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Authors: Engel, Michael S., and Grimaldi, David A.

Source: American Museum Novitates, 2006(3514) : 1-15

Published By: American Museum of Natural History

URL: [https://doi.org/10.1206/0003-0082\(2006\)3514\[1:TEWIE\]2.0.CO;2](https://doi.org/10.1206/0003-0082(2006)3514[1:TEWIE]2.0.CO;2)

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AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3514, 15 pp., 2 figures, 3 tables
May 17, 2006

The Earliest Webspinners (Insecta: Embiodea)

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ABSTRACT

A new genus and species of webspinner (Insecta: Embioidea = Embiidina, Embioptera *auctorum*) is described and figured from a well-preserved, alate male in mid-Cretaceous (latest Albian) amber from Myanmar (Burma). *Sorellembia estherae*, new genus and species, is distinguished from the only other Mesozoic webspinner, *Burmitembia venosa* Cockerell. Unlike the latter taxon, *S. estherae* embodies an array of notable plesiomorphies for the Neoembiodea (i.e., those Embioidea with strongly asymmetrical terminalia and the tenth tergum divided). Based on its phylogenetic position, *S. estherae* is placed in a new family, **Sorellembiidae**. *Burmitembia venosa*, on the other hand, possesses a synapomorphic suite of traits indicating placement in the Notoligotomidae (sensu novum) and as sister to the apterous subfamily Australembiinae (status novus). Past authors have considered *Burmitembia* as deserving of familial status, but it seems more conservative to combine the geographically restricted and species-poor sister families Notoligotomidae and Australembiidae and to consider *Burmitembia* as merely a subfamily therein (as Burmitembiinae). The phylogeny, classification, and geological history of the order are briefly reviewed.

INTRODUCTION

Among the smaller orders of polyneopteran insects, the webspinners (order Embioidea, approximately 360 species) are among the more biologically and anatomically distinctive. Embioideans are principally distributed pantropically, but some species extend into warm temperate or marginally into semixerid regions. Where known, species are gregarious, much like the closely related zorapterans. Individuals construct galleries from silk extruded from glands inside modified and enlarged probasitarsi. It is the presence of these glands that serves as the hallmark synapomorphy for the order, although embioideans are not without numerous other distinctive and derived traits. In addition to the probasitarsal glands (and associated modifications of the probasitarsus) and silken galleries, the embioideans are noteworthy for their trimerous tarsi, prognathous head closed ventrally by a gula, absence of ocelli, and specialized and reduced wing venation. The apomorphic peculiarities of the wings, when present (most embioideans are apterous), are associated with life within the network of silken tunnels in webspinner galleries. The venation is generally reduced, with few cross-veins, and for the most part desclerotized with sinuses running through some of the longitudinal veins. Thus, rather than forming rigid airfoils, the wings are flexible and collapsible. This flexibility permits winged males to reverse direction in tunnels without the wings becoming entangled in the silk and posing an imposition to movement. When flight is

necessary for dispersal such individuals pump hemolymph into the vein cavities, temporarily providing strength to the wing and permitting flight. Gallery life has likely also been responsible for the overall cylindrical body form of the species, a shape that lends itself well to deftly moving through the confines of tunnels.

Together with the orders Plecoptera and Zoraptera, the webspinners comprise the super-order Plecopterida within the Polyneoptera (Grimaldi and Engel, 2005). This clade is unified by the reduction and loss of the ovipositor, suppression of male styli, presence of an episternal sulcus on the trochantin, reduction in number of tarsomeres, and the presence of a ventromedian ostia in the dorsal vessel (unknown for Zoraptera). Embioidea and Zoraptera are most closely related as evidenced by the secondary reduction of the vannus to form a narrow, paddle-shaped wing; the enlarged metafemora with enlargement of the metatibial depressors (versus the metatibial levators in other lineages); dehiscent wings; presence of apterous morphs; and gregarious behavior (Engel and Grimaldi, 2000; Grimaldi and Engel, 2005).

For such a highly autapomorphic lineage one would expect paleontological data to provide the most critical insights into its phylogenetic affinities. Unfortunately, as might be expected for a lineage of small, soft-bodied, terrestrial arthropods the geological record of Embioidea is poor. Several Tertiary fossils have been described, almost exclusively from middle Eocene Baltic or Early Miocene Dominican amber (Ross,

1956, 2003b; Szumik, 1994, 1998), but a single compression fossil is also known from the Eocene-Oligocene boundary of Florissant, Colorado (Cockerell, 1908; Ross, 1984a). The sole Cretaceous record of a webspinner was *Burmitembia venosa* Cockerell (Cockerell, 1919; Davis, 1939a), from the Burmese amber deposits of northern Myanmar. The age of these deposits had been debated as being either Late Cretaceous (e.g., Cockerell, 1917) or Eocene (e.g., Stuart, 1923), but recent evidence has demonstrated Burmese amber to originate in the mid-Cretaceous (Zherikhin and Ross, 2000; Grimaldi et al., 2002; Cruikshank and Ko, 2003). Putative Paleozoic records of Embiodea are discussed later (vide Discussion, infra). Table 1 lists the described fossil Embiodea.

