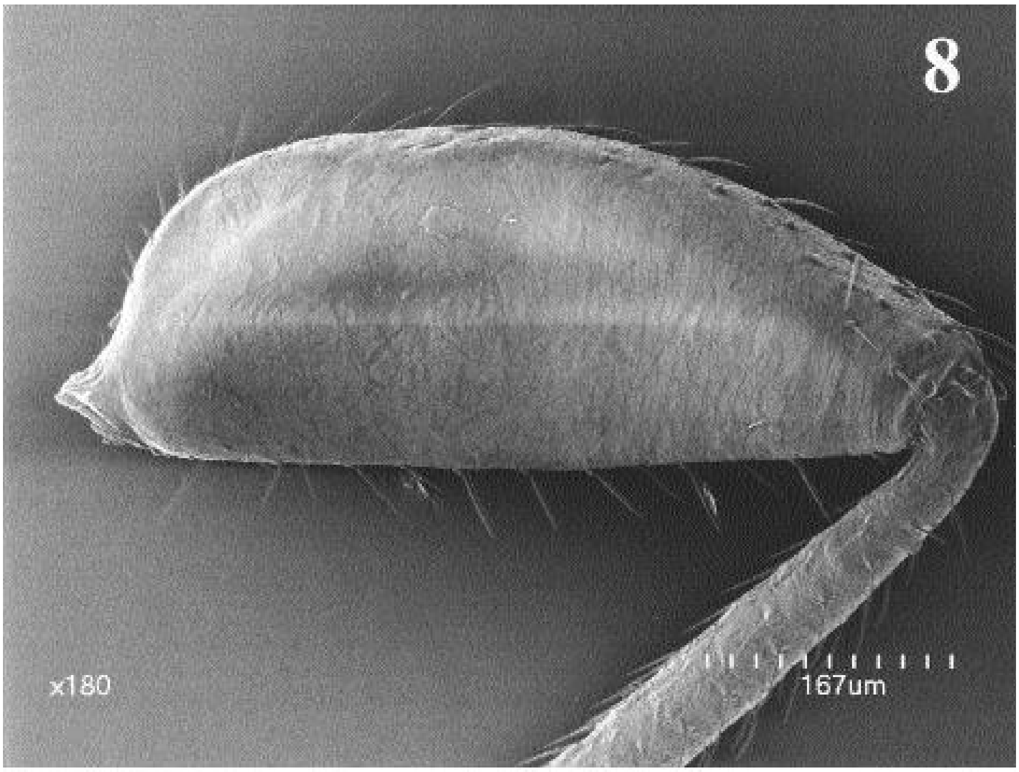
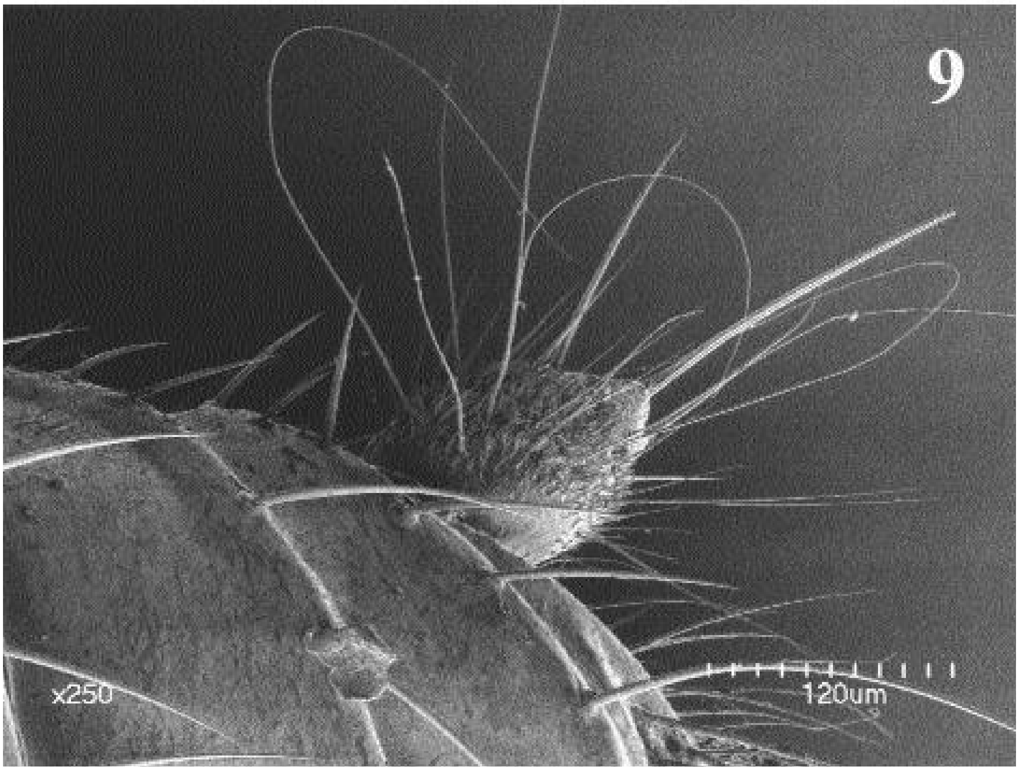


