Predatory behavior of the social orb-weaver spider, *Geratonephila burmanica* n. gen., n. sp. (Araneae: Nephilidae) with its wasp prey, *Cascoscelio incassa* n. gen., n. sp., (Hymenoptera: Platygasteridae) in Early Cretaceous Burmese amber

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Abstract

The present work shows predatory behavior of the social orb-weaver spider, *Geratonephila burmanica* n. gen., n. sp. (Araneae: Nephilidae) against a parasitic wasp, *Cascoscelio incassa* n. gen., n. sp., (Hymenoptera: Platygasteridae) in Early Cretaceous Burmese amber. An adult male and juvenile of *Geratonephila burmanica* n. gen., n. sp. in the same web provide the first fossil evidence of sociality in spiders. The spider is characterized by a pedipalp with a hemispherical tegulum, a subtegulum curved at 180 ˚ and an apical spiraled embolas- conductor bent approximately 45 ˚ at midpoint. The male wasp is characterized by an ocellar tubercle, 12 segmented antennae with a jointed, feeble 5-segmented clava, thick sensilla trichodea curvata with rounded ends on the claval antennomeres, a short uncus, a short postmarginal vein and a nebulose Rs vein extending from the uncus to the costal margin of the fore wing. This is the first fossil evidence of spider sociality and a spider attacking prey trapped in its web.

Keywords: Burmese amber, fossil nephilid spider, platygastrid wasp prey, Cretaceous

Introduction:

Fossil evidence of associations between a predator and its prey are extremely rare (Boucot 1990; Boucot and Poinar 2010). While amber contains many examples of insects captured in spider webs (Wunderlich 2004), there is no previous fossil record of a spider attacking its ensnared prey.

A piece of Early Cretaceous Burmese amber containing a spider web with a male and a juvenile spider as well as two captured insects (a neuropteran and a parasitic wasp) provides new insights into fossil predator-prey associations and sociality in spiders. The interacting biota offer an example of frozen behavior by portraying a scene from 100 million years ago. The present study describes the spider and entrapped parasitic wasp, characterizes the spider web and discusses sociality in spiders.

Materials and methods

The amber piece (Fig. 1) is roughly rectangular in shape with a greatest length of 12 mm, greatest width of 5.4 mm and greatest depth of 3 mm. The amber was obtained from a mine first excavated in 2001, in the Hukawng Valley, southwest of Maingkhwan in Kachin State (26º20´N, 96º36´E) in Burma (Myanmar). This new amber site, known as the Noije Bum 2001 Summit Site, was assigned to the Early Cretaceous, Upper Albian, on the basis of paleontological evidence (Cruickshank and Ko 2003), placing the age at 97 to 110 mya. Nuclear magnetic resonance (NMR) spectra and the presence of araucaroid wood fibers in amber samples from the Noije Bum 2001 Summit site indicate

an araucarian (possibly *Agathis*) tree source for the amber (Poinar et al. 2007). Observations, drawings, and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to 600X. Spider terminology follows that of Levi (2005) and Coddington (1990). Wasp terminology follows that of Masner (1976, 1980) and Masner et al. (2007). Higher wasp classification follows that of Sharkey (2007).

Descriptions

Spider

Family Nephilidae Simon, 1894

Geratonephila Poinar, new genus

Diagnosis: ovoid opistosoma; body and legs densely setose; male pedipalp with hemispherical tegulum; subtegulum curved 180 ˚; apical spiralled embolas wrapped by conductor long, curved approximately 45 ˚ at midpoint.

Type species: *Geratonephila burmanica* Poinar

Geratonephila burmanica Poinar, n. sp. (Figs. 1- 3)

Material examined: Holotype male and juvenile.

Description: Adult male. Length = 3.12 mm; width = 1.24 (ratio, 2.52); legs long, especially femora, tibiae and metatarsi of leg 1; walking leg formula, 1243; legs bearing both macrosetae and short setae; leg hair tufts absent; profemur, 3.30 mm; protibia, 3.24 mm; prometatarsus, 2.35 mm; rows of spines on legs; male pedipalp with hemispherical tegulum; subtegulum curved 180 ˚; apical spiralled embolas wrapped by conductor,

curved at midpoint approximately 45 ˚; length bulb, 323 µm, width bulb, 409 µm, length conductor, 540 µm; opistosoma ovoid, longer than wide, length, 1.76 mm, width, 1.24 mm.

Juvenile: Length, 1.4 mm; carapace wider than long; length carapace, 360 µm, width carapace, 410 µm; opistosoma ovoid; length opistosoma, 820 µm, width opistosoma, 620 µm; legs and body with dense covering of thick, setae.

Type: Holotype deposited in the Buckley amber collection (accession # E-2).