Herein we present the description of a second Burmese amber webspinner. Although apomorphic within the order the new fossil is considerably dissimilar to *Burmitembia* and modern webspinners and is described in a new family. Morphological terminology generally follows that of Ross (2000a) except in venational nomenclature.

SYSTEMATIC PALEONTOLOGY

ORDER EMBIODEA KUSNEZOV

Embiodea Kusnezov, 1903 [August]: 208. Originally proposed as suborder within Neuroptera.

Embiaria Handlirsch, 1903 [October]: 733.

Oligoneura Börner, 1904: 526. Originally proposed as suborder within Isoptera.

Embioptera Shipley, 1904: 260. Also proposed as French vernacular, Embioptères, by Lameere (1900).

Adenopoda Verhoeff, 1904: 196.

Embidaria Handlirsch, 1906: 33.

Aetioptera Enderlein, 1910: 171. *Partim* (= Embiodea + Isoptera).

Embiidina Enderlein, 1910: 172.³

Euplatyptera Crampton, 1916: 252.

Netica Navás, 1918: 88. Proposed as suborder (excluded suborder Oryttica: which was for *Cylindrachaeidae*, thus *Netica* = Embiodea).

Euembiararia Tillyard, 1937: 251. Proposed as suborder (excluded *Protembiararia*: which are not Embiodea, thus *Euembiararia* = Embiodea).

Euembioptera Davis, 1940a: 535. Proposed as suborder (excluded *Protembioptera*: which are not Embiodea, thus *Euembioptera* = Embiodea); proposed a second time in Davis (1940b: 677).

DIAGNOSIS: Small to moderate-sized hemimetabolous neopterans with typically slender, somewhat elongate bodies and short legs. Head prognathous, ventrally closed by gula between submentum and occipital foramen; mouthparts mandibulate; mentum reduced; submentum enlarged; dorsal paraglossa flexor present (also in Phasmatodea); compound eyes present, albeit typically not well developed; ocelli absent; antennae filiform (12–32 segments). Legs generally short; trochantin-episternal sulcus present; tarsi trimerous; probasitarsus greatly enlarged and containing silk glands (for gallery construction); metatarsus enlarged, with greatly developed metatarsal depressors (as in Zoraptera); metabasitarsus and metatarsomere II typically with plantulae; pretarsal claws simple. Females apterous (generally paedomorphic); males frequently winged, but shed wings; wings homonomous, dehiscent, with reduced venation; veins weak except R, Cu, and A typically thickened; blood sinuses formed of R, to a lesser extent around Cu and A, sometimes also weakly around Sc; Sc terminating before wing midpoint; stems of M and Cu fused at base; jugal lobe absent. Abdomen essentially 10-segmented (eleventh metamere is vestigial represented solely by cerci); first abdominal sternum reduced; cerci typically dimerous (cercal segments sometimes apomorphically fused, or with distal segments vestigial), typically asymmetrical in males; gonostylus absent; ovipositor absent; eggs tubular, with slanted and rimmed operculum. Gregarious; living in silken galleries (produced by probasitarsal glands) under bark, stones, or in soil.

COMMENTS: A universally employed name for this order, like some others, is not yet fixed. Although there are no rules governing

³ This name is often attributed to Enderlein (1903: published May 8, 1903, and therefore prior to Embiodea Kusnezov); however, in 1903 Enderlein employed the name strictly as a family-group taxon of suborder Isoptera; he explicitly indicated in that paper that he was recognizing three suborders in order Corrodentia (*Copeognatha*, Isoptera, and Mallophaga) and two superfamilies in Isoptera (*Embiidina* and *Termitina*); Enderlein, 1903: p. 424). Enderlein did not accord the name *Embiidina* as a taxon above the family group until his 1910 article. Similarly, Hagen (1861), who used the name *Embidina*, employed this name within what is today constituted as the family group.

ordinal names in zoology, Embiidina should perhaps not be employed owing to confusion with the standard suffix (i.e., *-ina*) for the rank of subtribe in the family group. Embioptera has been generally objected to by webspinner biologists on the grounds that it is not meaningful⁴ (Gr. *embios* + *pteron* = “lively wing”, clearly not descriptive of this order of less than spectacular fliers; a similar problem exists for Aetioptera and Oligoneura) and the more apt Adenopoda (Gr. *adenos* + *podos* = “gland foot”, a reference to the silk gland in the probasitarsus) has not been used since its original proposal just over a century ago. Embiodea is an appropriate, existing name for the order with a suffix not in conflict with any regulated within the family group (and, incidentally, similar to other insect lineages recognized at the same rank; e.g., Grylloblattodea, Mantodea, Blattodea, Phasmatodea). Embiodea is also not without modern usage (e.g., Beier, 1969). Protembioptera Davis (1940b) and Protembiarina Tillyard (1937), proposed for the Permian family Protembidae Tillyard (1937), are not included in the above synonymic listing despite