Figure 7. Ventral surface of head of *Zorotypus juninensis* ENGEL, scanning electron micrograph (from Engel, 2000); note that the right labial palp (left in the micrograph) is broken and missing its terminal segment while the right palpus (left in the micrograph and with its terminal segment labeled) is oddly appressed to the ventral side of the head and slightly broken between the terminal segment and the segment immediately preceding it. Ant = antenna, G = glossa, LP = labial palp, Md = mandible, MP = maxillary palp, Mx = maxilla.

short and rounded with numerous, fine scattered setae; labial palpal segments 1 and 3 elongate, segment 1 longest, narrow, and not widening towards apex, segment 2 short about one-third length of segment 1, segment 3 slightly shorter than segment 1, gently swollen on ventral surface, distal segment more densely setose than preceding segments. Mouthparts depicted in figure 4.

Thorax: Pronotal length subequal to anterior width (refer to metrics above); posterior width slightly less than anterior width, therefore pronotum is weakly constricted posteriorly. Two crescentic ridges running along anterior third of pronotum (Fig. 1). Longest setae of pronotum on lateral margins, smaller setae scattered on pronotum except for middorsal line; setae long and anteriorly directed except posterolateral-most setae, which are directed posterad with two minute setae just anterior to this. Mesonotum and metanotum each about as broad as anterior width of pronotum and slightly broader than long. Forewing venation faint with most veins represented by fuscous lines; pterostigma exceedingly lightly sclerotized; C+Sc becoming faint by base of pterostigma; R1 disappearing by base of pterostigma; Rs reaching nearly to wing apex before becoming slightly diffuse around apex of pterostigma; r-m present, very short, equal in length to basal section of Rs between stem of R and juncture with r-m; M reaching to posterior wing margin and equidistant from wing apex as is R_1; CuA_1 present and reaching to





Figures 8-9. Characters of *Zorotypus juninensis* ENGEL, scanning electron micrograph (from Engel, 2000). 8. Metafemur. 9. Abdominal apex, showing detail of unsegmented cercus.

posterior wing margin just beyond midwing; CuA_2 present as a short stub in basal third of wing; setae on wing membrane numerous and short, not concentrated in any portion of the wing. Hind wing with M+R running in anterior half, both R and M reaching respective wing margins; Cu absent. Marginal hairs on both fore and hind wings noticeably longer medially on posterior margin; lengths greater than twice that of setae on wing membrane. Legs with scattered setae of moderate length intermixed with much shorter and more numerous setae. Metafemur about three times longer than broad, not noticeably more swollen towards base than towards apex, gently but rapidly tapering at apex to join metatibia; ventral surface with four short, stiff spines (Fig. 5); proximal spine about one-third along length of metafemur, distinctly separated from remainder of spines beginning around midpoint. Proximal spine noticeably longest, apical series of spines of roughly equal length except distal spine slightly smaller. Metatibia slightly longer than metafemur. Metatarsomere II long, nearly one-half length of metatibia.

Abdomen: Posterior margin of each tergite with a single, transverse row of setae of moderate length, except such hairs longer laterally; T9 and T10 with two distinct apical setae and shorter laterals; T10 broadly rounded apically; sterna with scattered short setae; medio-apical margin of distal sternum shallowly and narrowly emarginate. Cerci not ovoid, instead strongly narrowed distad and apically pointed (Fig. 6); two-segmented, slight constriction just beyond midpoint with distinct annular ring; with numerous long preapical setae, of these outer-mediolateral seta longest; apical seta just longer than cercus, slightly shorter than outer-mediolateral seta.

