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Oldest webspinners from the Middle Jurassic of Inner Mongolia, China (Insecta: Embiodea)

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The oldest webspinners, ***Sinembia rossi* gen. et sp. nov.** and ***Juraembia ningchengensis* gen. et sp. nov.**, are described in the new family **Sinembiidae fam. nov.** from the Middle Jurassic of Inner Mongolia, China. They differ from the Cretaceous and more recent Embiodea in several plesiomorphic characters, namely they have a long ovipositor, three-segmented cerci, eyes situated on the posterolateral angles of the head, and the prothoracic prescutum is absent: these characters suggest habits that strongly differ from those of the recent taxa. The loss of the ovipositor and the reduction in the number of cerci can no longer be considered as synapomorphies of the ((Embiodea + Zoraptera) + Plecoptera) and (Embiodea + Zoraptera) clades, respectively.

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INTRODUCTION

Embiodea are a small enigmatic polyneopterous order, with rather uncertain affinities, and a still confusing classification. They are currently considered as a sister group of the Zoraptera (Grimaldi & Engel, 2005; Yoshizawa, 2007), although close relationships with Phasmatodea have been recently discussed (Dallai *et al*., 2007; Klug & Klass, 2007). Fossil webspinners are very rare, with only seven described species (Engel & Grimaldi, 2006). Some have been described from the Eocene Baltic and Miocene Dominican amber (Ross, 1956, 2003; Szumik, 1994, 1998). The sole described fossil compression is from Florissant (from the Eocene–Oligocene boundary, Colorado, USA; Cockerell, 1908; Ross, 1987). Mesozoic Embiodea are extremely rare: there are only two records, both of which are from the mid-Cretaceous Burmese amber (latest Albian), namely *Burmitembia venosa* (Cockerell, 1919) and *Sorellembia estherae* Engel & Grimaldi, 2006 (Davis, 1939; Engel & Grimaldi, 2006). Engel & Grimaldi (2006) suggested a Triassic origin and radiation of Embiodea, but they excluded the formerly reported Paleozoic fossil records. Thus, the present discoveries of two Middle Jurassic webspinners from China is of great interest for understanding the antiquity, morphology of the first Embiodea, and evolution of this order.

The volcanic deposits of the Middle Jurassic Jiulongshan Formation, near the Daohugou Village, Wuhua Township, Ningcheng County, Inner Mongolia, North-East China, have yielded very rich, exceptional fossils, such as plants, invertebrates (e.g. insects, conchostracans, anostracans, spiders, and harvestman), and vertebrates (e.g. salamanders, pterosaurs, and mammaliaforms) (Huang *et al*., 2006). The inanimate, rather small conchostracan carapaces preserved in normal bedding planes are the typical character of these rocks. The most common insects from Daohugou are nymphs of mayflies and aquatic bugs. This palaeoentomofauna is very diverse. Hitherto, more than 20 insect orders have been distinguished from our collections (of more than 40 000 specimens).

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SYSTEMATIC PALAEONTOLOGY

We follow the morphological terminology of Ross (2000), with the following abbreviations: CuA, cubitus anterior; CuBS, blood sinus of cubitus; CuP, cubitus posterior; MA, media anterior; MP, media posterior; RA, radius anterior; RBS, radial basal sinus; RP, radius posterior; ScBS, blood sinus of subcosta posterior. The fossils were studied using a binocular microscope (Olympus SZX9), drawings were made using a camera lucida, and photographs were taken with an Olympus Camedia C5060.

ORDER EMBIODEA KUZNEZOV, 1903

FAMILY **SINEMBIIDAE FAM. NOV.**

Type genus: Sinembia gen. nov., other genus *Juraembia* gen. nov.