⁴ It should be noted, however, that not all ordinal names in insects are truly “meaningful” (or necessarily need to be). For example, Psocoptera (Gr. *psocos* + *pteron*, meaning “rubbed small” and “wing”) is a reference to their gnawing habits, Zoraptera (Gr. *zoros* + *a* + *pteron*, meaning “truly”, “without”, and “wing”) is an erroneous indication that they are wingless, and Raphidioptera (Gr. *raphidos* + *pteron*, meaning “needle” and “wing”) is actually a reference to the ovipositor. The names, however, are still somewhat descriptive; in the same sense that Ephemeroptera is descriptive (i.e., Gr. *ephemera* + *pteron*, meaning “short-lived” and “wing”, not literally meaning “short-lived wings” but instead a reference to the fact that they are pterygotes that are noteworthy for being quite ephemeral). More *meaningful* constructions of these Greek names would be to remove the wing suffix and create Psocodea (once again for the gnawing habits of barklice, but this name is generally applied for the superorder consisting of Psocoptera + Phthiraptera), Raphidioidea or Ophiodera (for the snakelike neck of snakeflies), Ephemeroidea (for the all too brief lives of mayflies), and Dimeristopoda (Gr. *di* + *meristos* + *podos*, meaning “two”, “divided”, and “foot”; in this instance for the dimerous tarsi of zorapterans). For the sake of stability and effective communication concerning these more commonly discussed orders, however, there seems little reason to change the ordinal name; unlike the situation for Embiidina which is still somewhat in flux with the literature frequently employing alternatives, the name is easily confused with the standardized suffix (i.e., *-ina*) used for subtribes.

their names. This is, in actuality, not a lineage of webspinners at all (Carpenter, 1950). The same is true for Sheimiodea Martynova (1958) (vide etiam Discussion, infra).

Within the Embiodea the South and Central American family Clothodidae is excluded from the suborder Neoembiodea (vide appendix 1 and table 2) owing to the primitive retention of symmetrical genitalia and a complete tenth abdominal tergum (not divided into hemitergites). Clothodids possess other notable plesiomorphies (which are also found in basal Neoembiodea) such as the forked MA in the forewing (CuA is also forked except in *Chromatoclothoda*). It is not at present clear whether Clothodidae is monophyletic. Should synapomorphies of the family eventually be identified, then it might be warranted to recognize a separate, basal suborder for Clothodidae (perhaps as Clothododea). More likely Clothodidae as currently defined is paraphyletic since some species exhibit more typical “embiod” features such as a simple CuA and the beginning of asymmetrical genitalia. Indeed, a superficial examination of the distribution of clothodid traits implies that *Clothoda* is basal, with *Antipaluria* and *Chromatoclothoda* more closely allied to Neoembiodea (indeed, *Chromatoclothoda* may be the *living* sister group of Neoembiodea as among the clothodids with the beginning of genitalic asymmetry *Antipaluria* retains a primitively multibranching CuA and may, therefore, be more basal: vide Ross, 1987). Neoembiodea have strongly asymmetrical genitalia and the tenth abdominal tergum divided into hemitergites, notable apomorphies in the order.

SORELLEMBIIDAE, new family

TYPE SPECIES: *Sorellembia*, new genus.

DIAGNOSIS: Body slender, cylindrical, of small size (approximately 4.6 mm in total length). Male alate, with general habitus similar to modern Embiodea (figs. 1–2). Head elongate-oval, with well-developed compound eyes; mandibles prominent, with at least two teeth at apex. Metabasitarsus with two plantulae (medial and apical); metatarsomere II with plantula. Forewing with Rs + MA and MP arising from a common point after separation from Cu (fig. 2); crossveins few; crossvein present between R and Rs +

TABLE 1
Described Fossil Embiodea^a

—Teratembiiidae			
<i>Oligembia vetusta</i> Szumik	Miocene	Dominican amber	Szumik, 1994
—Anisembiiidae			
<i>Poinarembia rota</i> Ross	Miocene	Dominican amber	Ross, 2003b
<i>Glyphembia amberica</i> Ross	Miocene	Dominican amber	Ross, 2003b
<i>Glyphembia vetehae</i> (Szumik)	Miocene	Dominican amber	Szumik, 1998; Ross, 2003b
—“Embiidae”			
<i>Electroembia antiqua</i> (Pictet)	Eocene	Baltic amber	Pictet, 1854; Ross, 1956
“ <i>Lithembia</i> ” ^b <i>florissantensis</i> (Cockerell)	Eocene-Oligocene	Florissant, CO	Cockerell, 1908; Ross, 1984a
—Notoligotomidae: Burmitembiiinae			
<i>Burmitembia venosa</i> Cockerell	mid-Cretaceous	Myanmar amber	Cockerell, 1919; herein
—Sorellembiiidae			
<i>Sorellembia estherae</i> n.gen., n.sp.	mid-Cretaceous	Myanmar amber	herein

^a The fossil *Clothonopsis miocenica* Hong and Wang (1987) from the Miocene of China was originally described as a clothodid (a family today restricted to South and Central America), but is actually a bibionid fly (Zhang, 1993).