Male and apterous morphs. Unknown.

Holotype: Alate female; Miocene, Dominican Republic, AMNH, DR-14-34; from northern mines (specific mine unknown). Labeled “Holotype, *Zorotypus goeleti* Engel & Grimaldi”. In amber fossil collection, Department of Entomology, American Museum of Natural History.

Etymology: The specific epithet is a patronymic honoring a very generous benefactor of the American Museum of Natural History, Mr. Robert G. Goelet.

Preservation: The specimen is completely preserved in a piece of dark yellow amber originally 15 x 12 mm, 4 mm thick (oval), eventually embedded in epoxy and trimmed to better see details of the inclusion. The entirety of the dorsal surface is fully visible, with the wings overlapping slightly (Figs. 1-2). The ventral surface is also easily visible except for a few areas obscured by the legs. The ventral surface of the head is particularly well positioned so that the mouthparts can be examined with ease (Fig. 4).

DISCUSSION

Internal Affinities of *Zorotypus*

A specific-level phylogeny of Zoraptera has never been attempted and we do not undertake a cladistic analysis of the species here. This is due to the difficulty in comparing across all of the presently known taxa for two reasons; 1) most species are presently known from only one morph (apterous vs. winged) or sex; and 2) a world revision of the order is needed, since species are mostly known from a few, isolated specimens that are not well described and for which material is difficult to obtain (especially for African or southeast Asian species). Despite these difficulties, some comments can be made on possible affinities of species or species groups within the order, to provide a context for the new fossil species, *Z. goeleti*. This discussion will perhaps indicate characters that could be explored more fully for understanding *Zorotypus* phylogeny.

The new species presented above would appear to belong to a group of at least four western hemisphere species in which the row of metafemoral spines is interrupted. In some species (e.g., *Z. barberi*, *Z. snyderi*, *Z. shannoni*) the basal-most spine, or set of spines, is clearly separated from the apical series, whereafter the spines are evenly spaced. The alternative type (e.g., *Z. gurneyi*, *Z. neotropicus*, *Z. leleupi*, *Z. palaeus*, *Z. weidneri*, *Z. hamiltoni*, *Z. cramptoni*) have all the spines occurring at regular intervals. It is unclear whether this character is congruent with a species group that can be defined by the coiled intromittent organ positioned between the arms of the bifurcated basal plate in males (New, 1978; Choe, 1989); the inclusion of *Z. snyderi* within this group of “coiled” species appears to be the only exception. With respect to the metafemoral structure *Z. goeleti* falls into the first category and can be readily distinguished from the only other fossil zorapteran, *Z. palaeus*, which belongs to the other. The presence of CuA_1 in the forewing resembles the state seen in *Z. gurneyi*, *Z. brasiliensis*, *Z. leleupi*, and *Z. hubbardi*, but all of these species have ovoid cerci and metafemoral structures of both categories as do many of the other neotropical species. In *Z. goeleti* R_1 does not

SPECIES	DISTRIBUTION
Zorotypus barberi GURNEY	Costa Rica (Cocos), Panamá
Zorotypus brasiliensis SILVESTRI	Brazil
Zorotypus buxtoni KARNY	Samoa
Zorotypus caudelli KARNY	Indonesia (Sumatra)
Zorotypus ceylonicus SILVESTRI	Sri Lanka
Zorotypus congensis RYN-TOURNEL	Zaire
Zorotypus cramptoni GURNEY	Guatemala
Zorotypus delamarei PAULIAN	Madagascar
† *Zorotypus goeleti* ENGEL AND GRIMALDI	Dominican Republic
Zorotypus guineensis SILVESTRI	Guinea
Zorotypus gurneyi CHOE	Panamá
Zorotypus hamiltoni NEW	Colombia
Zorotypus hubbardi CAUDELL	United States
Zorotypus huxleyi BOLIVAR Y PIELTAIN AND CORONADO	Brazil, Peru
Zorotypus javanicus SILVESTRI	Indonesia (Java)
Zorotypus juninensis ENGEL	Peru
Zorotypus lawrencei NEW	Christmas Island
Zorotypus leleupi WEIDNER	Galapagos
Zorotypus longicercatus CAUDELL	Jamaica
Zorotypus manni CAUDELL	Bolivia
Zorotypus medoensis HWANG	Tibet
Zorotypus mexicanus BOLIVAR Y PIELTAIN	Mexico
Zorotypus neotropicus SILVESTRI	Costa Rica
Zorotypus newi (CHAO AND CHEN)	Taiwan
† *Zorotypus palaeus* POINAR	Dominican Republic
Zorotypus philippinensis GURNEY	Philippines
Zorotypus shannoni GURNEY	Brazil
Zorotypus silvestrii KARNY	Indonesia (Mentawai)
Zorotypus sinensis HWANG	Tibet
Zorotypus snyderi CAUDELL	Jamaica, United States
Zorotypus swezeyi CAUDELL	Hawaii
Zorotypus vinsoni PAULIAN	Mauritius
Zorotypus weidneri NEW	Brazil
Zorotypus zimmermani GURNEY	Fiji