Type locality: Amber mine at the Noije Bum 2001 Summit Site in the Hukawng Valley, southwest of Maingkhwan in Kachin State (26º20´N, 96º36´E) in Burma (Myanmar).

Etymology: The generic name is composed of the Greek "geratos" for old, in reference to the age of the fossil and the type genus of the family, *Nephila*.

Comments: The Nephalidae is currently composed of two subfamilies (Nephalinae and Clitaetrinae) with 58 species in four genera (Platnick, 2011). Since many characters on the fossil spiders are obscured it is not possible to assign them to an extant or extinct genus. This is the first member of the Nephalidae described from Burmese amber, however the family Nephilidae is fairly ancient and fossils occur in the Jurassic (Selden et al., 2011).

Wasp

The wasp is complete and perfectly preserved in spite of its capture in the spider web.

Family Platygasteridae

Cascoscelio Poinar, new genus

Diagnosis**.** Ocelli positioned on tubercle; weakly differentiated clava comprising terminal 5 antennomeres; thick sensilla trichodea curvata with rounded ends on claval antennomeres; fore wing with long, complete submarginal vein reaching wing margin; short postmarginal vein subequal to marginal vein; stigma vein subequal to marginal and postmarginal veins; short uncus directed toward apical wing margin; nebulose Rs vein extending from uncus to costal margin of fore wing; nebulase anal, cubital and medial veins; of these only cubital vein meets wing margin; marginal cilia fairly long; hind wing with submarginal vein complete, reaching costal margin beyond two frenal hooks; with long marginal cilia.

Type species *Cascoscelio incassa* Poinar, n. sp.

Etymology: Casco is from the Latin "cascus" for old.

Cascoscelio incassa Poinar, n. sp. (Figs 1, 2, 6-10)

With characters listed in the generic diagnosis.

Material examined: Holotype male

Description: Length, 1.2 mm; body and antennae brown; body shiny, with scattered, long setae (Fig. 4).

Head: Length, 336 µm; frons depressed; compound eyes large, bare, oval, greatest diameter 160 µm; ocelli positioned on tubercle; lateral ocelli positioned closer to compound eyes than to median ocellus; mandibles bidentate, 53 µm long; antennae long, length, 790 µm; 12-segmented with feebly 5- segmented clava; claval segments setose; scape elongate, more than 5 times longer than wide; flagellomeres 8-11 subequal,

quadrate; terminal flagellomere longer than preceding flagellomeres, with pointed tip; length antennomeres: scape, 126 µm; pedicel, 57 µm; 3rd antennomere, 86 µm; 4th antennomere, 57 µm; 5th antennomere, 46 µm; 6th antennomere, 52 µm; 7th antennomere, 52 µm; 8th antennomere, 57 µm; 9th antennomere, 57 µm; 10th antennomere, 52 µm;11th antennomere, 56 µm; 12th antennomere, 92 µm; elongate, thick sensilla trichodea curvata with rounded ends ranging from 7 µm to 13 µm in length on claval antennomeres.

Thorax: Mesonotum minutely punctate; propodium medially armed with short spine; trochantellus absent; tibial spur formula 1-1-1; fore wing length, 923 µm; wing membrane covered with thick short setae 18 µm in length directed toward wing apex; marginal cilia long, 14-60 µm in length; pigmented submarginal vein complete, tubular, reaching wing margin; postmarginal vein subequal to marginal vein and stigmal vein; uncus short with nebulose Rs vein extending from tip of uncus straight to wing margin; anal, cubitus and medial nebulose veins present; only cubitus vein reaching wing margin; hind wing length, 580 µm; membrane with short, thick setae 14 µm in length; marginal cilia long, 36-54 µm in length; submarginal vein complete, reaching costal margin and continuing beyond paired frenal hooks.

Metasoma: Brown, shiny, setose, 9-segmented; length, 568 µm; width, 186 µm; 2.9 times as long as wide; laterotergites narrow, forming sharp submarginal ridge (lateral margin); T2 longest; length first 6 segments: 1, 105 µm; 2, 114 µm; 3, 81 µm; 4, 65 µm; 5, 73 µm; 6, 65 µm; tip (14 µm) of ovipositor exposed.

Type: Holotype deposited in the Buckley amber collection (accession # E-2).
Type locality: Amber mine at the Noije Bum 2001 Summit Site in the Hukawng Valley, southwest of Maingkhwan in Kachin State (26º20´N, 96º36´E) in Burma (Myanmar).
Etymology: cassa is from the Latin "cassus" for spider web.

