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Anisopodidae (Insecta: Diptera) from Upper Cretaceous amber of northern Myanmar☆

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ABSTRACT

A new genus and three new species of Anisopodidae are described from the Cretaceous Burmese amber: *Cretolbia hukawnga* gen. et sp. nov., *Cretolbia burmitica* gen. et sp. nov., *Cretolbia zhuodei* gen. et sp. nov. Analyses of the morphological structures and taxonomical differences among representatives within the Anisopodidae have been carried out. A morphological comparison with their closest recent and fossil relatives is provided with the use of light and scanning electron microscopes.

1. Introduction

The Anisopodidae (wood gnats, window-gnats) are a small cosmopolitan family of relatively primitive flies. The wood gnats are found on all continents except Antarctica, on most major islands like Indonesia or Madagascar but are rather rare on smaller, "oceanic" islands (Thompson, 2006). The adults feed on nectar and other liquids, their saprophagous larvae occur under bark of decaying trees, and are associated with fungi or rotting vegetation, fermenting sap and mammal manure (Grimaldi and Amorim, 1995; Scudder and Cannings, 2006). Anisopodidae are represented by 15 genera with about two hundred of species, in fossil record 13 genera (four of them – extant ones) and about forty species have been described. The number of genera given herein is lower than that published earlier (Pape et al., 2011; Szadziewski et al., 2016; Evenhuis, 2017) because the mentioned authors did not take into account some previous transfers and synonimizations. In result of the revisions of type material and new finds *Oligophryne* Rohdendorf, 1962 and *Valeseguya* Colless, 1990 were transferred into Brachycera and the family of its own, respectively (Ansorge and Krzemiński, 1994; Amorim and Grimaldi, 2006), *Eoplecia* Handlirsh, 1920 was synonymized under *Mesorhyphus* Handlirsh, 1920 (Ansorge and Krzemiński, 1995) whereas *Mesobrachyopteryx* Hong and Wang, 1990, *Sinorhyphus* Hong, 1983 and *Sinotendipes* Hong and Wang, 1990 were transferred into Brachycera, Protorhyphidae and Blephariceridae, respectively, based on published illustrations (Blagoderov et al., 2002; Zhang, 2007).

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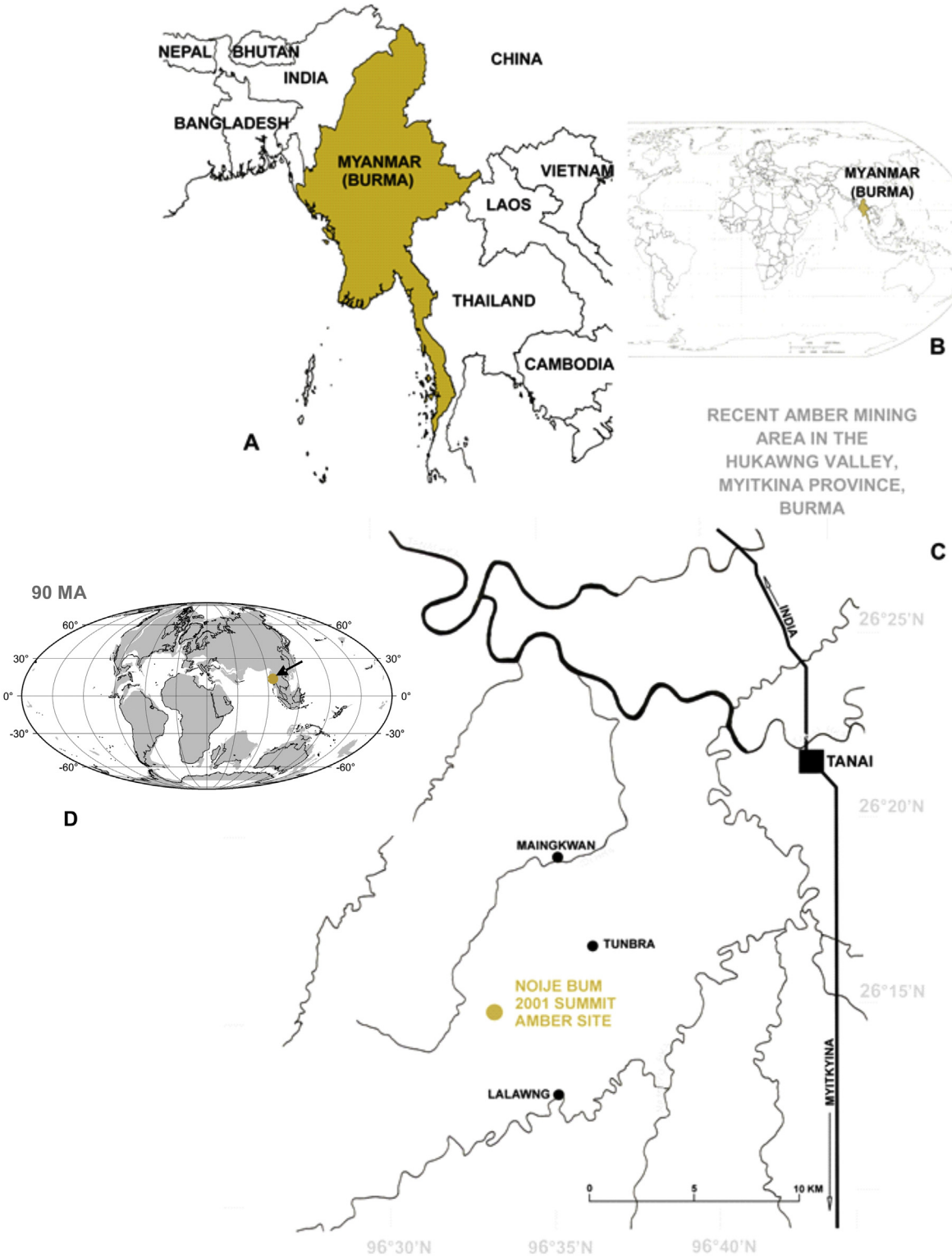

Fig. 1. A–C. Location of recent amber mining area in the Hukawng Valley, Myitkina Province, Myanmar. Compiled from data provided by Grimaldi et al. (2002), Cruikshank and Ko (2003) and Wandrey (2006), after Kania et al. (2015), modified; D. Position of Myanma on the Upper Cretaceous plate tectonics background.

The family Anisopodidae is known since the Early Jurassic: the oldest member, *Mesorhyphus rhaeticus* (Rohdendorf, 1962), was found in the Lower Jurassic of Kyrgyzstan near Lake Issyk-Kul, Sogyuty locality, Dzhil Formation, Sinemurian (Rohdendorf, 1962; Rasnitsyn and Zherikhin, 2002; Krzemińska and Lukashevich, 2018). Anisopodidae regularly occurs in the Euro-Chinese faunas of the Jurassic and Early Cretaceous age: all extinct genera (9 genera with 21 species) are known from this period but the number of extinct genera is still probably overestimated. The present consensus holds that only six extant genera exist although the classification of the Anisopodidae is still under discussion (Amorim and Tozoni, 1994; Michelsen, 1999; Thompson, 2006; Amorim et al., 2016). The extinct species of extant genera *Sylvicola* Harris, 1780, *Mesochria* Enderlein, 1910, and *Olbiogaster* Osten-Sacken, 1886 are described without hesitation only from the Cenozoic, *Mycetobia* Meigen, 1818 from the Cretaceous (Kania et al., 2018, in press), two remaining genera *Lobogaster* Philippi, 1865 and *Carreraia* Corrêa, 1947 are still unknown in the fossil record.

The three new species described herein within one new genus are the Anisopodidae from the Cenomanian Burmese amber and are classified to subfamily Olbiogastrinae which comprises also the oldest anisopodid species and most other Mesozoic members of the family.