Diagnosis: Female with ovipositor; cerci three-segmented, with (at least in the female) long setae; male genital appendages almost symmetrical; prognathous head; absence of ocelli; compound eyes in posterolateral position; thorax not very elongate; pronotum without visible prescutum; a median longitudinal furrow on prothoracic scutum; three-segmented tarsi; mid legs of normal size, not reduced; thickened hind femora; swollen fore basitarsus (visible in *Juraembia* gen. nov.); absence of bladders on hind basitarsus; both male and female fully winged; presence of blood sinuses ScBS (in both *Sinembia* gen. nov. and *Juraembia* gen. nov.) and CuBS (but only preserved in *Sinembia* gen. nov.); MA unforked.

SINEMBIA **GEN. NOV.**

Derivation of the name: Named after the Latin name for China and *Embia*.

Type species: Sinembia rossi sp. nov.

Diagnosis: Sinembia gen. nov. can be separated from *Juraembia* gen. nov. on the basis of the following characters: hind femur very long, instead of being short in *Sinembia* gen. nov.; second to fifth antennal segments short, instead of only the second being short in *Sinembia* gen. nov.

SINEMBIA ROSSI **GEN. ET SP. NOV.** (FIGS 1A–E, 2)

Derivation of the name: Named after Dr E.S. Ross, a specialist of Embiodea.

Material: A nearly complete specimen (NIGP 148119; male, part and counterpart), housed in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

Type locality: Near the Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, North-East China; Middle Jurassic, Jiulongshan Formation (*c*. 165 Mya).

Diagnosis: As for the genus.

Description: Body small, 6.5-mm long (smaller than *Juraembia ningchengensis* gen. et sp. nov.; see Fig. 1A–C).

Head: 0.9-mm long and 1.0-mm wide, prognathous, rather small, more or less triangular, a dorsal triangular structure could correspond to dorsal ecdysial suture; posterolateral compound eyes rather large and oval; no ocelli; clypeus transverse; mandible relatively small and strong, apical tooth developed, at least one molar tooth present, far from apical tooth; antenna thick, only five antennal segments preserved, scape large, located close to base of mandible, pedicel broad and very short, antenomeres 3–5 nearly uniform, broader than long (Fig. 1D).

Thorax: ~2.5-mm long and 1.5-mm wide, not very elongate; pronotum, mesonotum, and metanotum sclerotized; pronotum transverse, slightly broader than head, 0.6-mm long and 1.2-mm wide, with a median furrow, both anterolateral and posterolateral angles rounded, and no visible prescutum (Fig. 1D); no desclerotized zone between pronotum and mesonotum; mesonotum and metanotum transverse, mesonotum wider, but shorter than pronotum and metanotum.

Wing: brachypterous, relatively short compared with body length, only reaching apex of abdomen, and covered with very fine setae; forewing 4.7-mm long and 1.8-mm wide, brown, with a more hyaline longitudinal zone between main veins; large and dark (sclerotized) tubes are present as basal parts of veins Sc and Cu, corresponding to the hemolymph sinuses ScBS and CuBS; ScBS is 2.7-mm long; RA is weaker than ScBS (not developed into an RBS), and reaches the wing apex; MA is basally fused with RP, with RP + MA probably emerging from R, but the basal part is not preserved; MA separates from RP a few millimeters from the wing base; RP with two distal branches parallel with simple distal part of MA; MP simple, parallel with RP and MA; MP emerging at arculus between R and CuBS; distal part of Cu emerging from CuBS, divided into a simple CuP and a forked CuA; crossveins are probably present between the main veins, but they are weakly indicated (Fig. 1A, C).

Hindwing: nearly identical to forewing, but slightly shorter, at 4.2-mm long and 1.7-mm wide; numerous crossveins are present between the main veins (Fig. 1C).