Comments: The fossil wasp falls into the scelionid section of the Platygastridae. It is not possible to assign the fossil to an extant or extinct genus based on the works of Masner (1976, 1980) and Masner et al., (2007). The presence of an ocellar tubercle (Figs. 5,8C), a jointed 5-segmented feeble club, short postmarginal vein and other wing characters (Figs. 6, 8A) separates *Cascoscelio* from Tertiary members of platygastrids described from Baltic amber, which includes species in the genera *Aneurobaeus* Kieffer, 1912, *Archaeoscelio* Brues, 1940, *Brachyscelio* Brues, 1940, *Ceratobaeoides* Dodd, 1913, *Ceratoteleia* Kieffer, 1908, *Dissolcus* Ashmead, 1893, *Electroteleia* Brues, 1940, *Gryon* Holiday, 1833, *Hadronotoides* Dodd, 1913, *Hoploteleia* Ashmead, 1893, *Microtelenomus* Dodd, 1913, *Proplatyscelio* Brues, 1940, *Pseudobaeus* Perkeins, 1910, *Sembilanocera* Brues, 1940, *Trachelopteron* Brues, 1940 and *Uroteleia* Brues, 1940. While the Baltic amber *Sparaison simplicifrons* Brues, 1940 has a broad tubercle between the face and vertex that is somewhat similar to the ocellar tubercle on *Cascoscelio,* no ocelli are associated with the tubercle of *S. simplicifrons* and that species has a 7-jointed club, the postmarginal vein extends to the tip of the radial cell and the stigmal vein is curved (Brues, 1937, 1940; Cockerell, 1909; Masner et al., 2007).

Cobaloscelio Masner & Johnson, 2007 from Baltic amber has the mesopleuron and metapleuron completely fused, the frons with a well developed median longitudinal

carina, a 7-segmented clava, short marginal cilia on the forewing, a short submarginal vein remote from the costal margin, R_1 not reaching the wing margin and Rs as an arched nebulous vein (Masner et al., 2007). The Baltic amber *Chromoteleia theobaldi* Maneval (1938) has a 7-segmented clavus, the mandibles are tri-dentate and the postmarginal vein is much longer than that of *Cascoscelio*.

The Mexican amber *Palaeogryon muesebecki* Masner (1969) is only 0.6 mm in length, antennomeres 3-6 are transverse and the club is only 3-segmented. The genus *Moravoscelio* (Nel & Prokop, 2005) in Eocene Moravian amber has reduced antennal segments 3-6 and a completely different fore wing venation than *Cascoscelio*. The genus *Galloscelio* Nel & Prokop (2005) in French Eocene Oise amber has a 6-segmented club and the venation in both fore and hind wings differs significantly from that of *Cascoscelio*.

Three species of scelionids were described from Upper Cretaceous Canadian amber (Brues, 1937). Of these, *Baryconus fulleri* Brues, 1937 has a 6-segmented club, the 3rd tergite is much longer than T1 and T2 combined and the marginal vein is short, only half as long as the stigmal vein. *Baeomorpha dubitata* Brues, 1937 has 9-segmented antennae inserted high on the face with a large compact club. *Proteroscelio antennalis* Brues, 1937 has a flattened head and 14-segmented antennae. The Late Cretaceous *Cenomanoscelio pulcher* Schlüter (1978) from French amber has 11-segmented antennae and antennomeres 4-6 are reduced and transverse. Also this wasp has a large head with the eyes occupying most of the lateral surface. The Early Cretaceous Lebanese amber *Proteroscelio gravatus* Johnson, Musetti & Masner (2008) has 14-segmented antenna. All of the above characters differ from those of *Cascoscelio*.

Discussion

Geratonephila burmanica provides fossil evidence of sociality in spiders. The presence of a male and juvenile in the same web implies the presence of a female since extant male nephilids live in female webs (Fig. 9) (Comstock 1948). Spider sociality involves the cohabiting of juveniles and adults in a common web and cooperating in web construction and/ or the acquisition of food. The advantage of sociality is an extended web to cover more area and maximize prey acquisition. The adults and pre-adults show a tolerance towards each other and their common young (Buskirk 1981). The males (extant webs of *Nephila* often contain more than one male) attend the female and share her food (Vollrath 1980). The presence of the juvenile spider indicates that intraspecific aggression and cannibalism were maintained at a minimal level, which are characteristics of social spiders. Although sociality in extant spiders evolved in several independent lineages, there was no previous fossil record of this behavior, making its evolution difficult to interpret (Buskirk 1981).

At least 15 unbroken strands of spider silk extend through the entire length of the amber piece (longest continuous silk strand = 12.7 mm) and these major strands (1.6 µm - 2.0 µm in diameter) are crisscrossed by numerous thinner strands (0.5 µm - 0.7 µm in diameter)(Fig. 1). The adhesiveness of the web is not only demonstrated by the variously sized viscid droplets (4 µm - 25 µm in diameter) attached to the strands, but also the captured insects and attached lepidopteran scales (102-122 µm in length and 45-50 µm in

width)(Fig. 10). Many of the viscid droplets are covered by aerial plankton (pollen, spores, dust particles), which can be explained if the fossil clade had similar habits to extant nephilids that do not re-build their webs at frequent intervals, but only repair damaged parts (Nentwig, 1985). The large viscid droplets noted on the fossil strands (Fig. 10) occur on webs of extant *Nephilia* as well, where the larger drops often can be detected with the unaided eye (Comstock 1948). The use of viscid droplets by spiders to entrap their prey extends back at least to the Early Cretaceous (Zschokke 2003).