2. Material and methods

The studied specimens are amber inclusions from the Hukawng Valley in northern Myanmar (Fig. 1) that was studied and named

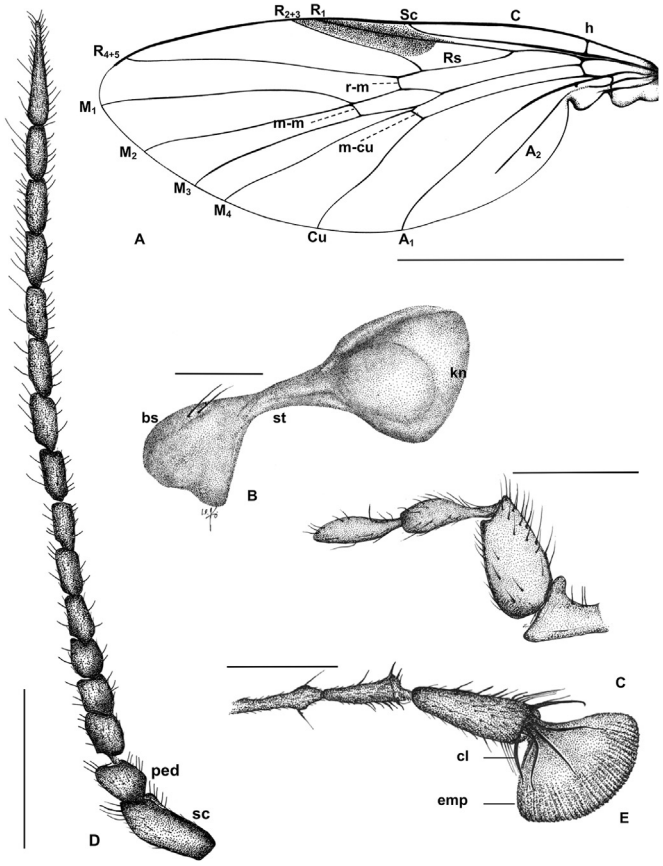

Fig. 2. *Cretolbia hukawnga* gen. et sp. nov., holotype, No. MP/3657 (male): A. wing venation; B. halter; C. palpus; D. antenna; E. last segments of tarsus. Abbreviations: bs – base; cl – claw; emp – empodium; st – stem; kn – knob; ped – pedicel; sc – scape. Scale bar = 1 mm for A; scale bar = 0.1 mm for B and E; scale bar = 0.2 mm for C and D.

'burmite' (Helm, 1892, 1893) although the only commercial source is the Hukawng Valley in the Myitkyina and Upper Chindwin districts (Zherikhin and Ross, 2000; Cruikshank and Ko, 2003; Ross et al., 2010). Shi et al. (2012) dated zircons from the amber-bearing bed which gave an age of 98.79 ± 0.62 Ma; therefore, the amber is likely to be of early Cenomanian age (Smith and Ross, 2017).

The study was based on specimens from the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China (three specimens) and Institute of Systematics and Evolution of Animals Polish Academy of Sciences, Kraków, Poland (ISEA PAS) (two specimens). All five inclusions in Burmese amber were studied using a Nikon SMZ 1500 stereomicroscope equipped with a Nikon DS-Fi1 camera and the measurements were taken with NIS-Elements D 3.0 software. The drawings for the analysis were based on the specimen and photographs and were made by the first author.

Additionally, for comparison of morphology of chosen structures the recent species *Sylvicola* (*Sylvicola*) *cinctus* (Fabricius, 1787) were studied. The some structures, e.g. antenna, apical combs and tarsus of *S.* (*S.*) *cinctus* were analyzed under the scanning microscope Hitachi SU 8010 SEM at the Podkarpacie Innovative Research Center of the Environment (PIRCE) at the University of Rzeszów. For scanning electron microscope (SEM) observations, the material was attached to aluminum stubs and sputtered with 20 nm of gold using a Turbo-Pumped Sputter Coater Quorum Q 150OT ES.

The measurements were made as follow: the length of head—length of head capsule; the length of discal cell was measured from its posterior edge to the point of connection of vein m-m with vein M_3. The measurements were given only in case when relevant structures were not distorted.

The classification of Anisopodidae used here is conservative and follows mainly from Edwards' *Genera Insectorum* (Edwards, 1928) updated by Michelsen (1999) and Thompson (2006) without over splitting the wood gnats into numerous genera and tribes. The family includes 15 genera totally (six of them extant) classified in four subfamilies, three extant Anisopodinae, Mycetobiinae and Olbiogastrinae and one extinct Teginae as was adopted by one of us earlier (Shcherbakov et al., 1995; Lukashevich, 2012). In the Olbiogastrinae three extant genera *Olbiogaster*, *Lobogaster* and *Carreraia* and most of Mesozoic ones are included (except for *Tega* Blagoderov, Krzemińska and Krzemiński, 1993).

The nomenclature of wing venation follows that used in literature on Anisopodidae (e.g. Ansorge and Krzemiński, 1995; Krzemińska et al., 2010) and differs from the system of Wootton and Ennos (1989) accepted by one of the co-authors (Shcherbakov et al., 1995; Lukashevich, 2012). The terminology of the external structures of *S.* (*S.*) *cinctus* was used after Friedemann et al. (2014), Meyer-Rochow (2015), Yang and Zhang (2014).

3. Systematic palaeontology

Order: Diptera Linnaeus, 1758
Suborder: Nematocera Duméril, 1805
Infraorder: Bibionomorpha Hennig, 1954
Superfamily: Anisopodoidea Knab, 1912
Family: Anisopodidae Knab, 1912
Subfamily: Olbiogastrinae Hennig, 1973

Most of Mesozoic anisopodids have been described in this extant subfamily. In their wings, R_{2+3} is gradually approaching C, without a strong curve in the distal third; the branches of Rs are not

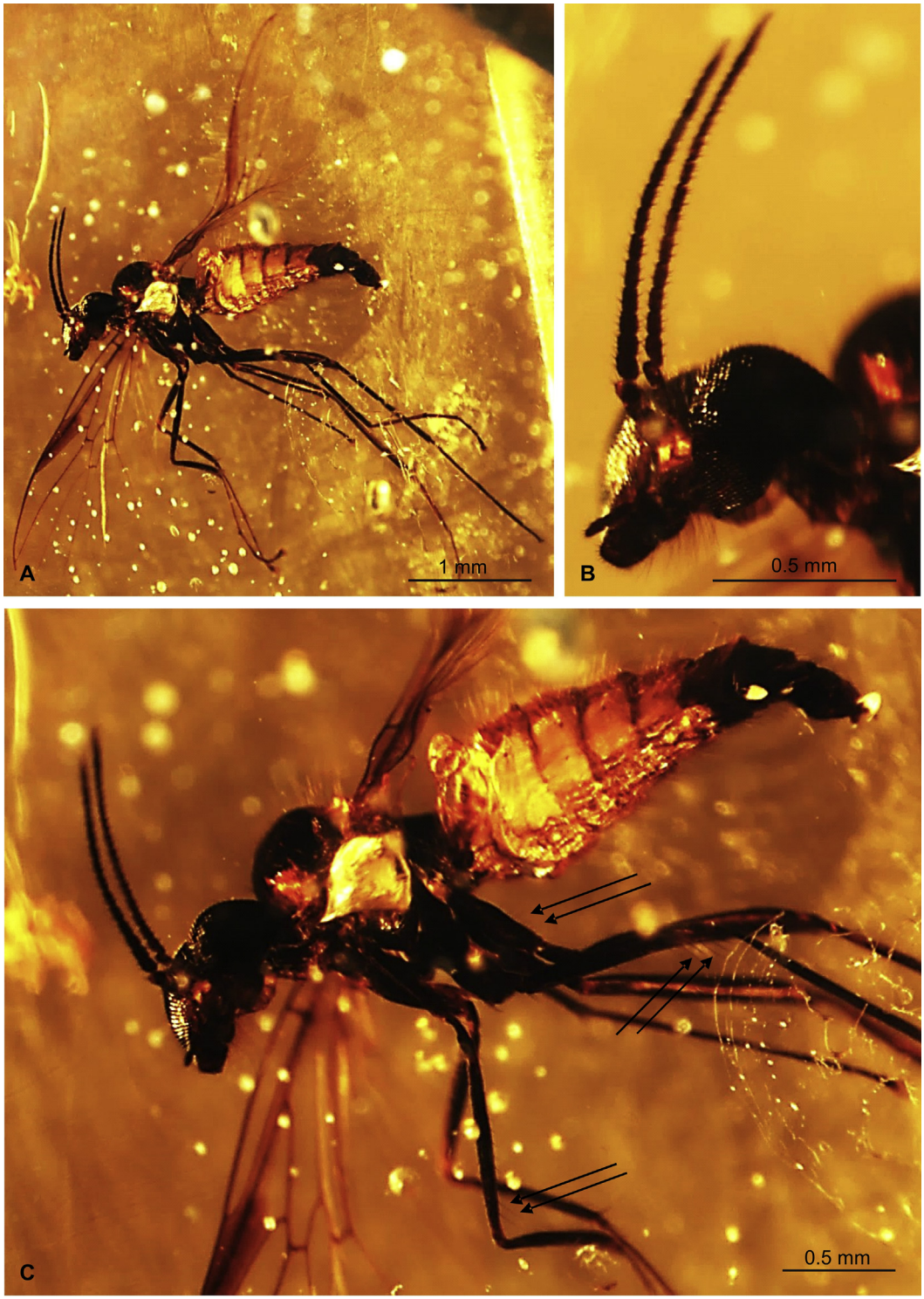

Fig. 3. *Cretolbia hukawnga* gen. et sp. nov.; holotype, No. MP/3657 (male). A. habitus, lateral view; B. head; C. enlarged lateral view of body with elongated setae on coxa and femur visible, pointed by arrows.