Table 1. List of presently known Zoraptera species (updated from Choe, 1992), alphabetical by species*. Daggers indicate fossil taxa. A species, excluded from this list, is recorded from Angola under the *nomen nudum Zorotypus machadoi* (Delamare-Deboutteville, 1951). * The names *Z. chinensis* given in Hwang (1974), *Z. hubbardis* given in the title of Crampton (1920), and *Z. guineen*is listed in Choe (1992) are all *lapsus calami* for the species *Z. sinensis*, *Z. hubbardi*, and *Z. guineensis*, respectively. Abundant material, perhaps of *Z. barbieri*, is kown from the Dominican Republic (M. Ivie, pers. comm.)

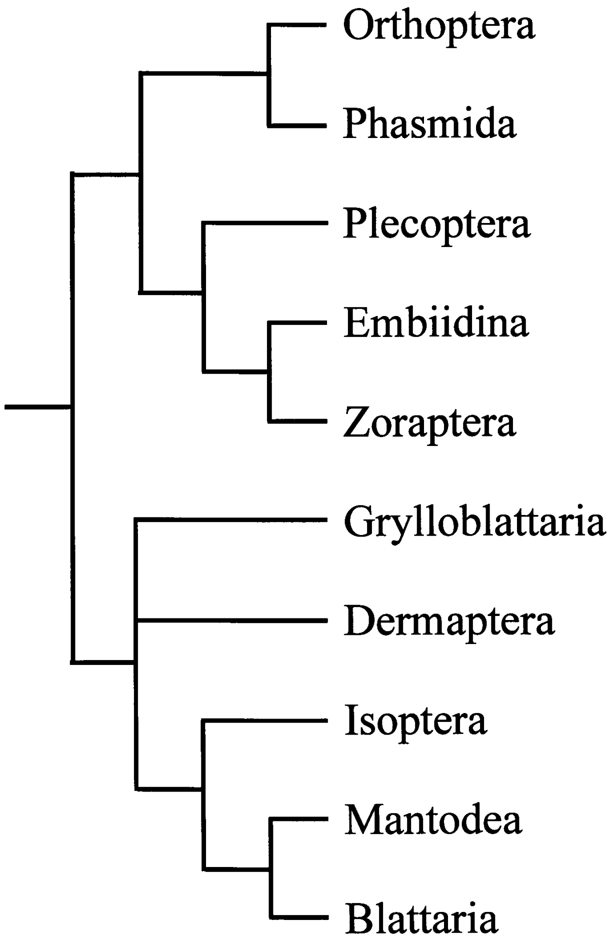


Figure 10. Preferred hypothesis of phylogenetic relationships within Polyneoptera.

reach the wing apex as a well defined vein and instead becomes entirely fuscous and diffuse at the base of an exceedingly faint pterostigma, differing from species such as *Z. gurneyi*, *Z. snyderi*, and *Z. caudelli* in this respect. The new species also lacks vein Cu in the hind wing and has the fine hairs noticeably longer on the posterior margins of the fore and hind wings. The pronotum is slightly narrowed posteriorly, somewhat similar to the African species *Z. congensis*, *Z. delamarei*, and *Z. vinsoni*, but the structure of the cerci and metafemur can quickly distinguish *Z. goeleti* from these species. The second metatarsomere is elongate in *Z. goeleti* (and in *Z. neotropicus*), being nearly one-half the length of the metatibia. This differs from the United States species in which this structure is only about one-third the length of the metatibia. If *Z. goeleti* is sister to the remainder of *Zorotypus* species owing to the plesiomorphic segmentation of the cercus, then some of the above similarities may also prove to be plesiomorphic or convergent.