Parasitoid wasps usually have some type of sensory organs on their terminal antennomeres to detect hosts or mates. In platygasterids, several types of sensilla occur on the antennae of both males and females (Bin 1981; Cave and Gaylor 1987). It is difficult to determine how many sensilla are present on the claval antennomeres of *Cascoscelia* and only nine are clearly visible on the ventral surface of the terminal three antennomeres (Fig. 7), with four on the terminal antennomere (Figs.7, 8D). They are similar in size (7-13 µm) to the sensilla trichodea curvata (STC) in males of *Telenomus reynoldsi* Gordh & Coker,1973(10-14 µm), however those of the fossil are thicker and have more rounded rather than pointed ends.

Aside from *Cascoselio*, a second captured insect is a partially wrapped neuropteran (length of remaining body, 2 mm) adjacent to the male spider (length, 3mm) (Fig. 1). *Cascoselio* is attached to the web by at least 6 strands of silk and three legs of the juvenile *Geratonephila burmanica* are in contact with the wasp (Fig. 2). It would appear that *Cascoselio* was entrapped only seconds before the resin covered the web, which appears to have occurred just as the arachnid was preparing to feed on its prey. Studies on the extant *Nephila clavipes* (L.) that forms nests in shrubs and trees showed

that over 9 % of the total insect prey captured were parasitic Hymenoptera ranging between 1 and 2 mm in length (Nentwig 1985).

Aside from providing the first fossil preservation of an orb web together with its spider builder and captured prey, the present study demonstrates the existence of spider sociality in the Early Cretaceous. The author could find no previous descriptions of platygastrids in Burmese amber.

Acknowledgments

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Figures

Figure 1. Entire piece with juvenile (J) and adult male (M) *Geratonephila burmanica* spiders together with neuropteran (N) and *Cascoscelio incassa* wasp (W) prey in Early Cretaceous Burmese amber. Bar = 1.05 mm.

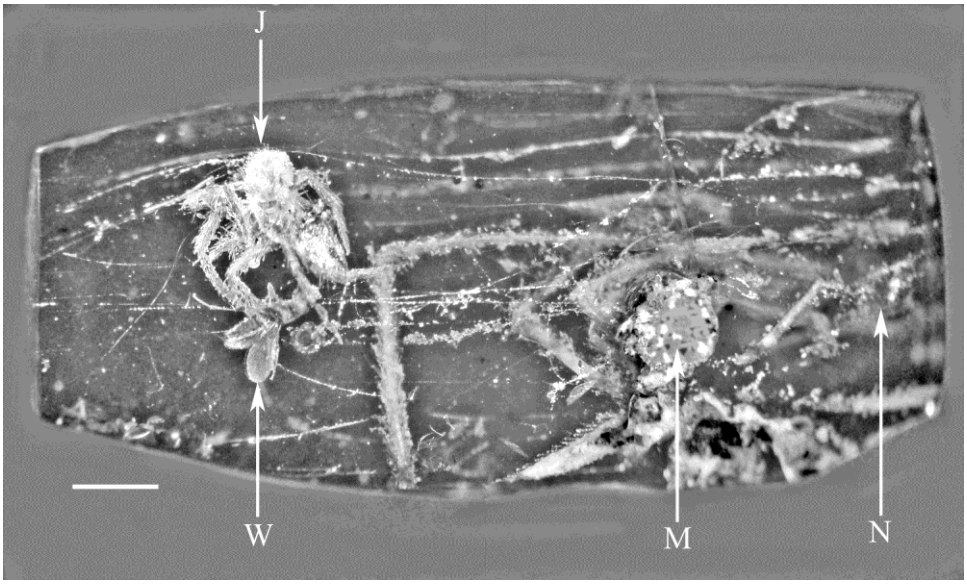

Figure 2. Juvenile *Geratonephila burmanica* in contact with the prey wasp, *Cascoscelio incassa*, in Early Cretaceous Burmese amber. Bar = 440 µm.