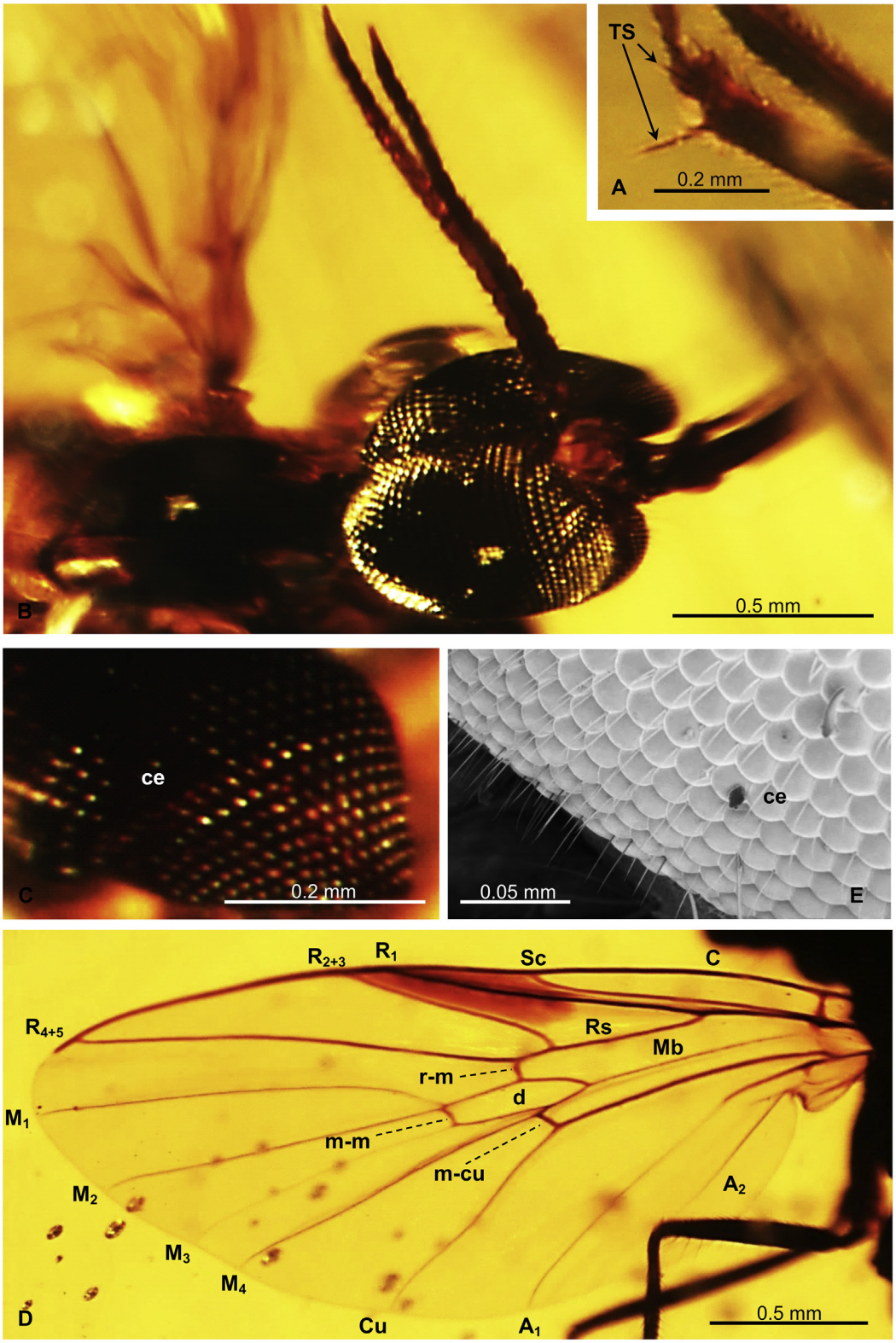

Fig. 4. A – D. *Cretolbia hukawnga* gen. et sp. nov., holotype, No. MP/3657 (male): A. tibial spurs of fore leg; B. head with holoptic compound eyes; C. compound eyes without long pilosity; D. wing venation; E. *Sylvicola* (*S.*) *cinctus* (Fabricius, 1787), ommatidia of compound eye with short microommatrichia, SEM. Abbreviations: ce – compound eye, TS – tibial spurs.

lying close to each other, both flowing into C; media has four branches; discal cell of usual size with m-m lying in the distal half of the wing (Lukashevich, 2012). In the new genus described herein one can see a main peculiarity of adults, which was used by Hennig for establishing the subfamily, absence of macrotrichia on wing membrane (Figs. 13D, 14E). In contrast to the extant members of the family, the antennae in all Mesozoic genera are much shorter than the body (not longer than head and thorax together) and the number of spermathecae is sometimes two, rather than usual three. In the new species described herein spermathecae are invisible. Anisopodid larvae (important for subfamilial attribution) are unknown in the fossil record.

***Cretolbia* gen.** nov. Kania, Wojtoń, Lukashevich, Wang and Krzemiński
(Figs. 2–15)

LSID urn:lsid:zoobank.org:act:7C7854E2-BB51-4AE9-9F23-9F624825D8CE

Type species. *Cretolbia hukawnga* sp. nov. Kania, Wojtoń, Lukashevich, Wang and Krzemiński.

Etymology. The species name is derived from "creta" (Latin) = Cretaceous and "olbios" (Greek) = happy. Gender: feminine.

Diagnosis. Small body; huge holoptic (male) or dichoptic (female) eyes without long pilosity (Fig. 4B, C); raised large ocelli formed equilateral triangle (Fig. 9A); antennae approximately as long as head and thorax combined or slightly shorter, 16-segmented, flagellomeres cylindrical, twice as long as wide (Figs. 2D, 10A, B); maxillary palpus longer than proboscis, 5-segmented, first palpomere greatly reduced (Figs. 6C, 9B); katepisternum bare; wing (Figs. 2A, 4D) wide, membrane hyaline without distinct coloration pattern except for very dark pterostigma surrounding apical part of R_1, C distinctly extending approximately 1/3-1/4 distance between R_{4+5} and M_1 apices; radial veins strongest; distance between R_1 and R_{2+3} apices short, only 0.25 distance between Sc and R_1 apices; R_{4+5} ending well before wing tip; Rs approximately as long as d-cell; M stem weaker than M_1 and M_2, diverging from pentagonal d-cell independently; M_{1+2} fork narrower than fork of Rs; M_3 out of d-cell weaker than other M veins; distance between M_2 and M_3 apices one and half to twice the distance between M_3 and M_4 apices; M branches with macrotrichia (at least M_1 and M_2, Fig. 8B); d-cell much longer than wide; Cu curved at m-cu, slightly S-shaped distally; reduced vein A_2 comparatively short, all veins except A_2 meeting wing margin. Maximum width of wing between Cu and A_1; anal lobe well developed, alula strongly differentiated (Figs. 8C, 12A, 14B); halter more or less elongated with very wide, rounded knob and rather short stem (Figs. 2B, 14H); all tibia slender, tibial