Additional characters appear to be useful in picking out species groups but are not known for enough taxa for consideration at this time. The presence/absence of a medio-apical cleft on S8 in females; the shape, position, and size of the anterior arms on S9 in females; the general structure of the male genitalia; the relative sizes and shapes of the maxillary and labial palpi; and the structure of the mandibles all deserve detailed study.

Ordinal Phylogeny

As was alluded to in the Introduction, the phylogenetic placement of the Zoraptera has been of considerable interest and legitimate debate. For our discussion we shall only briefly touch on the more significant studies addressing zorapteran affinities.

Hennig (1969, 1981) considered the Zoraptera to be the basal-most Paraneopteran lineage, based on the development of the "areola postica" in the forewing, the reduced number of tarsomeres, and the reduced number of abdominal ganglia. Later, Minet and Bourgoin (1986) associated the Zoraptera with the order Embiidina based on the development of the metafemur and tibial musculature (both orders share a number of characteristics which are detailed further below). This is perhaps the best supported position for Zoraptera among other insects. Most recently, Rasnitsyn (1998) hypothesized that Zoraptera is allied with the extinct order Caloneurodea and represents the sister group of the Holometabola. His position was based on evolutionary hypotheses of particular characters that were overlooked because of their apparent lability, or homoplasy. Most notably, the medial mesocoxal articulation was used along with the presence of the "discrimen" (impressed line indicating sternal invagination) to unite Zoraptera with the endopterygote orders. Although Zoraptera lack a medial mesocoxal articulation, the presence of a medial mesocoxal swelling in was argued to be an incipient precursor to a true articulation and homologous with the articulation in Holometabola. Rasnitsyn's own evidence, however, suggests a gladular function for this structure by the presence of secreted substances and numerous secretory cells under the integumental surface. Thus, the homology between the medial mesocoxal articulation in Holometabola and the glandular swelling in Zoraptera does not seem well justified. The discrimen of Rasnitsyn

(1998), however, seems more well founded and may truly represent remnants of an invaginated sternum. Taken in context with the numerous characters uniting Zoraptera with lower Neoptera, however, it must be interpreted as convergent. Many of the musculature characters discussed by Rasnitsyn (1998) are homoplastic across all of the insect orders (occurring in groups as diverse as Ephemeroptera and Coleoptera) while the fossil orders with which he attempts to unite major groups are unknown for these characters. Also, some of the external characters he used are ambiguous for the extinct orders, and the position of the Caloneurodea is even of serious question. Sharov (1966) and Rasnitsyn (1980) both considered the order to show affinity with neuropteroids and the Coleoptera while Kukalová-Peck (1991) considered it to be allied with the hemipteroid assemblage. The order is perhaps best classified as a relative of the extinct order Protorthoptera (Carpenter, 1992; Burnham, 1984: This order is itself an extremely diffuse, certainly paraphyletic group.) and no characters conclusively support Caloneurodea as basal to the Holometabola.