Legs: well-developed; tarsi three-segmented; fore coxae approximated; elongate drop-shaped trochant-

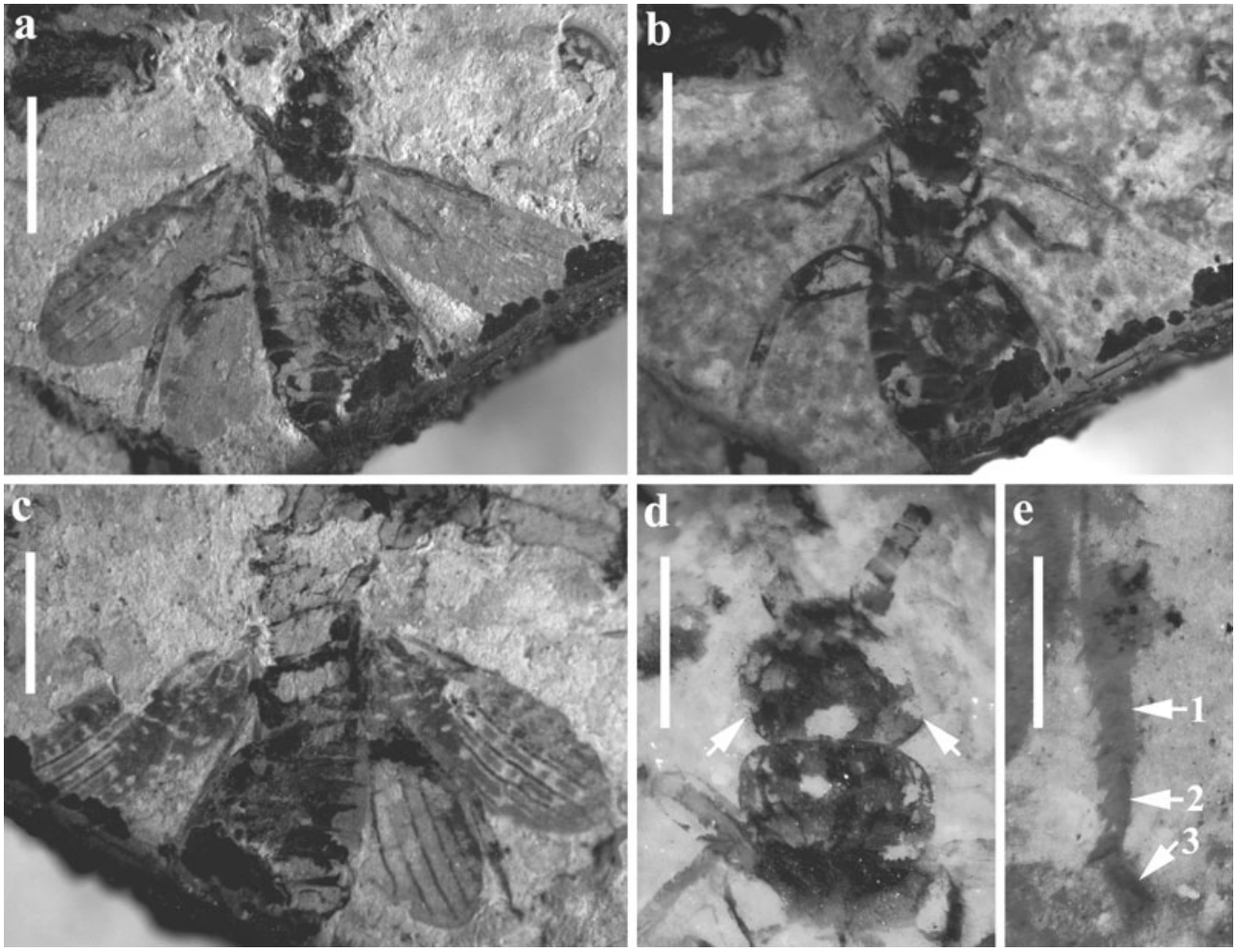

Figure 1. ***Sinembia rossi*** **gen. et sp. nov.**, holotype NIGP 148119. A, print (148119a), general habitus; B, print under alcohol, showing details of body (e.g. mid and hind legs); C, counterpart (148119b), general habitus; D, enlargement of (B), showing details of head and pronotum; white arrows indicate eyes; E, enlargement of (C), showing detail of hind leg (under alcohol); white arrows show details of hind tarsi. Scale bars: 2 mm in (A), (B), and (C); 1 mm in (D); 0.5 mm in (E).