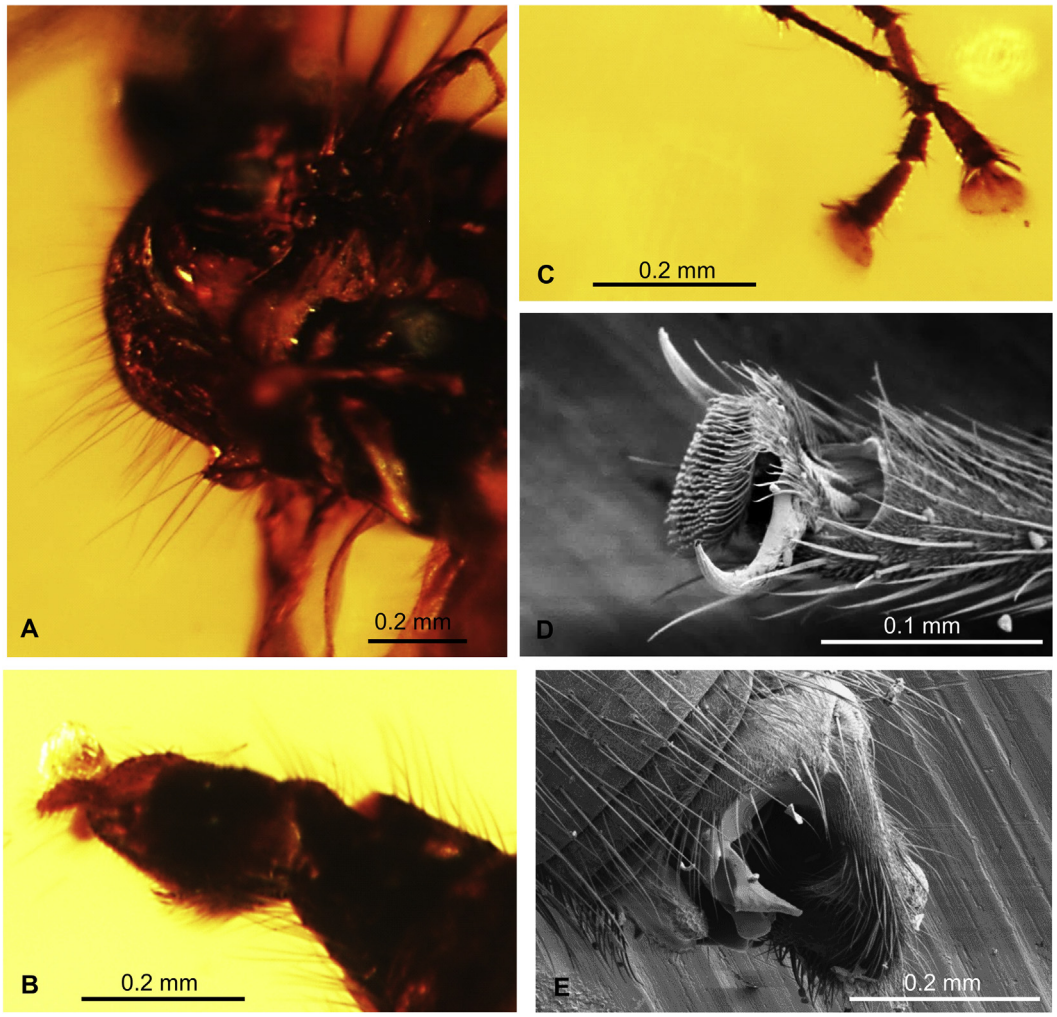

Fig. 5. A – C. *Cretolbia hukawnga* gen. et sp. nov. holotype, No. MP/3657 (male): A. thorax, latero-dorsal view; B. male terminalia, lateral view; C. last segments of tarsi; D – E. *Sylvicola* (*S.*) *cinctus* (Fabricius, 1787), SEM: D. last segment of tarsus with empodium visible; E. male genitalia, latero-ventral view.

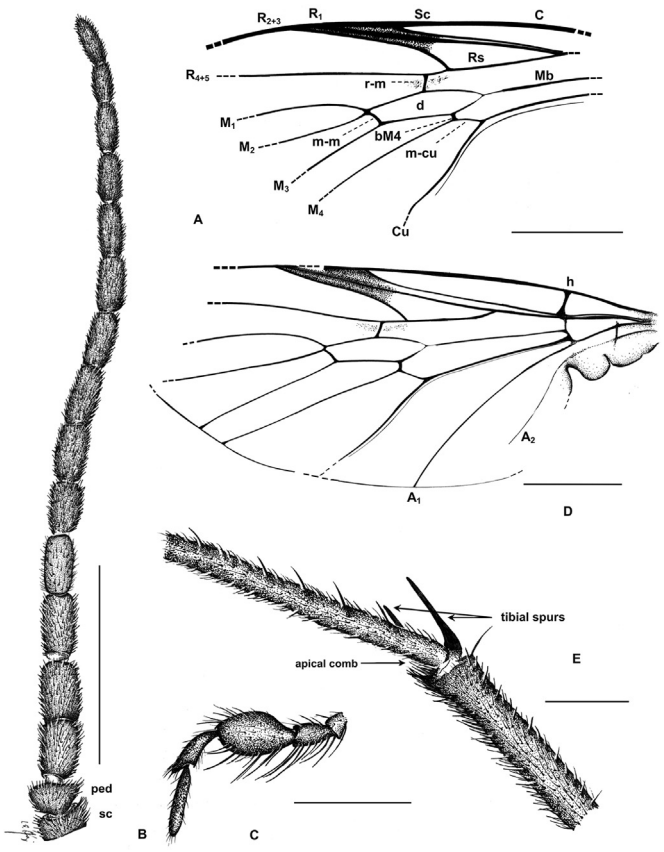

Fig. 6. A – C. *Cretolbia burmitica* sp. nov., holotype, No. NIGP168837 (female): A. wing venation; B. antenna; C. palpus; D – E. No. NIGP168838 (sex unknown): D. wing venation; E – part of middle leg with tibial spurs visible. Abbreviations: ped – pedicel, sc – scape. Scale bar = 1 mm for A and D; scale bar = 0.5 mm for B; scale bar = 0.1 mm for C; scale bar = 2 mm for E.

spur formula 2:2:2 with subequal spurs of fore legs (Fig. 11C-E); empodium large in female, very large in male (Figs. 2E, 5C); female cerci rather short (Fig. 11F); male terminalia complex, unrotated, comparatively elongated, with fleshy, somewhat conical rather short cerci (Fig. 5B).

Comparison. The new genus differs from other Euroasian Mesozoic genera with the wide distribution (*Mesorhyphus* Handlirsh, 1920, *Pachyrhyphus* Kovalev, 1986 and *Megarhyphus* Kovalev, 1990) in a slender male habitus and longer antenna which is not longer than thorax in all aforementioned genera (Kovalev, 1990). Additionally, it distinct from *Megarhyphus* in a smaller size, a bare katepisternum, wing venation (narrow M_{1+2} fork, m-m connecting with M_2, M_3 weaker than other medial veins) and maximal width of wing at level of Cu-A_1, from *Mesorhyphus* – in slender, not clavate hind tibia, from *Pachyrhyphus* – in elongated flagellomere (with length twice longer than wide) and maxilary palpi longer than proboscis.

Among extant genera *Cretolbia* gen. nov. is more similar to *Olbiogaster* (see Table 1) but differ mainly in shorter antenna, holoptic male eyes, two spurs on fore and hind tibia, a large empodium, rather short cerci of male, and presence of macrotrichia on medial veins, at least on M_1 and M_2 (Peterson, 1981; Amorim and Tonzoni, 1994). Such short antenna and holoptic male eyes are unknown among extant Olbiogastrinae.

Remarks. For comparison SEM images of eyes with short ommatrichia (Figs. 4E, 9C) and wing membrane with macrotrichia (Fig. 14F) of *Sylvicola* (*S.*) *cinctus* is given. The strongly differentiated alula, found in *Cretolbia* gen. nov. (Figs. 8C, 12A, 14B), is also known in extant *Sylvicola* (Fig. 14A) and *Olbiogaster* (Peterson, 1981) and is described in Mesozoic *Pachyrhyphus* (Lukashevich, 2012).

Cretolbia hukawnga sp. nov. Kania, Wojtoń, Lukashevich, Wang and Krzemiński
(Figs. 2–5)

LSID urn:lsid:zoobank.org:act:7A544010-1656-41C7-B128-26B5A9F14D89

Etymology. The species name is derived from Hukawng Valley in Myanmar.
Material examined. Holotype, No. MP/3657 (male), Institute of Systematic and Evolution of Animals, Polish Academy of Sciences, Kraków.
Horizon and locality. Lowermost Cenomanian, Hukawng Valley, northern Myanmar. The mining is done at a hill named Noije Bum, near Tanai Village (26°21′33.41″N, 96°43′11.88″E).
Diagnosis. Sc short, ending before r-m level; R_{4+5} almost straight; any sclerotization across r-m absent; M stem and d-cell connection

Table 1
Characters of *Cretolbia* gen. nov. compared to extant anisopodid genera (mainly based on Edwards, 1928, additional or corrected data are marked with references below [1]Peterson, 1981; [2]Amorim & Tozoni, 1994; [3]Thompson & Rogers, 1992; [4]Thompson, 2006).