A recent comprehensive analysis of hexapod ordinal relationships has been presented by Carpenter and Wheeler [1999: a summary of Wheeler et al. (in press)], based on a combination of molecular characters and previously published morphological and ethological characters. In their simultaneous analysis cladogram Zoraptera is placed in a polytomy with Grylloblattaria and Dermaptera basal to the Dictyoptera, and the position of the order within the Polyneoptera corroborates the conclusions of Boudreaux (1979) and Minet and Bourgoin (1986) even though disagreeing in finer details of relationship. In 21 of their 25 analyses the Zoraptera are supported as sister group to the Dermaptera. This novel grouping is not well supported, (a conclusion even reached by Carpenter and Wheeler, op. cit.) and corrections to their morphological interpretations might explain the result and perhaps revise future analyses. Conical coxae [a character extracted from Boudreaux (1979)] are used to unite Zoraptera, Grylloblattaria, Dermaptera, and some Dictyoptera; yet, the Clothodidae, a basal or the most basal group of Embiidina, show a similar coxal structure to that seen in Zoraptera (personal obs.). This character needs to be more carefully explored across the insect orders since it does seem to appear outside of the aforementioned six groups. The reduced indirect flight musculature, which is incompletely surveyed, and a discoid pronotum are the only characters which appear to unite this purported clade. A discoid pronotum, however, also occurs in some Archaeognatha, Ephemeroptera, Coleoptera, some orthopterans, and Plecoptera. This is an exceptionally generalized character based on shape which is exceedingly difficult to homologize. The Zoraptera were excluded from a clade containing the Orthopteroidea, Plecoptera, and Embiidina on the basis of characters of antennal circulatory development, which are actually unknown in the Zoraptera, and by the free premental lobes. In their “minimal incongruence” tree Dermaptera and Dictyoptera are united by the fusion of MA with the radial system in the forewing (a character adapted from Kukalová-Peck, 1985; Kukalová-Peck and Peck, 1993). While this coding is accurate for Dictyoptera and the fusion of R+MA+Cu is accurate for Zoraptera, the coding of this feature for Dermaptera needs revision. This character was coded as present for Dermaptera even though the hemelytra of earwigs lack venation of any sort. The coding was based on Kukalová-Peck and Peck’s (1993) assertion that the extinct order Protelytroptera are primitive relatives of or stem-group dermapterans. This position is not entirely justified, and has been based on the convergence of a large anal fan in hemelytrous insects [e.g., Umenocoleidae, placed in Protelytroptera by Kukalová-Peck (1991), but based on abundant Cretaceous material they are actually roaches (personal obs.)]. Large, fan-like anal lobes occur throughout the insects, correlated with tegminous or elytrous forewings (Orthoptera, Blattaria, Mantodea, Coleoptera), so basing a protelytropteran-dermapteran relationship on this feature is unsupported. There are indeed fossils which can be positively assigned to Dermaptera which do possess some venational details in the hemelytra; these being members of the extinct suborder Archidermaptera (Martynov, 1925; Bey-Bienko, 1936; Vishniakova, 1980; Carpenter, 1992). In the Archidermaptera, however, MA and R are not fused in the forewing at any point. Dermaptera, therefore, should be considered as lacking this feature, thereby failing to link this order with Zoraptera or Dictyoptera.

Five characters were proposed that specifically united Dermaptera and Zoraptera in some analyses. The characters optimized at this node, however, are quite homoplasious. Not discussed by Carpenter and Wheeler (1999) is the presence of maternal brood care (a groundplan feature of Embiidina), and the reduction of male gonostyli, which is present in Embiidina and Plecoptera. With regard to the remaining three characters, Zoraptera do not share states with Dermaptera nor any of the other closely allied orders (i.e., Dictyoptera and Grylloblattaria). The first of these is the development of the ovipositor which they coded as present in the Dictyoptera (actually, it is vestigial and internal in the living Blattodea and Isoptera) and Grylloblattaria, and vestigial in Dermaptera [where it is actually more developed than in most Dictyoptera, particularly in the Pygidicranidae (cf. Fig. 23.5, Rentz and Kevan, 1991)]. The Zoraptera, however, have lost the ovipositor, in this way again resembling the Embiidina and Plecoptera. The tarsomere count is autapomorphic for Zoraptera, which has two tarsomeres; Dermaptera and Embiidina have three; and the Dictyopteran orders have five tarsomeres each in the groundplan (reduced to four in all but the most basal Isoptera). Lastly, the development of the antennal circulatory organs is completely unknown for Zoraptera and thereby cannot convincingly serve to unite it with any other order.

Carpenter and Wheeler (1999) did not advocate a [Dermaptera + Zoraptera] clade even though this grouping appeared in their simultaneous analysis. As we have discussed, reconsidering the distribution and polarities of many of the non-molecular characters they cited may account for such a novel result. We suggest that the Embiidina and Zoraptera share numerous synapomorphic traits, that Polyneopteran phylogeny more closely resembles that depicted in figure 10, and that future cladistic analyses will likely recover such a grouping. Such synapomorphies for [Zoraptera + Embiidina] include:

1. Loss of Gonostyli: As noted above, the loss of the gonostylus in the male genitalia is also a feature of Embiidina and Plecoptera, as well as Zoraptera and Dermaptera. No other insect orders have this in their groundplan.

2. Cerci Reduced: The reduced number of cercal segments is found in both orders, and two-segmented cerci in *Z. goeleti* is particularly tantalizing given the presence of two-segmented cerci in Embiidina. Embiidina are autapomorphic for asymmetrically-shaped cerci (although some, like Oligotomidae, may plesiomorphically have symmetrical cerci). A definite annular ring occurs on the cerci of *Z. goeleti* beyond their midpoint (refer to the description above). Examination of some living zorapterans failed to find any evidence of segmentation and thus *Z. goeleti* likely represents the sister group to all other *Zorotypus* species (see Conclusions below).