ers; femora broad, with two inner ridges, and with armed setae near the apex; tibiae short; mid femora broad, 1.1-mm long and 0.4-mm wide; tibia thin, with apical setae, 1.0-mm long; sizes of tarsomeres decrease backwards, first 0.3-mm long, second 0.25-mm long, and third 0.25-mm long, with a pair of claws that are simple and small; hind femora very broad and relative short, 1.6-mm long and 0.7-mm wide, with inner ridge, and with outer side armed with sparse, long setae (Fig. 1B); tibia rather thin and short, 1.3-mm long, with outer side setose, with tarsi-armed setae, the length and width of which decrease from the first tarsomere to the third, width of tarsomeres increase backwards, first tarsomere 0.4-mm long, second tarsomere 0.3-mm long, armed with a strong tooth at apex, third tarsomere 0.2-mm long, and with no middle or apical bladder; claws are small but thick (Fig. 1D).

Abdomen: ~3.0-mm long and 1.7-mm wide, with ten visible tergites, wider than thorax, length and width of tergites increases backwards, narrowed apically; apex of abdomen with at least two symmetrical sclerotized structures, cerci incompletely preserved, if visible (?).

Discussion: The wing venation of this fossil is very similar to those of the recent webspinners, especially to the 'plesiomorphic embiid' *Clothoda* (Ross, 2000: fig. 24). The presence of blood sinuses (ScBS and CuBS) is one of the main synapomorphies of the Embiodea, allowing an accurate attribution of *Sinembia* gen. nov. to this order. Other synapomorphies visible in *Sinembia* gen. nov. are: three-segmented tarsi, absence of ocelli, prognathous head, and thickened hind femora (Szumik, 1996). Unfortunately, the structure of the fore tarsus is unknown in *Sinembia*

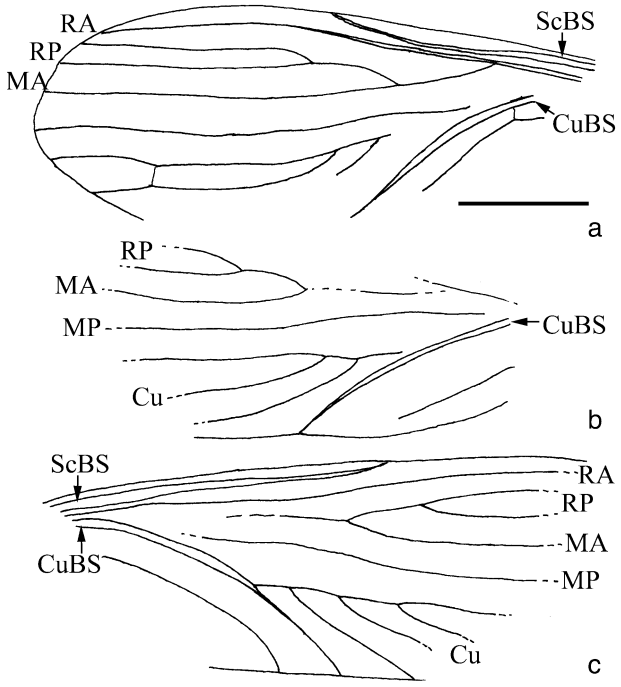

Figure 2. ***Sinembia rossi*** **gen. et sp. nov.**, holotype NIGP 148119. Line drawings of wing venations. A, part of left forewing; B, counterpart of right forewing; C, part of right forewing. See Systematic palaeontology for a list of the abbreviations. Scale bar: 1 mm.