Characters of *Cretolbia* gen. nov.	*Sylvicola*	*Olbiogaster*	*Lobogaster*	*Carreraia*	*Mycetobia*	*Mesochria*
Antenna not longer than head and thorax together	+	–	–		+	+
Male eyes holoptic	+ or –	–	–	–[2]	– or +[2]	+ or –[4]
Eyes with short pubescence or bare	+	+	–	+[3]	+	+
Ocelli large	+	–	+		–	– or +[4]
Palpomere I-III not fused	+	+	+	+	–	–
Katepisternum bare	+	+	–	–[3]		
Thorax with long dense setae	+	+ or –[1]	+		–	+ or –[4]
Wing without macrotrichia	–	+	+	+	+	+
R_{2+3} – in C	+	+	+	+	+	–
R_{2+3} not curved	–	+	+	+	+	+
Rs branches not closed	+	+	+	+	+	+
R_{4+5} well before apex	–	–	+		–	–
M_3 present	+	+	+	+	–	–
M_3 weaker than others	–	+ or –[2]	–		Absent	Absent
M stem distinct	+	+	+	+	–	–
d-cell present	+	+	+	+	–	–
Metatibia with apical comb	+	–/+[1]	–		+	
Empodium large	+	–	+		Absent	
Unrotated male terminalia	+	–			–	+[4]

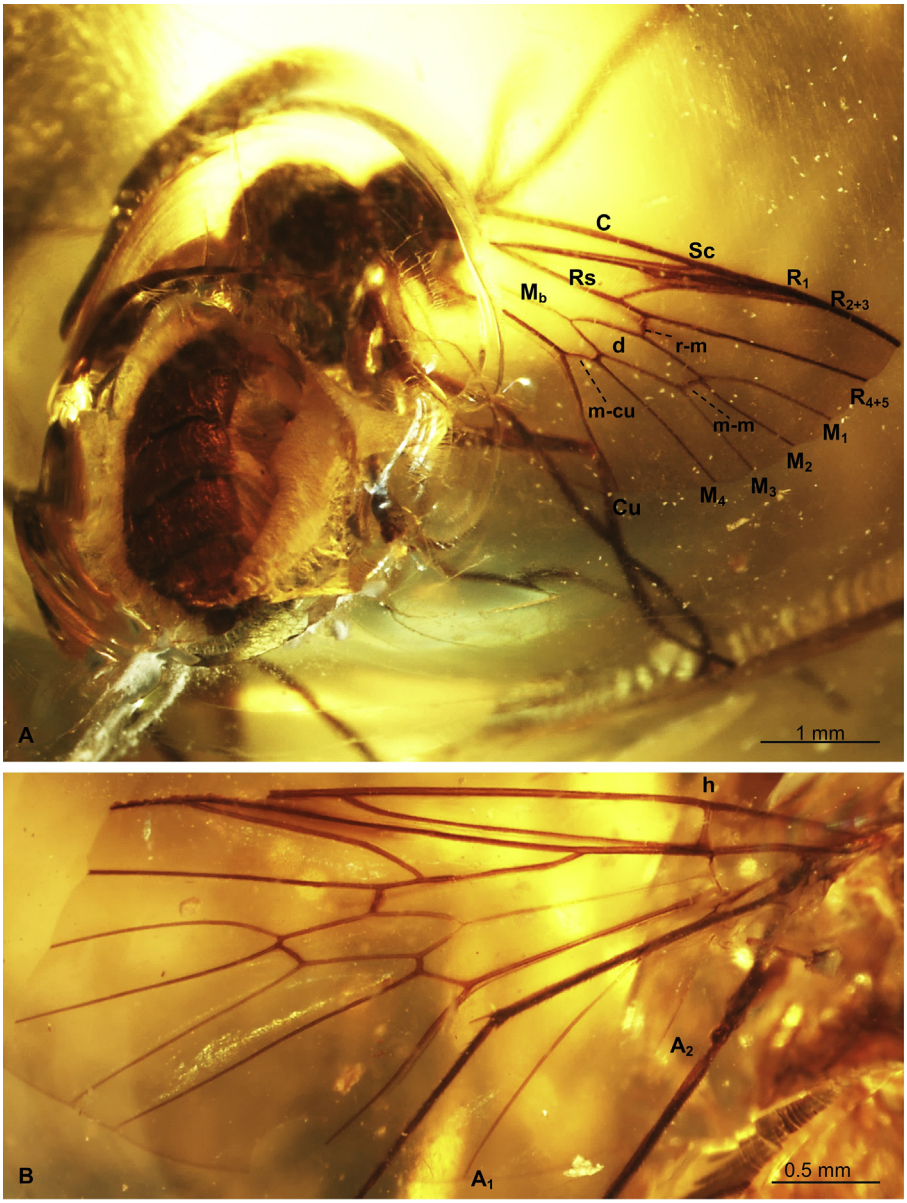

Fig. 7. *Cretolbia burmitica* sp. nov.: A. Holotype, No. NIGP168837 (female), habitus, latero-dorsal view; B. No. NIGP168838 (sex unknown): wing venation.

without desclerotization; scape cylindrical; flagellomeres with elongated sparse setae; terminal flagellomere longer than penultimate one, tapered at apex; III maxillary palpomere strongly dilated; elongated dense bristles on thorax, coxae and femora; abdomen yellow with almost black last segments; spots on femur and tibia absent.

Description. Body (Fig. 3) 2.90 mm long. Head, thorax and legs dark brown, almost black, I-V abdominal segments pale, yellow instead dark brown distal part; head and thorax combined 1.09 mm long, head width 0.69 mm. Antenna (Figs. 2D, 3B, 4B), comparatively long (1.05 mm); scape elongated, twice as long as wide; pedicel very short, approximately as long as wide; terminal flagellomere longer than penultimate one, tapered at apex; all flagellomeres with elongated sparse setae, subequal to width of bearing segments; additionally very short setae on all flagellomeres; maxillary palpus 0.5 mm (Figs. 2C, 3B) with third palpomere dilated, massive and longest, penultimate and terminal palpomeres subequal, approximately 0.30 mm, elongated and narrow; sparse short setae on all palpomeres.

Thorax: mesoscutum (Fig. 5A) with very elongated dense setae, scutellum with probably four such setae. Wing (Figs. 2A, 3A, 4D): 2.66 mm long, 0.89 mm wide; very dark pterostigma in half length of wing, surrounding apical part of R_1 to 3/5 length of R_1 from edge of wing and extending to 5/6 of R_{2+3} from edge of wing, distinctly separated from other part of wing by arched/rounded line of dark tint. Sc comparatively short, ending in proximal part of wing, approximately in 2/5 from base, beyond Rs bifurcation, but before r-m, opposite approximately 1/3 of d-cell length and A_1 apex; R_1 apices in about 3/5 of wing length, distance between R_1 and R_{2+3} apices very short, subequal to m-m, only 0.25 distance between Sc and R_1 apices. Rs separate Rb in proximal 1/5 of wing length from wing base; Rs stem longer than half R_{2+3} and as long as d-cell, constituting approximately 2/3 of R_{2+3}. D-cell pentagonal, 4× longer than wide, in proximal wing half, margins of d-cell evenly