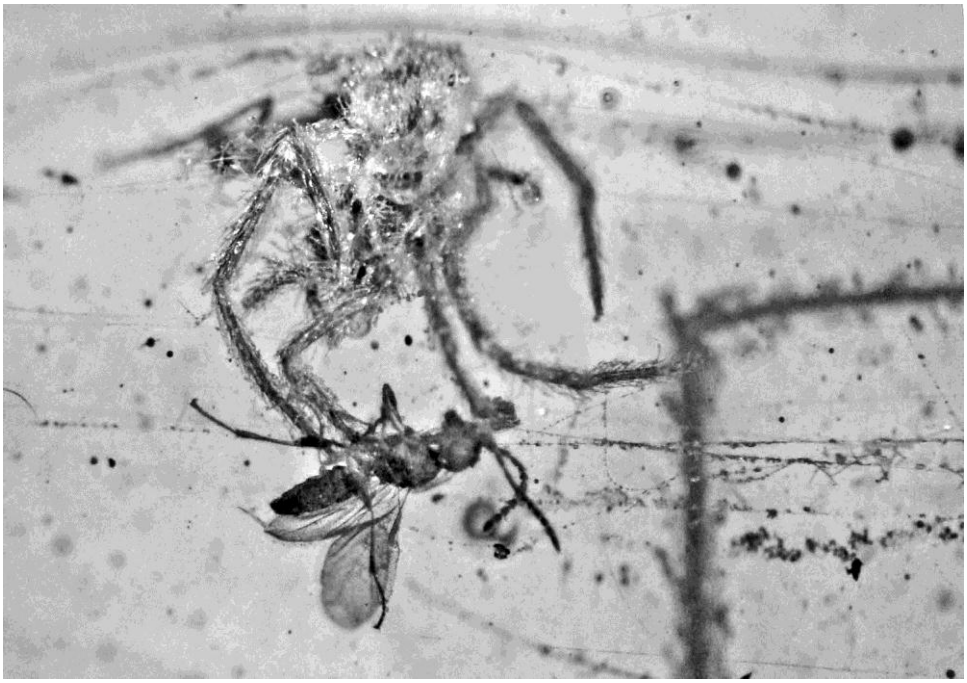

Figure 3. Pedipalp of male *Geratonephila burmanica* in Early Cretaceous Burmese amber. C-E = conductor with embolus; ST = subtegulum; T = tegulum. Bar = 140 µm.

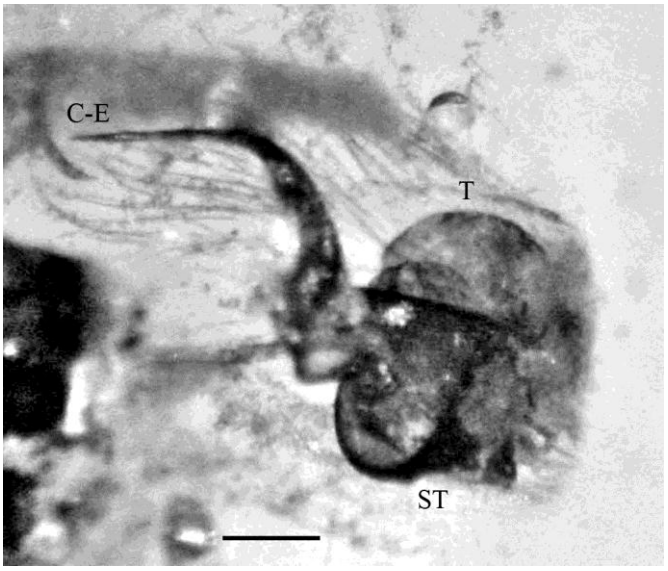

Figure 4. Habitus of *Cascoscelio incassa* in Early Cretaceous Burmese amber. Arrows show spider legs in contact with the captured wasp. Bar = 240 µm.