^b The genus-group name *Lithembia* Ross (1984a) cannot be considered available. The criterion for availability requires that after 1930 every new name must “be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon” (ICZN, 1999: Art. 13.1). The “diagnosis” given by Ross (1984a) for *Lithembia* is only, “The type is a large adult male with well preserved wings displaying typical embiid venation (MA forked). Abdominal terminalia represented by only a dark blotch.” These descriptive comments do not state “characters that are purported to differentiate the taxon”, but instead merely describe the state of preservation of the holotype and why it is perhaps an embiid. No single trait is given to diagnose the taxon, and even in the key to species the fossil is separated at the first couplet by “Tertiary fossil from Florissant shales”. The same is true for the brief accounts of *Lithembia* by Carpenter (1992) and Ross (2001). Thus, *Lithembia* should very likely be considered a nomen nudum and unavailable as proposed by Ross (1984a), unless one considers “large adult male” a diagnosis. Instead, we recommend that the fossil be re-examined, diagnostic characters extracted, and the genus newly proposed (otherwise it would appear that a petition to the ICZN is necessary in order to validate *Lithembia* as it stands; the likelihood of such a petition being approved is slim).

MA; MA forked near wing apex beyond evanescent rs-ma crossvein; MP simple. Terminalia strongly asymmetrical; 10RP prominent and evident ventrally (mostly owing to damage to ninth sternum), elongate, thin, and pointed at apex; right cercus entirely vestigial (including basal section); left cercus with both sections complete and separate, with elongate setae on outer surface, distal section slightly more slender and longer than basal section.

COMMENTS: Plesiomorphies worthy of mention for Sorellembiiidae are the forked MA, the common point of separation for Rs + MA and MP, and the possession of a large, median metabasitarsal plantula. Absence of the right cercus is a significant autapomorphy for the family. The absence does not appear to be a result of imperfect preservation as that portion of the terminalia is not damaged and there appears to be no site of articulation for the cercus.

Sorellembia, new genus

TYPE SPECIES: *Sorellembia estherae*, new species.

DIAGNOSIS: As for the family (vide supra).

ETYMOLOGY: The new genus-group name is a combination of *sorelle* (Greek nickname for “old man”) and *Embia* (Gr., *embios*, meaning “lively”), the stem generic name in the order. The name’s gender is feminine.

Sorellembia estherae, new species

Figures 1–2

DIAGNOSIS: As for the genus (vide supra).

DESCRIPTION: The same characters as provided for diagnosing the family with the following additions: **Male (alate)**. Total body length (excluding antennae) approximately 4.6 mm; forewing length approximately 3.5 mm. Integument dark brown, apparently smooth (microsculpturing not evident). Head longer than wide; compound eyes prominent,

TABLE 2
Comparison of Three Classifications

Davis (1940a)	Ross (1970, 2001, 2003a, 2003b) ^a	Herein (with updates by Szumik, 2004)
Order Embioptera	Order Embiidina	Order Embioidea
Suborder †Protembioptera ^b	Suborder Embioptera	Family "Clothodidae"
Family †Protambiidae	Family Clothodidae	Suborder Neoembioidea ^c
Suborder Euembioptera	Family Embiidae	Family †Sorellembiidae
Family Clothodidae	Subfamily Archemiinae (A)	Family Anisemiidae ^d
Family Oligemiidae	Subfamily Scelemiinae (B)	Subfamily Anisemiinae
Family Teratemiidae	Subfamily Microemiinae (C)	Subfamily Scolemiinae
Family Oligotomidae	Subfamily Embiinae	Subfamily Aporembiinae
Family Notoligotomidae	Subfamily D	Subfamily Chorisebiinae
Family Anisemiidae	Subfamily E	Subfamily Platyemiinae
Family Embiidae	Subfamily F	Subfamily Cryptemiinae
	Subfamily Pachylemiinae	Subfamily Chelicercinae
	Family Notoligotomidae	Family Andesebiidae
	Family Embonychidae	Family "Oligotomidae"
	Family A	Family Teratemiidae
	Family B	Family Archemiidae
	Family Andesebiidae (C)	Family "Embiidae"
	Family Anisemiidae	Family Embonychidae
	Suborder A	Family Notoligotomidae
	Family Australemiidae	Subfamily Notoligotominae
	Family D (<i>Burmitemia</i>)	Subfamily †Burmitemiinae
	Suborder B	Subfamily Australemiinae
	Family (<i>Enveja</i>)	
	Suborder C	
	Family Oligotomidae	
	Family E	
	Family Teratemiidae	

^a Letters for suborders, families, and subfamilies follow those of Ross (1970). When the group has been subsequently named we have indicated the name followed by Ross's original letter designation in parentheses.