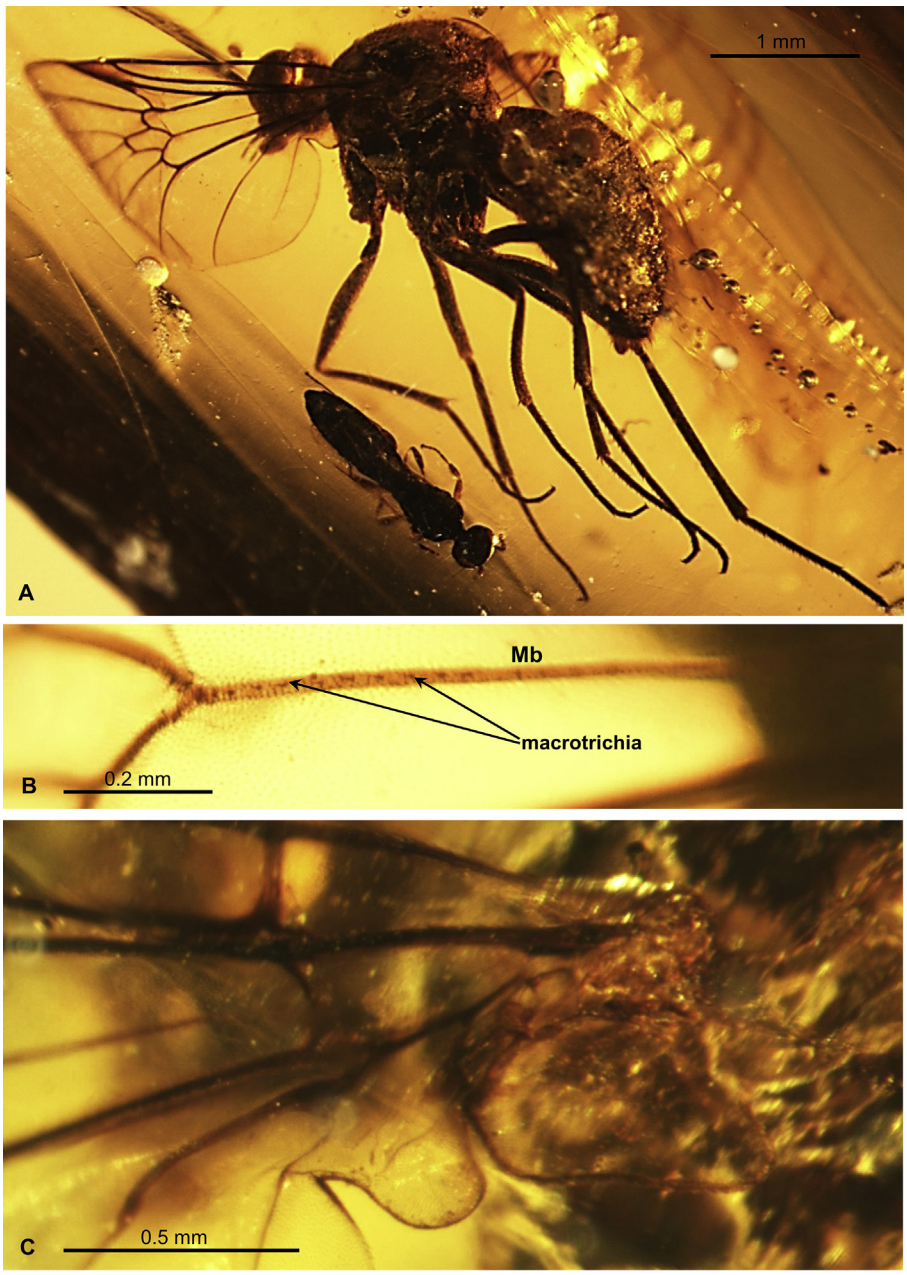

Fig. 8. *Cretolbia burmitica* sp. nov., additional material, No. MP/3682 (female): A. habitus, latero-dorsal view; B. macrotrichia on Mb stem; C. base of wing with strongly differentiated alula.

sclerotized, m-m almost straight. Segment bM_4 much shorter than m-cu, diverging from d-cell in proximal 1/3. Crossvein r-m shorter than m-m, r-m positioned just before d-cell midlength, approximately right angle to d-cell. Halter uniformly yellow, 0.39 mm long (Fig. 2B), not very elongated with short stem, shorter than knob and base of halter.

Legs (Figs. 3A, B, 4A, 5C): all coxae long, coxae and femora with very long, sparse bristles on inner surface of apical part and rare short setae. Tarsus (Figs. 2E, 5C) comparatively elongated with last tarsomere wide and longer than penultimate, simple claw shorter than very large empodium. Fore leg 3.01 mm long, middle 3.41 mm, hind leg 4.09 mm. Fore coxa 0.48 mm, trochanter 0.08 mm, femur 0.77 mm, tibia 0.61 mm, tarsus 1.07 mm long (0.51/0.27/0.13/0.07/0.09). Middle coxa 0.32 mm, trochanter 0.12 mm long, femur 1.07 mm, tibia 0.82 mm, tarsus 1.08 mm long (0.47/0.26/0.15/0.07/0.13). Hind coxa 0.45 mm, trochanter 0.14 mm, femur 1.11 mm, tibia 1.04 mm, tarsus 1.35 mm long (0.46/0.29/0.17/0.09/0.13).

Abdomen (Fig. 5B): male terminalia 0.22 mm long.

Comparison. The new species can be distinguished from other species of the genus described below in the shortest Sc, ending in proximal part of the wing and in color pattern of the body, in the shape and length of terminal flagellomere, the setation of antenna and pubescence of mesoscutum, scutellum, coxae and femora.

Remarks. For comparison scanning electron micrograph of the empodium (Fig. 5D) and male terminalia (Fig. 5E) of *Sylvicola* (*S.*) *cinctus* is given. In both genera the male terminalia are unrotated and structure of empodium is probably similar but in *Cretolbia* gen. nov. the empodium larger than in both extant species of *Sylvicola*, examined by us and previously (Peterson, 1981; Friedemann et al., 2014).

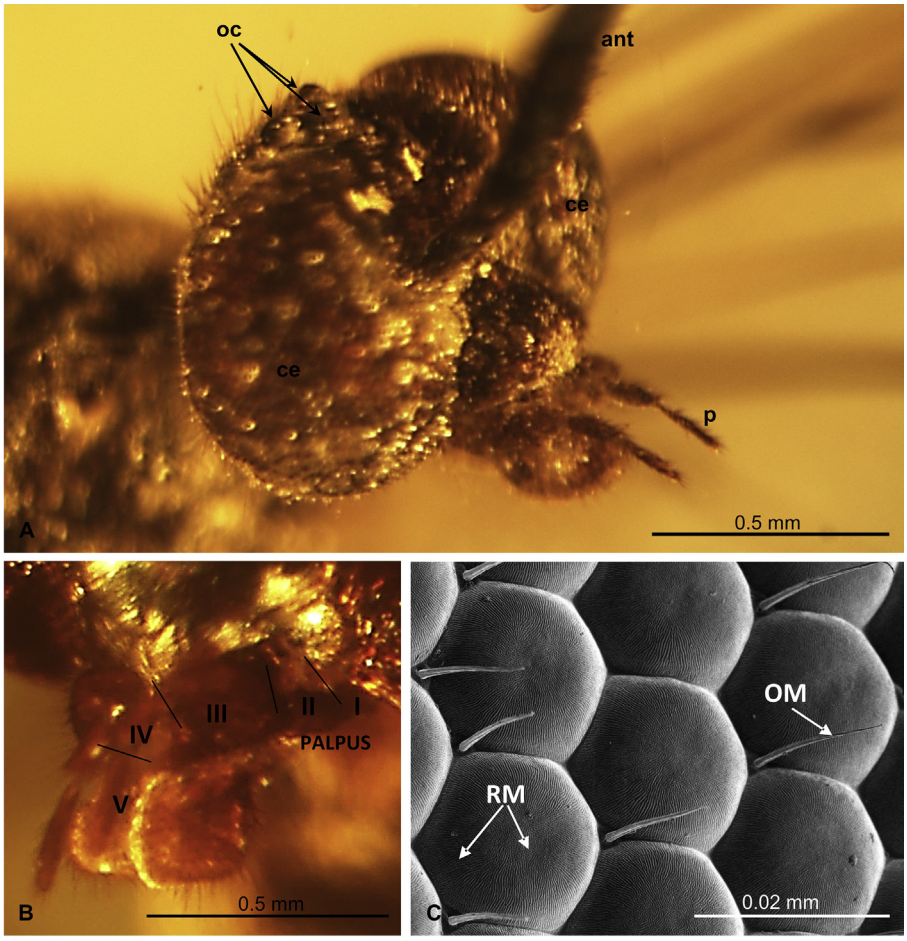

Fig. 9. A– B. *Cretolbia burmitica* sp. nov., A. additional material, No. MP/3682 (female), head with ocelli and palpi visible; B. Holotype No. NIGP168837 (female), head with palpi visible; C. *Sylvicola* (*S.*) *cinctus* (Fabricius, 1787) (female), SEM, the corneal surface with radial microridges and short ommatrichia arranged irregulary. Abbreviations: ant – antenna; ce – compound eye; oc-ocelli; p – palpus.; OM – ommatrichia; RM – radial microridges; I-V – palpomeres I–V.