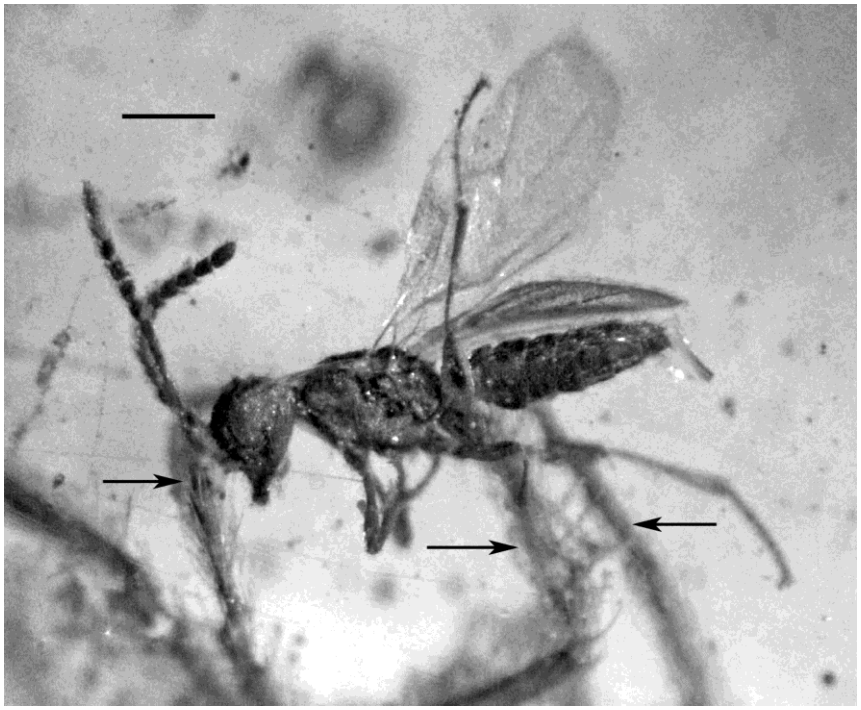

Figure 5. Head of *Cascoscelio incassa* in Early Cretaceous Burmese amber showing antenna and ocellar tubercle (arrow) Bar = 127 µm.

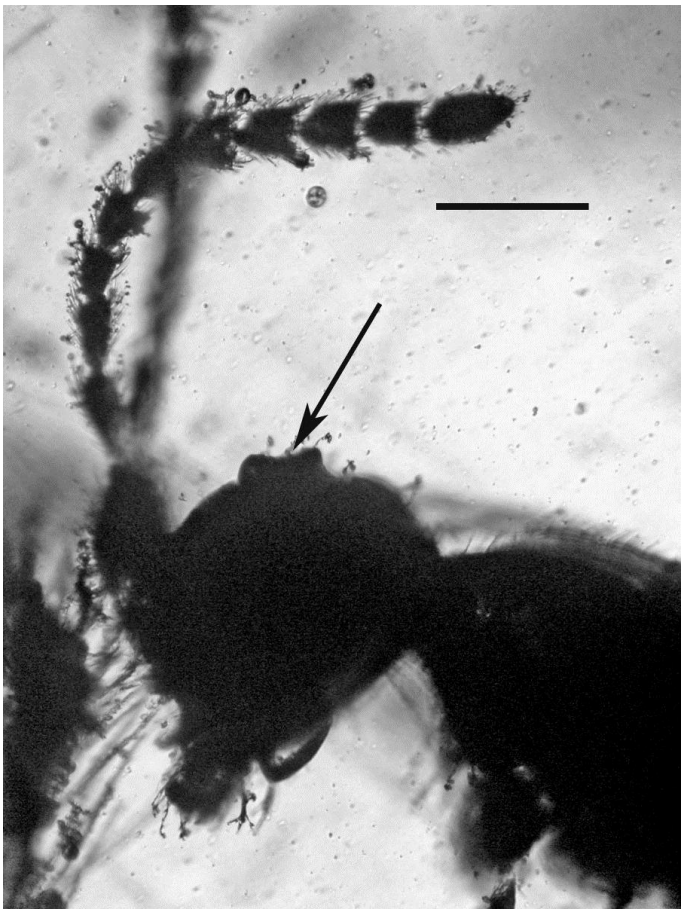

Figure 6. Forewing of *Cascoscelio incassa* in Early Cretaceous Burmese amber. Bar = 114 µm.

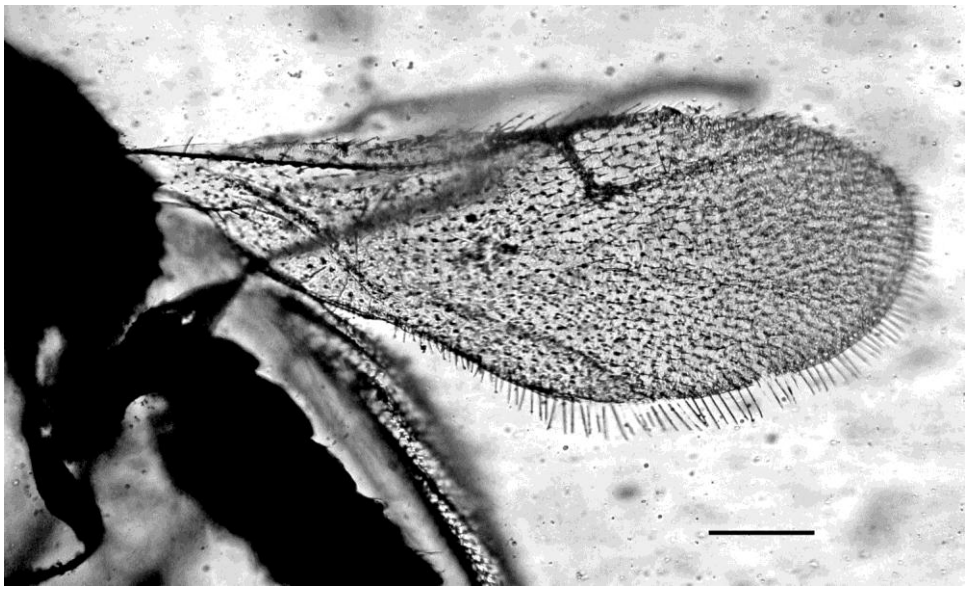

Figure 7. Sensilla trichodea curvata (arrows) on terminal three antennomeres of *Cascoscelio incassa* in Early Cretaceous Burmese amber. Bar = 28 µm.