gen. nov., and thus it is not possible to determine if it had a swollen fore basitarsus (producing silk), as found in the recent taxa. A further potential synapomorphy with other Embiodea is the presence of a median longitudinal furrow on the prothoracic scutum, which is a character absent in Zoraptera. The unforked MA of *Sinembia* gen. nov. corresponds with an apomorphy present in the recent Anisembiidae, but it is also present in some Oligotomidae and Embiidae. Thus, it is not sufficient for a phylogenetic placement of *Sinembia* gen. nov. *Sinembia* gen. nov. differs from recent webspinners and the Cretaceous Sorrelembiidae in the following characters: (1) compound eyes in posterior part of head; (2) absence of bladders on the hind basitarsus. The second character is probably a plesiomorphy. Such bladders are absent in Zoraptera. *Sinembia* gen. nov. shares with Clothodidae the presence of (nearly) symmetrical male genitalia, a character that is also probably plesiomorphic, and is not shared by the Cretaceous family Sorrelembiidae. Clothodidae is currently considered as the most 'primitive' or inclusive in the phylogeny, but note that Szumik (1996) used *Clothoda* as an out-group in his phylogeny, and Ross (1987, 2000) did not perform a cladistic analysis . . . Finally, the posterolateral position of the compound eyes of *Sinembia* gen. nov. differs from the anterolateral position in other Embiodea, but is very similar to the position in Zoraptera. Thus, it is probably a plesiomorphy. The available data suggest that *Sinembia* gen. nov. would be in a very inclusive position in the Embiodea: more basal than the mid-Cretaceous *S. estherae*, which indeed displays rather 'modern' characters present in the most recent webspinners, e.g. cerci, male genitalia, enlarged and short hind femora, etc.

JURAEMBIA GEN. NOV.

Derivation of the name: Named after the Jurassic period and *Embia*.

Type species: Juraembia ningchengensis gen. et sp. nov.

Diagnosis: See that of *Sinembia* gen. nov. above.

JURAEMBIA NINGCHENGENSIS GEN. ET SP. NOV.

(FIG. 3A–D)

Derivation of the name: Named after Ningcheng County, where the type was found.

Material: A nearly complete specimen (NIGP 148120) (female), with part and counterpart, housed in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

Type locality: Near the Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, North-East China; Middle Jurassic, Jiulongshan Formation (*c.* 165 Mya).

Diagnosis: That of the genus.

Description: Body elongate and rather small, ~8.0-mm long (Fig. 3A).

Head: prognathous, subrounded, rather small, 1.2-mm long and 1.1-mm wide, and with a Y-shaped suture dorsally, probably corresponding to dorsal ecdysial sutures; labrum rectangular; mandible relatively small, with two nearly equally sized sharp incisor teeth and one molar tooth; last segment of maxillary palpus very large; antenna thick, with only 16 segments preserved, scape very large, pedicel very short, antenomeres 3–5 wide and short, more distal antenomeres narrower, and with gradually increased lengths; posterolateral compound eyes oval; no ocelli (Fig. 3B).

Thorax: 2.7-mm long and 1.4-mm wide, not very elongate; pronotum rather strongly sclerotized, subrectangular, transverse, 0.9-mm long and 1.3-mm wide, broader than head, with a median furrow,