^b Protembioptera are not Embioidea (Carpenter, 1950, 1992) and are, therefore, not considered in later classifications.

^c The recognition of superfamilies would greatly aid the recognition of a natural hierarchy within Neoembioidea (e.g., Anisembioidea for Anisemiidae + Andesebiidae; Oligotomoidea for Teratemiidae + Oligotomidae + any new families resulting from the break up of the likely paraphyletic oligotomids; Embioidea for Archemiidae + Embiidae + Embonychidae + Notoligotomidae).

^d The validity of the various anisemiid subfamilies requires cladistic investigation.

moderate-sized; set anteriorly on head near antennal sockets; portion of head behind posterior tangent of compound eyes approximately 1.5 times length of compound eyes; posterior border rounded. Mandibles large, prominent, apically dentate; incisor with at least two teeth. Forewing with membrane hyaline; Sc disappearing rapidly in basal third of wing, weakly arched posteriorly; R terminating into C well before wing apex; 1r-rs + ma crossvein and three r-rs crossveins (fig. 2); single evanescent (i.e., faint to nearly obsolete medially) rs-ma crossvein present, positioned at midpoint between distalmost r-rs crossveins

(i.e., at midpoint between 2r-rs and 3r-rs), meeting MA at distal quarter of abscissa of M between MA origin and MA bifurcation; MA separating from Rs near wing midpoint, shortly after 1r-rs + ma crossvein; single evanescent ma-mp crossvein present before midpoint of MA origin and MA bifurcation; MA bifurcating prior to point at which R terminates; short mp-cua crossvein present shortly after separation of Rs + MA from MP; MP simple; more posterior portions of forewing obscured. Male terminalia as depicted in figure 2 and as described for the family. **Female.** Unknown.



Fig. 1. Dorsal photomicrograph of *Sorellembia estherae* n.gen., n.sp., holotype male (Bu-227).

MATERIAL: **Holotype.** Male alate, AMNH Bu-227, Myanmar (Burma): Cretaceous, Kachin, Tanai Village (on Ledo Road 105 km NW Myitkyna). Deposited in the Amber Collection, Division of Invertebrate Zoology, American Museum of Natural History, New York. This is the material discussed and figured as an undescribed Cretaceous amber embiodean by Grimaldi et al. (2002: their fig. 22a) and Grimaldi and Engel (2005: their fig. 7.13).

ETYMOLOGY: The specific epithet is a matronymic honoring Mrs. Esther Pratt (1911–

2005) whose passing on May 18 marked the close of a special life; though short in stature she was powerful in spirit. Lucan (nephew of the Stoic philosopher Seneca the Younger) wrote, “The gods conceal from men the happiness of death, that they may endure life.” Having joyfully endured these many years on Earth, may she now know a more complete and eternal happiness.