Cretolbia burmitica sp. nov. Kania, Wojtoń, Lukashevich, Wang and Krzemiński
(Figs. 6–11)
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Etymology. The species name is derived from the mineralogical name of the resin containing inclusions – burmite.
Material examined. Holotype, female, No. NIGP168837; additional material: sex unknown, No. NIGP168838, deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, P.R. China; female, No. MP/3682, Institute Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków.
Horizon and locality. Lowermost Cenomanian, Hukawng Valley, northern Myanmar. The mining is done at a hill named Noije Bum, near Tanai Village (26°21′33.41″N, 96°43′11.88″E).
Diagnosis. Sc ending just behind of r-m level, but before M_{1+2} bifurcation level; R_{4+5} almost straight; small sclerotization across r-m; M stem and d-cell connection desclerotized; scape saucer-shaped; flagellomeres without elongated sparse setae; terminal oval flagellomere subequal to penultimate one; III maxillary palpomere strongly dilated; thorax, coxae and femora without elongated dense bristles; abdomen brown; spots on femur and tibia absent.
Description. Body (Figs. 7A, 8A) uniformly pale brown, 3.85–5.54 mm long. Head (Fig. 9A): small, 0.73–1.23 mm high, 0.95–1.55 mm wide; eyes widely separated; antenna (Figs. 6B, 10A, B) comparatively massive, elongated, approximately as long as head and thorax combined, 1.65–2.22 mm long, scape and pedicel short, wider than long, both saucer-shaped, flagellomeres elongated, distinctly longer than scape and pedicel, comparatively equal in length, last oval flagellomere subequal to penultimate one; all segments of antenna densely covered by thick and very short setae only; maxillary palpus (Figs. 6C, 9A, B) 0.36–0.54 mm long, second palpomere elongated with elongated and strong setae at apex, third one strongly dilated, twice as long as wide, with strong elongated setae, fourth one short, slightly widened distally, with elongated and strong apical setae, last one twice as long as penultimate, with strong setae arranged evenly, additionally on all palpomeres short and thick setae arranged evenly.
Thorax: with not numerous, elongated setae on mesoscutum; head and thorax combined 2.01–2.40 mm; wing (Figs. 6A, D, 7A, B): 1.68–1.78 mm wide; very dark pterostigma in distal wing half, beyond Rs bifurcation, small sclerotization across r-m. Sc long, ending in distal half of wing, approximately in 2/3 from wing base, beyond Rs bifurcation and r-m, but before M_{1+2} bifurcation, just beyond d-cell midlength; Rs setose, separate Rb in distance 2/3 of its length from cross-vein h, Rs stem 0.75–0.89 mm long. R_1 terminating in 2/3 from wing base, 1.3 times longer than Rs. Crossvein r-m subequal to m-m, positioned aslant, in d-cell midlength; M stem with macrotrichia (Fig. 8B), bM_2 extremely short, almost entirely reduced, bM_4 much shorter than m-cu, diverging from d-cell in proximal part, d-cell four times longer than wide, 0.95–0.97 mm long, 0.19–0.26 mm wide,

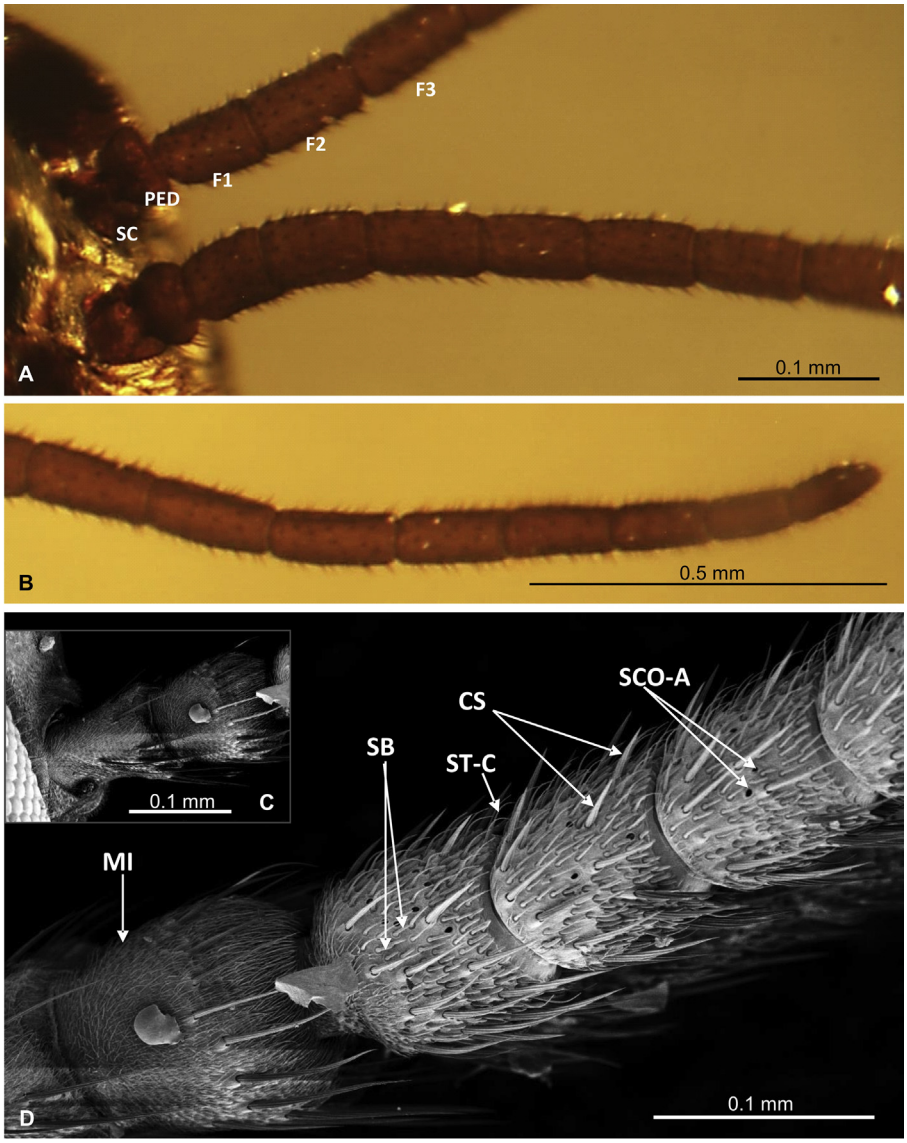

Fig. 10. A – B. *Cretolbia burmitica* sp. nov., holotype, No. NIGP168837, morphology of antenna: A. saucer-shaped scape and pedicel, and cylindrical flagellomeres 1–3; B. elongated flagellomeres; C, D. *Sylvicola* (*S.*) *cinctus* (Fabricius, 1787) (female), SEM: D. scape and pedicel; E. comparatively short flagellomeres with stout chaetic sensilla. Abbreviations: CS – chaetic sensilla; F1-F3 – flagellomeres; PED – pedicel; SB – sensilla basiconica; SC – scape; SCO-A – sensilla coeloconica type A; ST-C – sensilla trichoidea; MI – microtrichia.

M stem and d-cell connection desclerotized. A_1 almost straight; A_2 slightly waved. Halter uniformly yellow, comparatively elongated.

Fore, middle and hind tibia (Fig. 11C-E) with two equal tibial spurs each, 0.17 mm long, middle and hind legs with apical combs (Figs. 6E, 11E). Coxa of fore leg 0.65 mm; trochanter 0.20 mm; femur 0.91–1.16 mm long, tibia 1.04–1.11 mm; tarsus 1.21 mm long. Coxa of middle leg 0.46 mm; trochanter 0.15 mm; femur 0.80 mm; tibia 0.85 mm; tarsus 1.37 mm long. Coxa of hind leg 0.51 mm; trochanter 0.17 mm; femur 0.80 mm; tibia 1.14 mm; tarsus 1.75 mm long. Empodium small, shorter than claw.

Abdomen (Fig. 11F): female terminalia not very elongated.

Comparison. The new species can be distinguished from *C. hukawnga* sp. nov. by having a saucer-shaped scape, absence of elongated sparse setae (subequal to flagellomere width) on antenna, terminal oval flagellomere subequal to penultimate one, longer Sc, desclerotization of M stem and d-cell connection.

Remarks. Holotype: female terminalia not well visible, partially destroyed, distal portion of wings absent. Specimen No. NIGP168838: antenna, palpi, wings partially cut.

For comparison scanning electron micrographs of ommatidia with ommatrichia (Fig. 9C), antenna (Fig. 10C, D), female terminalia (Fig. 11G) and apex of tibia (Fig. 11A, B) of *Sylvicola* (*S.*) *cinctus* are given. Sensilla which are visible on first flagellomere of extinct species are comparable to sensilla coeloconica of *Sylvicola* (*S.*) *cinctus.* Apical combs of bristles look similar in both extinct and extant anisopodids and differ only in the degree of development but in extant species combs are known on hind tibia only (Peterson, 1981).