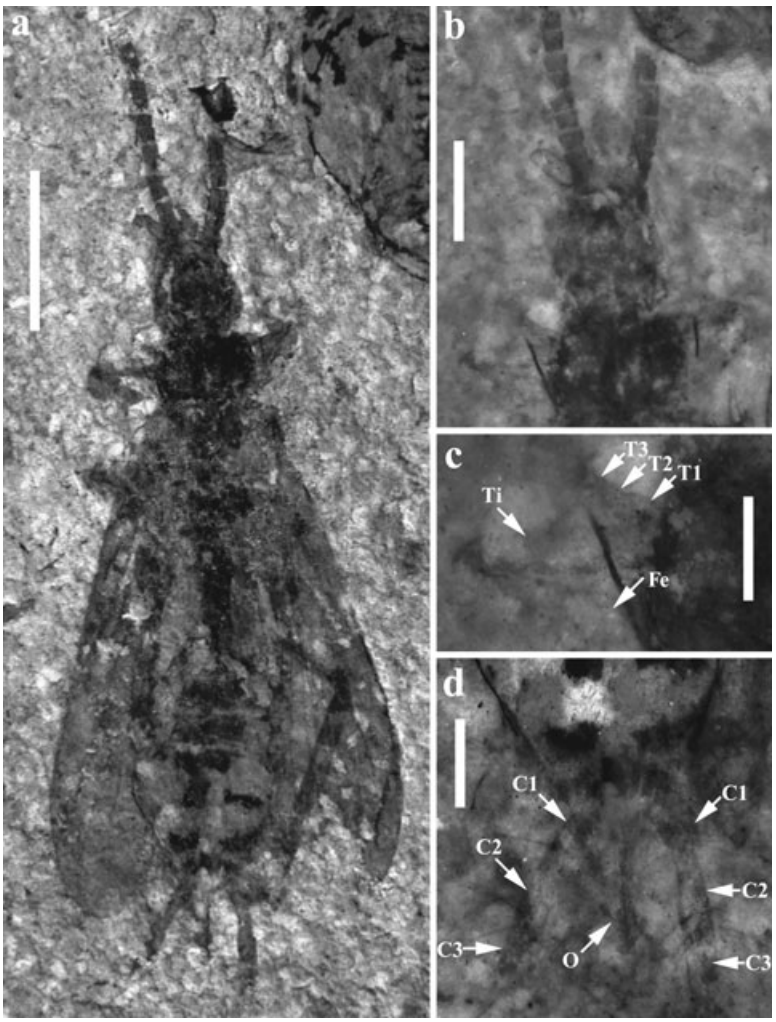

Figure 3. ***Juraembia ningchengensis*** **gen. et sp. nov.**, holotype NIGP 148120a. A, part, general habitus; B, enlargement of head and pronotum (under alcohol); C, enlargement of fore tarsi (under alcohol); D, enlargement of ovipositor and cerci (under alcohol). Scale bars: 2 mm in (A); 1 mm in (B) and (D); 0.5 mm in (C). Fe, femur; O, ovipositor; T, tarsi; Ti, tibia.

anterolateral angles rounded, and no prescutum (Fig. 3A, B); mesonotum and metanotum longer than pronotum.

Wings: well-developed; forewing 6.2-mm long and ~1.5-mm wide, covering hindwings; venation hardly visible; four parallel and straight longitudinal veins visible in distal half of forewing; at least one very large and dark (sclerotized) tube at the Sc, corresponding to the haemolymph sinus ScBS; RA apically merging with RP (Fig. 3A).

Ltiposer posterior tergums wider than head, and throx legs well-developed; fore femora broad, tibia relatively short and broad, with sparse setae, tarsi three-segmented, with setae, basal tarsomere distinctly swollen, second tarsomere rather short, inserted on apex of basal tarsomere, third tarsomere small, claws small and simple (Fig. 3C); mid legs larger than forelegs, tibia narrowed apically, basal tarsomere the largest; hind legs well-developed, femora extremely large, widest at base, 2.3-mm long and 0.9-mm wide, with inner ridges, tibia slender, 2.1-mm long, with outer side setose, tarsi short, setose, first tarsomere the largest, second and third tarsomeres thinner; no visible bladders on hind basitarsus.

Abdomen: 4.3-mm long and 2.0-mm wide, relatively wide, ten visible tergites, with widths and lengths increasing backwards, posterior tergites broader than head and thorax; ovipositor long, thick, 1.2-mm long, cone-like, with a median longitudinal furrow (Fig. 3D); cerci well-developed, 1.4-mm (right) or 1.5-mm (left) long, symmetrical, three-segmented,

with long setae arranged in crowns at the joints between segments, basal segment short, second segment very long and slightly curved, with posterior part slightly swollen, third segment small, and armed with numerous long apical setae; remnants of three small segments fused with the second one (left cercus), and two small segments fused with the third one are possibly present (Fig. 3D).