FAMILY NOTOLIGOTOMIDAE DAVIS

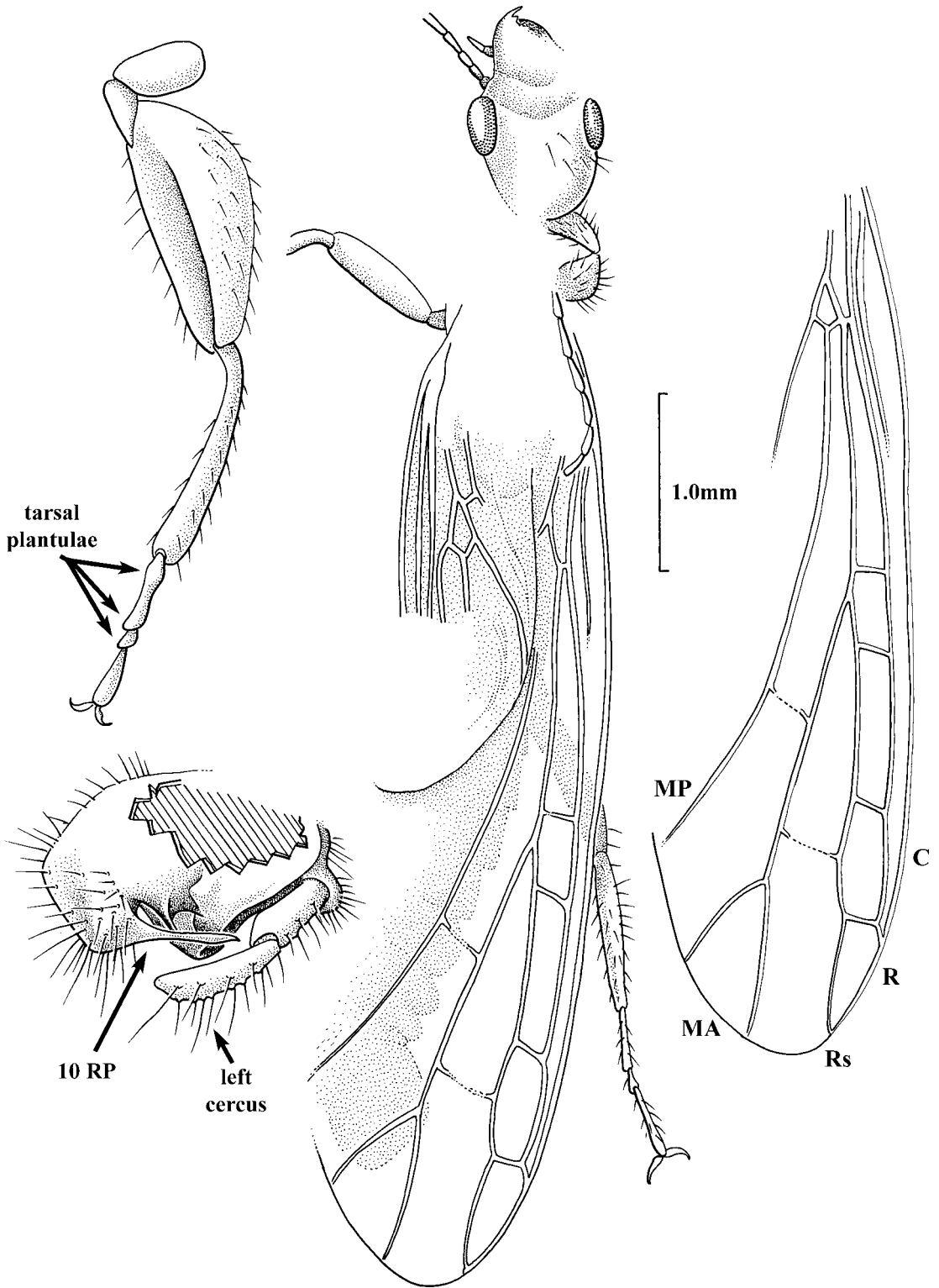
COMMENTS: The family is used herein in a slightly expanded sense than as employed by many recent authors. Instead, our usage of the family is closer to that of Davis (1940a, 1940b). We have considered the family *Australembiidae* as a subfamily of *Notoligotomidae* as both of these small, Australian families (*Notoligotominae* may also contain some undescribed Southeast Asian species) share the distinctive combination of a greatly reduced right cercus and have the two sections of the left cercus fused. The fusion of the left cercal sections is incomplete, with the two sections still distinguishable, in the basal subfamily *Notoligotominae*, while these sections are indistinguishably fused in *Burmitembiinae* and *Australembiinae*. Males of *Notoligotominae* and *Burmitembiinae* primitively retain wings, while *australembiines* are completely apterous. *Burmitembia* is an intermediary between *Australembiinae* and typical *Notoligotominae*. As more phylogenetic work on the Embioidea is conducted it may be warranted to recognize *Burmitembiinae* as a tribe of an expanded *Australembiinae*, thereby more completely reflecting hierarchical relationships of *Notoligotomidae* in the classification.

Burmitembiinae, new subfamily

Burmitembiidae Zherikhin, 1980: 78 (nomen nudum).
Type genus: *Burmitembia* Cockerell, 1919. Ross and York, 2000: 11 (nomen nudum).

TYPE GENUS: *Burmitembia* Cockerell, 1919.

DIAGNOSIS: Males fully winged, of small size (approximately 4.5 mm in total length). Forewing with Sc terminating in basal third of wing; R terminating into C well before wing



apex; crossveins relatively sparse but more numerous than many living species; three rs-ma crossveins, distalmost crossvein (i.e., 3rs-ma) evanescent (i.e., vanishing medially) and positioned before distalmost r-rs crossvein; MA simple; at least four ma-mp crossveins present, all apparently evanescent; MP, CuA, CuP, and A simple; wing membrane hyaline. Metabasitarsus with two ventral plantulae (one medial, one apical); metatarsomere II with single ventral plantula. Right cercus with basal section enlarged, distal section vestigial; left cercal sections indistinguishably fused (as in *Australembiinae*).

Genus *Burmitembia* Cockerell

Burmitembia Cockerell, 1919: 194. Type species: *Burmitembia venosa* Cockerell, 1919, monobasic. Davis, 1939a: 369. Carpenter, 1992: 190.

DIAGNOSIS: As for the subfamily (vide supra, and Davis, 1939a). Ross and York (2000) provide a photograph of the holotype of *B. venosa* (their fig. 4).

Embiodea sp. indet.

MATERIAL: Fragments of a male alate (presumed to be a male owing to wing fragment, but sex is otherwise indeterminable). AMNH Bu-200, Myanmar (Burma): Cretaceous, Kachin, Tanai Village (on Ledo Road 105 km NW Myitkyna). These fragments were briefly mentioned by Grimaldi et al. (2002).