3. Enlarged Metafemora: The tibial depressor muscles and metafemora are greatly developed and expanded in both Embiidina and Zoraptera, a derived feature unique to these two orders. A similar but convergent condition is seen in saltatorial groups (e.g., Orthoptera). The orthopteroid condition is easily distinguished from the state found in webspinners and zorapterans since the highly developed metafemoral muscles in Orthoptera are tibial levators, versus tibial depressors in the Embiidina and Zoraptera.

4. Fore and Hind Wings Narrow, Paddle-Shaped (reduction of anal region): The anal region of the wing is greatly reduced in both Embiidina and Zoraptera resulting in a distinctive “paddle-shaped” wing. This is also somewhat true in Plecoptera but in forewings only, and for all except the most basal Isoptera.

5. Apterous Morphs: Zorapterans occur in both winged and apterous morphs while the same condition occurs among some Embiidina males. Embiidina females are always wingless.

6. Dehiscent Wings: The orders Embiidina, Zoraptera, and Isoptera all possess dehiscent wings that are shed by a basal fracture, although the basal fracture in Isoptera differs significantly from that seen in the previous two orders.

7. Gregarious (maternal behavior): Both Embiidina and Zoraptera are gregarious. Neither possesses societies which can be classified as social (e.g., communal or better) but both do exhibit an extended maternal care.

8. Tarsomere Reduction: Both orders share a reduced tarsomere count; two in Zoraptera, three in Embiidina. This latter number is homoplasious and shared with Dermaptera.

CONCLUSIONS

With the sole exception of the interesting and highly significant character of segmented cerci, *Z. goeleti* in Dominican amber is very similar to living species. If the segmented cerci are viewed as a retention of the plesiomorphic condition, and unsegmented cerci as a synapomorphy linking all modern species, then the other features that the fossil shares with some of the living species (e.g., pattern of metafemoral spination) would be due to convergence. The new fossil provides little evidence to address phylogenetic relationships of the Zoraptera to other polyneopterous orders, although its modernity probably reflects the antiquity of the order. Also, a reconsideration of the morphological and behavioral characters used by Carpenter and Wheeler (1999) and Wheeler et al. (in press) as well as consideration of additional characters, indicates a sister-group relationship of the zorapterans and webspinners.

Zorapterans and embiids share several very interesting biological traits (dehiscent wings with reduced venation, and aptery), which are obviously adaptations for a cryptic way of life; this lifestyle probably fostered development of social behavior, analogous to the situation in termite colonies. Given the rich pre-Cenozoic record of orders in the Polyneoptera (e.g., Carpenter, 1992), it should be expected that pre-Cenozoic fossils of Zoraptera and Embiidina will eventually be found. These fossils will certainly be more phylogenetically significant than *Z. goeleti*. Unfortunately, outside of an undescribed, Permian fossil of a putative embiid (Kukalová-Peck, 1991), there are no Mesozoic or Paleozoic fossils of the Zoraptera or Embiidina, only embiids in Baltic and Dominican amber. Kukalová-Peck (1991: Fig. 6.19B) figured an undescribed fossil from the Permian of the Urals, which has virtually no thoracic differentiation, and a pair of terminal appendages that are either cerci or male genitalia. The right appendage is either smaller or else has only the base intact (e.g., if genitalic, the gonostylus is lost); apparent asymmetry has led Kukalová-Peck to conclude that the fossil is of embiid affinities. Wing venation is weakly preserved, and what little venation that is figured shows no diagnostic features for Embiidina. When the Zoraptera-Embiidina divergence took place is, thus, purely conjectural at this point.

ACKNOWLEDGEMENTS

MSE was supported by the generosity of Mr. Robert G. Goelet, Trustee and Chairman Emeritus of the American Museum of Natural History board of trustees, who also provided funds for the acquisition of this wonderful specimen. His sense of museum priorities - collections and collection-based research - is deeply appreciated. We are grateful to Dr. Edward S. Ross for the donation of specimens of Clothodidae and information on Embiidina; to Molly G. Rightmyer for commenting on the manuscript and assistance in preparing the figures; to Drs. Niels P. Kristensen and J. Minet for valuable reviews of the manuscript; and, even though we could not agree with their conclusions, to Drs. Ward C. Wheeler, Michael Whiting, Quentin D. Wheeler, and James M. Carpenter for sharing with us their paper on hexapod phylogeny.

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