Discussion: The attribution of *Juraembia* gen. nov. to the Embiodea is based on its close similarity to *Sinembia* gen. nov. in habitus. Although its wing venation is poor, a broad blood sinus ScBS is visible. The visible parts of the wing venation also agree with an attribution to Embiodea. This fossil strongly differs from Cretaceous and recent webspinners in several plesiomorphies: wings are present in females; female basal segment of fore tarsus is much less enlarged; hind legs are strongly developed; symmetrical cerci have three segments, instead of two or less; female has a large ovipositor, which is nearly completely reduced in recent taxa. Also, *Juraembia* gen. nov. has long setae on its cerci, unlike other Embiodea, but rather similar to those in Zoraptera (Engel & Grimaldi, 2000: figs 6, 9). The posterolateral position of the eyes in *Juraembia* gen. nov. is similar to the situation in *Sinembia* gen. nov. The presence of cerci with more than two segments in *Juraembia* gen. nov. is another probable plesiomorphy. Thus, as for *Sinembia* gen. nov., *Juraembia* gen. nov. probably has a very inclusive position near the very base of the webspinner's phylogeny.

Differences between *Sinembia* gen. nov. and *Juraembia* gen. nov. are as follows: (1) female *Juraembia* gen. nov. larger (body 8.0-mm long instead of 6.5-mm long); (2) female *Juraembia* gen. nov. wings very elongate, instead of being short and broad in the male *Sinembia* gen. nov.; (3) female *Juraembia* gen. nov. hind femur very long, instead of being short in male *Sinembia* gen. nov.; (4) female *Juraembia* gen. nov. second to fifth antennal segment short, instead of only the second antennal segment being short in male *Sinembia* gen. nov. The first and second differences can be considered as less important than the third and fourth, because they can be of specific or even sexual origin.

Although *Sinembia* gen. nov. and *Juraembia* gen. nov. can both be accurately attributed to Embiodea, they have synapomorphies of the whole order or plesiomorphies. Finding characters that are synapomorphies of a Jurassic family comprising these two fossils will be tricky. *Sinembia* gen. nov. has a simple MA, which is currently considered as a derived character, but it is unknown in *Juraembia* gen. nov., and is present in some recent taxa. *Sinembia* gen. nov. and *Juraembia* gen. nov. have distinctly shorter thoraxes than other Embiodea, mid legs that are moderately developed, and an absence of a prothoracic prescutum, which is a character of ambiguous state, as this structure is also not visible in Zoraptera. It could well be a plesiomorphy.

CONCLUSIONS

Recent female webspinners are apterous, but Ross (2000) supposed that their ancestor had wings present in both sexes. The presence of normal wings in the type specimen of *Juraembia ningchengensis* gen et sp. nov., a female, supports this hypothesis.

The cerci of *Juraembia* gen. nov. are three-segmented, unlike all other Embiodea. Grimaldi & Engel (2005) proposed the presence of two- (or less) segmented cerci as a potential synapomorphy of the clade (Embiodea + Zoraptera). Thus, the present discoveries contradict this hypothesis, and suggest rather that the reduction in the number of cerci occurred convergently in these two orders.

Grimaldi & Engel (2005) suggested placing Embiodea, together with Zoraptera and Plecoptera, within a superorder Plecopterida. They suggested that the reduction and loss of the ovipositor is one of the synapomorphies of this clade. However, a somewhat large and distinct ovipositor is present in our Middle Jurassic female webspinner. Similar ovipositors are also known from the Jurassic earwigs, the Orthoptera, and the Paleozoic and many Mesozoic blattid-like Dictyoptera. Thus, the presence of an ovipositor is probably a plesiomorphic character for *Juraembia* gen. nov. The loss of the ovipositor can no longer be considered as an accurate synapomorphy of the potential clade ((Embiodea + Zoraptera) + Plecoptera).