COMMENTS: A small piece of Burmese amber containing fragments of an embiodean as evidenced by the distinctive probasitarsus. The foreleg is preserved from the profemur to the pretarsus. The profemur and protibia are typical in construction for most Embiodea; the probasitarsus is greatly enlarged, being slightly longer than the protibia and similar in length to the profemur and about 2.5 times wider than protarsomere II; protarsomere II is

the shortest and about as long as wide, with protarsomere III arising from its surface, protarsomere III slender and elongate, about 1.75 times as long as protarsomere II; the pretarsal claws are short and simple. In addition, the apical portion of a forewing is preserved with the foreleg fragment. The evident venation is nearly identical to that of the apical portion of the forewing of *B. venosa* (e.g., MA is simple, well separated from MP; Rs and MA connected prior to termination of R by evanescent rs-ma crossvein: the only apparent differences are that the apical r-rs crossvein is shorted and more bowed in Bu-200 and that the rs-ma crossvein is slightly more distal in position in Bu-200, but this latter difference might be the result of r-rs being shorter). Similarly, the foreleg structure is identical to that of *B. venosa*. It is possible that these are fragments of a male *B. venosa* but it must be noted that these are not diagnostic traits and do not permit authoritative identification except to confirm that the fragments are that of an embiodean. Nonetheless, the combination of these similarities is tantalizingly suggestive of *B. venosa*.

DISCUSSION

Historically, the Embiodea have been considered of Permian origin. Tillyard (1937) proposed the suborder Protembliaria (renamed Protembioptera by Davis, 1940a, 1940b) for what he believed to be the earliest representatives of the webspinners. *Protembia permiana* Tillyard (Protembliidae) was recovered from the Early Permian deposits of central Kansas. Carpenter (1950), however, demonstrated that these Permian fossils were not webspinners and removed the group from the Embiodea. Similarly, Martynova (1958) proposed a suborder, Sheimiodea, for a Late Permian fossil from Russia that she believed to be a basal webspinner. As demonstrated by Carpenter (1976: vide etiam Ross, 2000a), this fossil, like *Protembia*, is not allied to Embiodea. Lastly, a putative Permian webspinner was reported by Kukalová-Peck (1991). The figure of the specimen is consistent with the overall shape of Embiodea, such as the homonomous wings with narrow bases and apparently asymmetri-

←
 Fig. 2. Dorsal habitus of *Sorellembia estherae* n.gen., n.sp., holotype male (Bu-227), including a reconstruction of the forewing venation and an oblique, ventral view of terminalia as preserved. Scale bar for wing and full-body habitus only; leg and terminalia enlarged.

cal male genitalia (characteristic though not unique to the order; e.g., Grylloblattodea). However, there is no single apomorphy that unites this fossil with the Embiodea and its attribution to the order must be considered dubious at best.

The removal of these Paleozoic fossils from the order leaves *Sorellembia* and *Burmitembia* as the sole pre-Tertiary webspinners. However, Embiodea are certainly more ancient than the Cretaceous. The presence of the parasitic wasp family Sclerogibbidae, obligate parasites of Embiodea (Callan, 1939; Yokoyama and Tsuneyoshi, 1958; Ross, 2000b), in Early Cretaceous amber from Lebanon (Engel and Grimaldi, 2006) indirectly suggests the presence of webspinners at that time. Furthermore, neither *Sorellembia* nor *Burmitembia* are primitive webspinners. The most plesiomorphic family for the order is the Clothodidae (Davis, 1938, 1939b, 1940a, 1940b; Ross, 1987; Szumik, 1996) and to date no fossil of this lineage has been discovered. Thus, the more basal cladogenetic events in the order must be prior to the mid-Cretaceous. At present the origin and radiation of the order is speculative but may be as old as the Triassic, a period when most polyneopteran orders appear to have radiated following the End Permian Event and the disappearance of ecologically dominant taxa such as †Palaeodictyoptera. Interestingly, the oldest records of the Zoraptera, sister-group of Embiodea, also originate from Burmese amber (Engel and Grimaldi, 2002) and, as is the case for the webspinners, most Cretaceous zorapterans are not particularly plesiomorphic in character. The recovery of pre-Cretaceous webspinners and zorapterans will be difficult since these typically small, soft-bodied insects are not well-preserved as compressions or replacements.

ACKNOWLEDGMENTS

We are abundantly grateful for detailed and thorough critiques of the manuscript by Michael Ohl and an anonymous reviewer. Partial support for this work was provided by NSF EF-0341724 (to MSE) and NSF DBI-9987372 (to DAG). This is contribution No. 3435 of the Division of Entomology,

Natural History Museum, University of Kansas.

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See Appendix 1 on pages 14 and 15.

APPENDIX 1

CURRENT HIERARCHICAL CLASSIFICATION OF EMBIODEA

The classification of the order is presently under intense investigation by Drs. Edward S. Ross and Claudia Szumik, the latter based on rigorous cladistic analyses (e.g., Szumik et al., 2003; Szumik, 2004). Many new taxa will be added to this listing soon (e.g., Ross, 1970, 2001, 2003a, 2003b, in prep.), and it is hoped that the phylogenetic studies of the order will shed light on the evolution and natural classification of Embioidea. There are, however, great differences of opinion concerning the hierarchical classification of the order. We have employed what we believe to be the most conservative arrangement of higher groups (vide infra). Szumik (2004) has been followed in the treatment of Archemiidae and thus Scelembiinae and Pachylembiinae (both of Ross, 2001) are considered synonyms of the former, while Microembiinae (also of Ross, 2001) belongs to Anisembiidae. Table 2 summarizes three different classifications of Embioidea (authorship of higher taxa is provided, however, only in the summarized classification, infra).