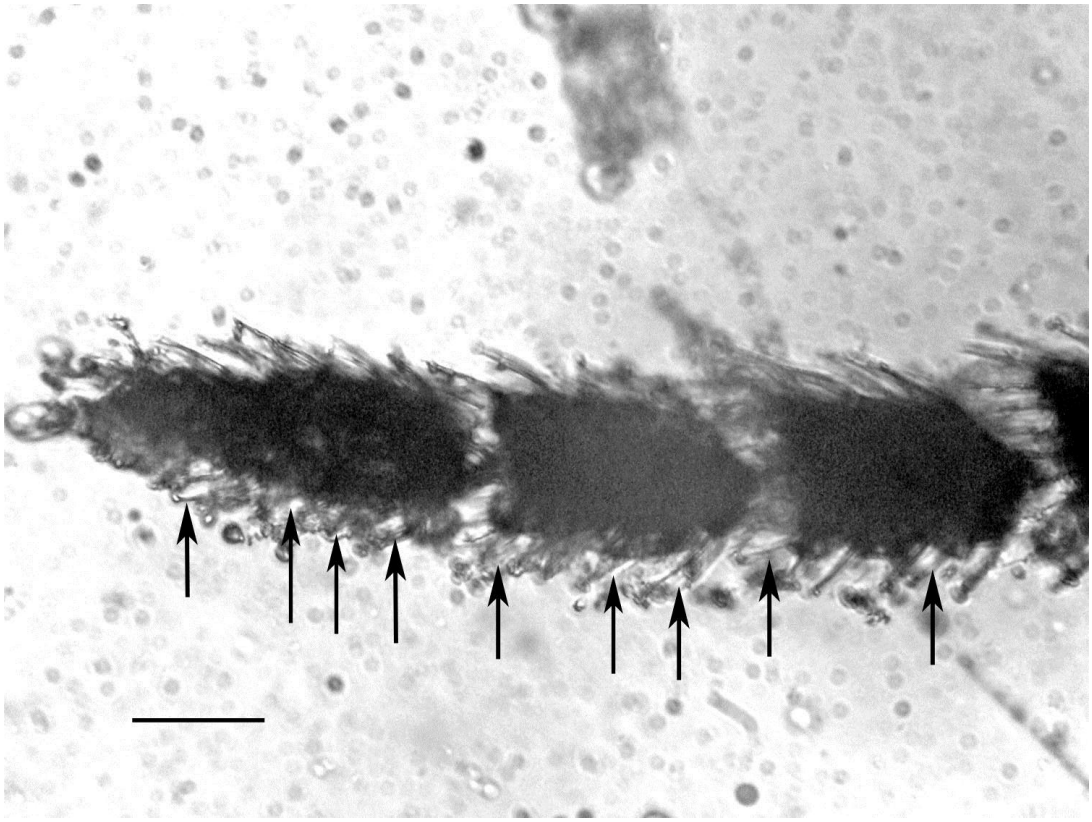

Figure 8. *Cascoscelio incassa* in Early Cretaceous Burmese amber. A. forewing: A = nebulose anal vein; Cu = nebulose cubital vein; fg = frenal gutter; M = marginal vein; Me = nebulose medial vein; Pm = postmarginal vein; Rs = radial sector; S = stigmal vein; Sm = submarginal vein; U = uncus. Only a few setae on wing membrane are shown. Bar = 95 µm. B. hind wing. Bar = 93 µm. C. Head showing antennae with claval segments stippled. Bar = 90 µm. D. Terminal antennomere with sensilla trichodea curvata (stippled) on ventral surface. Bar = 22 µm.