The modern webspinners use the spinning organs in their greatly swollen fore basal tarsomeres to make galleries, which is the major specialized habit of Embiodea. Their greatly enlarged femur of the hind legs indicates an adaptation of backward movement (Ross, 2000). Rapid reverse movement in narrow galleries has been a major factor in the evolution of many adaptive characteristics of webspinners, such as wing modifications and wing elimination in female individuals, as well as in males of many species (Ross, 2000). The general body patterns of our Middle Jurassic webspinners are strongly similar to those of recent Embiodea. The silk-spinning habit probably developed in these Middle Jurassic animals, as evidenced by the enlarged basal segment of fore tarsus, at least in *Juraembia* gen. nov. Strongly enlarged hind femora of both *Sinembia* gen. nov. and *Juraembia* gen. nov. support possible reverse movements. Unlike the more or less smooth cerci of recent forms, the very long setae on the cerci of *Juraembia* gen. nov. probably had

a sensorial function during the reverse movements. Both *Sinembia* gen. nov. and *Juraembia* gen. nov. bear very long hind legs that contradict a habitat in galleries. Thus, perhaps these Middle Jurassic webspinners had a 'primitive' silk-spinning habit under weathered outer bark and dead leaf litter, where they developed the ability to move backwards. The presence of a developed ovipositor also suggests that these insects put their eggs in a substrate (soil, plants, or leaves), unlike the recent taxa that attach them on the surface of the silky galleries where they live. This Jurassic mode of egg-laying is probably not compatible with taking care of the offspring, unlike what is observed in recent forms.

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REFERENCES

Cockerell TDA. 1908. Description of Tertiary insects. *American Journal of Science* **25:** 51–52 & 227–232.

Cockerell TDA. 1919. Two interesting insects in Burmese amber. *The Entomologist* **52:** 193–195.

Dallai R, Machida R, Jintsu Y, Frati F, Lupetti P. 2007. The sperm structure of Embioptera (Insecta) and phylogenetic considerations. *Zoomorphology* **126:** 53–59.

Davis C. 1939. Taxonomic notes on the order Embioptera. III. The genus *Burmitembia* Cockerell. *Proceedings of the Linnean Society of New South Wales* **64:** 369–372.

Engel MS, Grimaldi DA. 2000. A winged *Zorotypus* in Miocene amber from the Dominican Republic (Zoraptera: Zorotypidae), with discussion on relationships of and within the order. *Acta Geologica Hispanica* **35:** 149–164.

Engel MS, Grimaldi DA. 2006. The earliest webspinners (Insecta: Embiodea). *American Museum Novitates* **3514:** 1–15.

Grimaldi DA, Engel MS. 2005. *Evolution of the insects*, Vol. 755. Cambridge: Cambridge University Press.

Huang D-Y, Nel A, Shen Y-B, Selden PA, Lin Q-B. 2006. Discussions on the age of the Daohugou fauna – evidence from invertebrates. *Progress in Natural Science* **16** (Special Issue)**:** 308–312.

Klug R, Klass K-D. 2007. The potential value of the mid-abdominal musculature and nervous system in the reconstruction of interordinal relationships in Lower Neoptera. *Arthropod Systematics and Phylogeny* **65:** 73–100.

Ross ES. 1987. Studies in the insect order Embiidina: a revision of the family Chothodidae. *Proceedings of the California Academy of Science* **45:** 9–34.

Ross ES. 2000. EMBIA. Contributions to the biosystematics of the insect order Embiidina. Part 1. Origin, relationships and integumental anatomy of the insect order Embiidina. *Occasional Papers of the California Academy of Sciences* **149:** 1–53.

Szumik CA. 1996. The higher classification of the order Embioptera: a cladistic analysis. *Cladistics* **12:** 41–64.

Yoshizawa K. 2007. The Zoraptera problem: evidence for Zoraptera + Embiodea from the wing base. *Systematic Entomology* **32:** 197–204.