Order EMBIODEA Kusnezov, 1903

Family Clothodidae Enderlein, 1910

Suborder Neoembiodea, subordo novum

Family †Sorellembiidae, familia novum

Family Anisembiidae Davis, 1940a

Subfamily Anisembiinae Davis, 1940a^{a,b}

Subfamily Scelembiinae Ross, 2003b

Subfamily Aporembiinae Ross, 2003b

Subfamily Chorisembiinae Ross, 2003b

Subfamily Platyembiinae Ross, 2003b

Subfamily Cryptembiinae Ross, 2003b

Subfamily Chelicercinae Ross, 1984b

Family Andesembiidae Ross, 2003a^c

Family Oligotomidae Enderlein, 1910

Family Teratembiidae Krauss, 1911 (= Oligembiidae Davis, 1940a)

Family Archemiidae Ross, 2001^d

Family Embiidae Burmeister, 1839

Family Embonychidae Navás, 1917

Family Notoligotomidae Davis, 1940a (sensu novum)

Subfamily Notoligotominae Davis, 1940a

Subfamily †Burmitembiinae, subfamilia novum

Subfamily Australembiinae Ross, 1963 (status novus)

^a Authorship is Davis (1940a), not Ross (1940) as erroneously indicated in Ross (2003b). Davis (1940a) appeared 15 days prior to Ross (1940) and, therefore, has priority. Owing to the Principle of Coordination (ICZN, 1999) once a family-group name is established for a particular type genus, it must take the same authorship and date, regardless of rank within the family group.

^b Ross (2003b) proposed a tribal classification for the genera included in Anisembiinae. However, there are numerous nomenclatorial difficulties and of the six tribes recognized only two are valid under the Code (ICZN, 1999). Under the current Code three criteria must be met in order to validate a family-group name: **1.** the name must be explicitly indicated as new; **2.** the type genus must be explicitly cited; and **3.** a description of characters that serve to distinguish the higher taxon must be provided in words. In the body of the text, Ross (2003b) does not indicate that any of his tribes are new; however, in the table preceding the systematic section of the paper he does state “new” and thus the first criterion may be considered as having been met. However, his tribe Isoembiini is not listed in the table (indeed the type genus *Isoembiia* is placed in “Stenembiini”), and so for this name the first criterion is not met, as its treatment in the text is not accompanied with a statement that it is explicitly intended as new, and thus the name cannot be considered valid. For none of the tribes is the type genus explicitly indicated, thus, even though they can be inferred, the names fail to meet the second criterion.

APPENDIX 1

(Continued)

These difficulties are, however, minor as only Saussurembiini, Isoembiini, and Poinarembiini are described (these three tribes are monogeneric, and so the generic diagnoses can be considered as a joint diagnosis of the tribes). The remainder—Stenembiini, Anisembiini, Exochosembiini—are comprised of multiple genera and must, therefore, be diagnosed separate from their included genera. For Anisembiini this is merely academic as the name is already available from Davis (1940a). The only place characters might be sought for Stenembiini and Exochosembiini is in the key to tribes. However, both tribes key out in multiple places, and a suite of traits that distinguish the tribes as a whole from the remainder is lacking (even if the keys are used as satisfying criterion 3, both names still fail criterion 2). In summary, Isoembiini fails criteria 1 and 2, Saussurembiini fails criterion 2, Exochosembiini fails criteria 2 and 3 (and is erroneously named as Exochembiini in the key), Poinarembiini fails criterion 2, and Stenembiini fails criteria 2 and 3. The tribe Stenembiini, however, is further complicated in that it contains the genus *Mesembia* for which a family-group name is already available. Ross (1940) proposed Mesembiinae for *Mesembia*, and according to the Principle of Coordination (ICZN, 1999), this name must be applied to the lineage known as “Stenembiini” in Ross (2003b). Thus, this tribe is valid, but under a different name—Mesembiini. Only Mesembiini and Anisembiini can be considered valid names under the Code (ICZN, 1999). Owing to the confusion resulting from these errors we have chosen not to list tribes within Anisembiinae until such time as the nomenclatorial status of these names is clarified.

^c This family is almost assuredly sister to Anisembiidae as evidenced by the apomorphic combination of a simple MA and absence of the metabasitarsal median plantula (a.k.a., papilla or bladder). The family does not appear to have been derived from within Anisembiidae as all anisembiids are united by the simple mandibular dentition (a single incisor tooth and a single molar tooth).

^d The family-group name Olynthidae Krauss, 1911, while older, is not available owing to homonymy of the type genus *Olyntha* (today known as *Embolynta*).

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