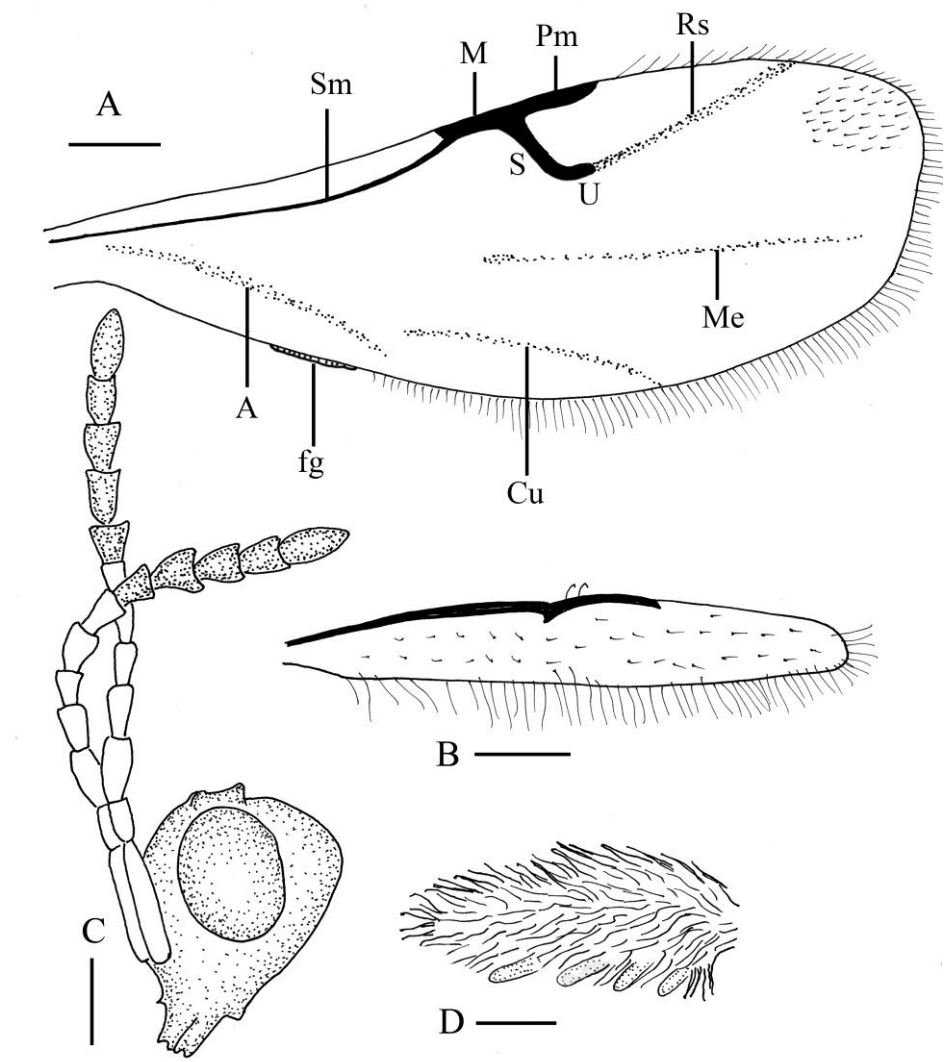

Figure 9. Small male of the extant *Nephila clavipes* living in the web of the larger female. (photo taken by the author in Chiapas, Mexico). Bar = 13 mm.

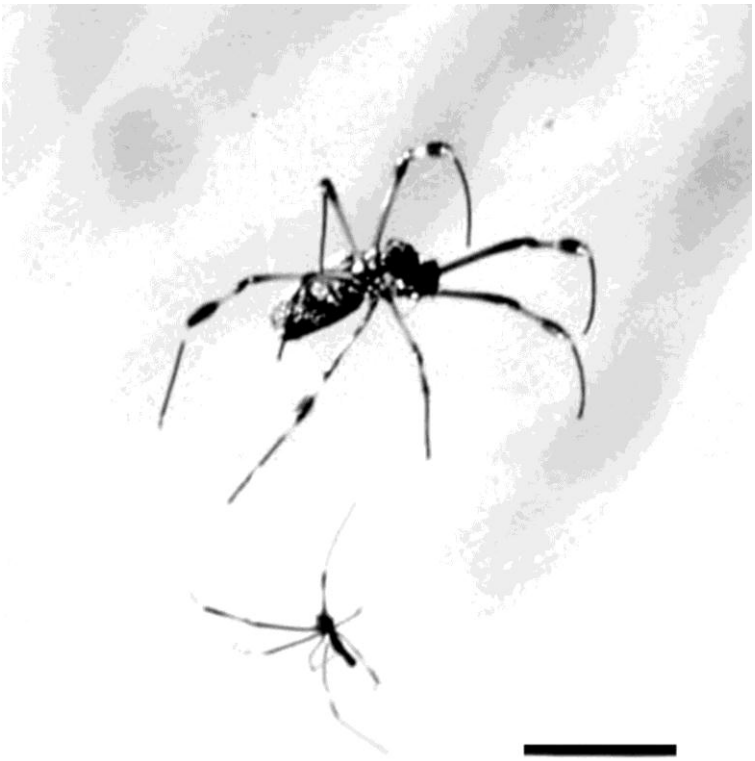

Figure 10. Scales attached to web of *Geratonephila burmanica* in Early Cretaceous Burmese amber. Note also large viscid droplets. Bar = 38 µm.