Cretolbia zhuodei **sp. nov. Kania, Wojtoń, Lukashevich, Wang and Krzemiński**

(Figs. 12–15)

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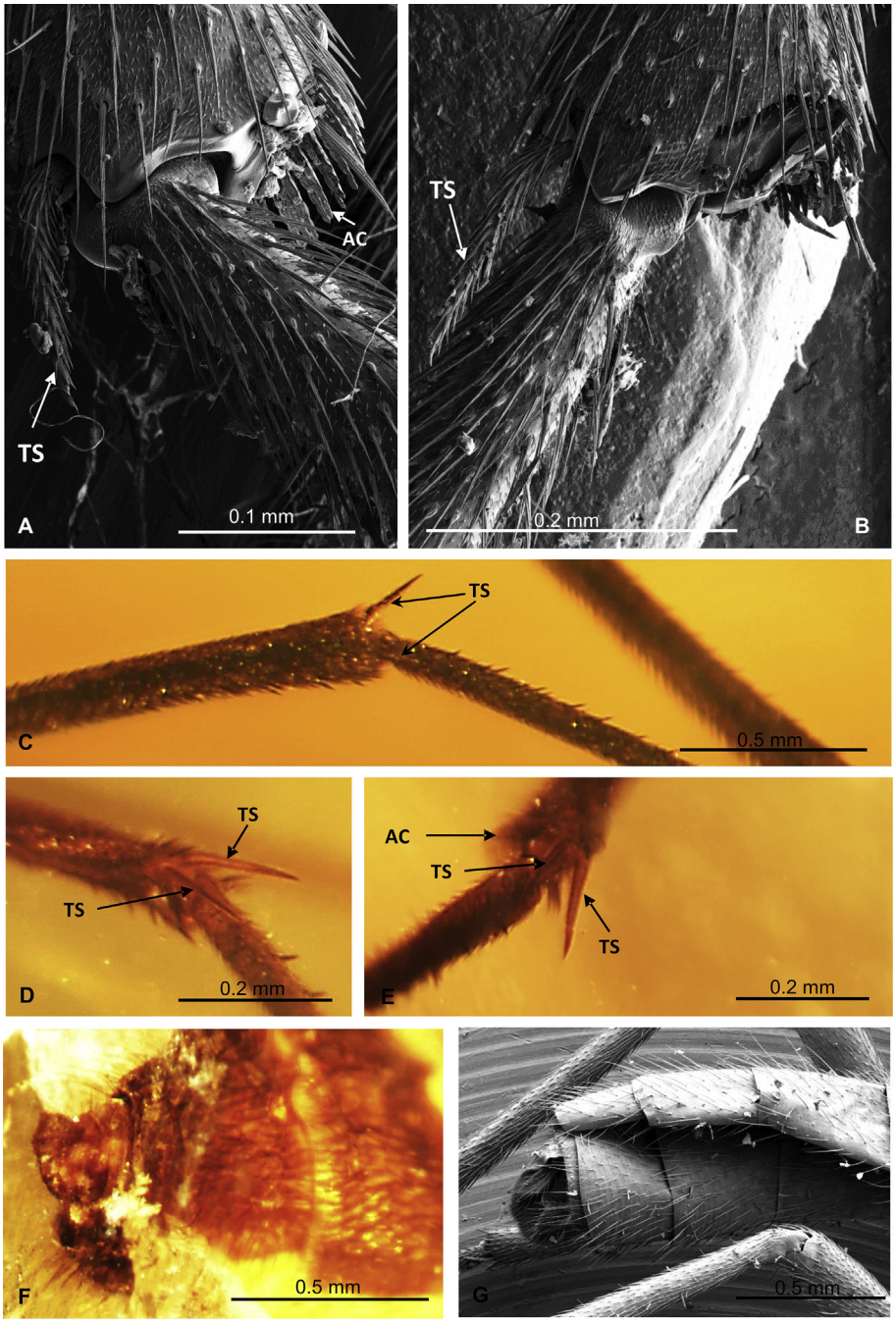

Fig. 11. A, B, G. *Sylvicola* (*S.*) *cinctus* (Fabricius, 1787), SEM: A. apex of tibia with tibial spur and apical comb (female); B. apex of tibia with tibial spur and apical comb (male); G. female terminalia; C – F. *Cretolbia burmitica* sp. nov., additional material, No. MP/3682: C. tibial spurs of fore leg; D. tibial spurs of middle leg; E. tibial spurs of hind leg; F. female terminalia. Abbreviations: AC – apical comb; TS – tibial spurs.

Etymology. The species name is dedicated to private collector Zhuo De.

Material examined. Holotype, female, No. NIGP168839, deposited in the collections of Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, P.R. China.

Horizon and locality. Lowermost Cenomanian, Hukawng Valley, northern Myanmar. The mining is done at a hill named Noije Bum, near Tanai Village (26°21′33.41″N, 96°43′11.88″E).

Diagnosis. Sc long, ending before M_{1+2} bifurcation level; R_{4+5} sinuous; small sclerotization across r-m; short and very thick setae on all flagellomeres; terminal flagellomere slightly narrowed in distal part, subequal to penultimate one; uniform, slender maxillary palpomeres; thorax, coxae and femora without elongated dense bristles; abdomen brown; small dark spots on femur and tibia.

Description. Body (Fig. 13A) 4.15 mm long, uniformly pale brown, with dark small spots on femur and tibia (Fig. 15B). Head: not very small, 0.92 mm high, 0.58 mm wide; antennae comparatively massive (Fig. 12B), elongated, as long as head and thorax combined, 1.48 mm long, flagellomeres elongated, subequal in length; all flagellomere covered by very thick and short uniform setae, almost perpendicular to surface of bearing flagellomere; elongated sensilla not visible on flagellomeres; maxillary palpus (Fig. 12C) with

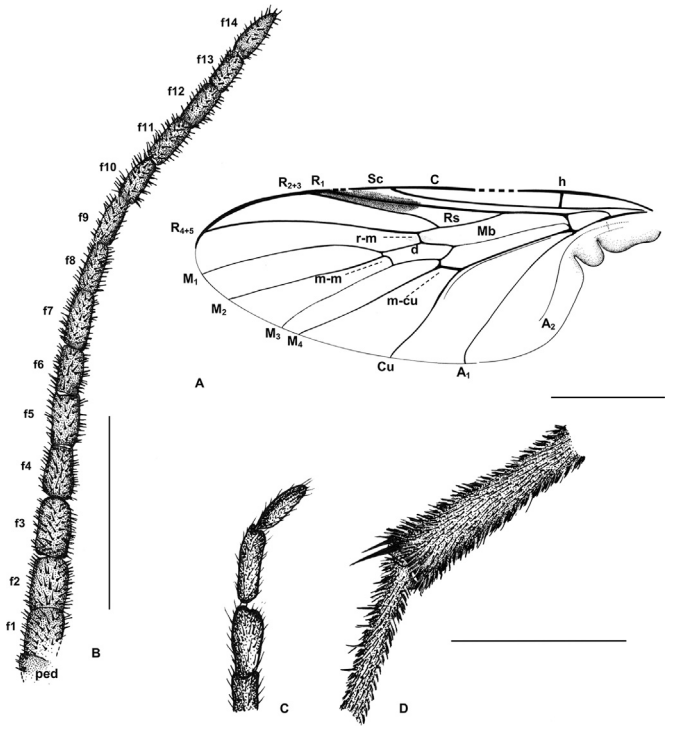

Fig. 12. *Cretolbia zhuodei* sp. nov., holotype No. NIGP168839: A. wing venation (reconstruction); B. antenna; C. palpus; D. part of fore leg with tibial spurs. Abbreviations: f1-f14 – flagellomeres; ped – pedicel. Scale bar = 0.5 mm for A and D; scale bar = 0.2 mm for B and C.

uniform slender palpomere, third one only slightly widened apically, twice as long as wide, with not very elongated setae, fourth one smooth, three times as long as wide; last one shortest.

Thorax: wing (Figs. 12A, 13A-D, 14B-E): 4.05 mm long, 1.65 mm wide; very dark pterostigma surrounding apical part of R_1 to 5/6 of R_{2+3}, distinctly separated from other part of wing by arched/rounded line of dark tint. Sc ending approximately in 3/5 from wing base, distal to r-m, and before M_{1+2} bifurcation level; r-m positioned aslant, directed to wing apex; Rs separate Rb at distance equal of its length from cross-vein h, Rs short, half of R_{2+3}, 0.53 mm long. R_1 about 4/6 of wing length. R_{4+5} sinuous. Crossvein r-m shorter than m-m, just before d-cell midlength, with small sclerotization across r-m. D-cell (Fig. 13D) 0.60 mm long, approximately 3.5× longer than wide, m-m arched to wing base. Distance between M_3 and M_4 apices about half of that between M_2 and M_3 apices (Figs. 13C, 14D). Vein bM_4 much shorter than m-cu, diverging from d-cell proximal 1/4; A_1 slightly arched at end, reduced A_2 comparatively short, waved. Halter (Fig. 14H) uniformly yellow, 0.62 mm long, with elongated sensilla.

Legs: Apical combs invisible. Subequal tibial spurs of fore legs 0.18 mm long (Figs 12D, 15C). Fore trochanter 0.19 mm, femur 0.92, tibia 1.11 mm long. Middle trochanter 0.23 mm, femur 0.84 mm, tibia 1.20 long. Hind trochanter 0.21 mm, femur 1.27 mm long.

Abdomen: female terminalia not very elongated (Fig. 15D).

Comparison. The species is distinguished from both other species described here in wing venation with extremely long Sc and sinuous R_{4+5}, thick setae on flagellomeres, uniform, slender maxillary palpomeres and small dark spots on femur and tibia.

Remarks. For comparison scanning electron micrograph of base, membrane of wing (Fig. 14A, F), halter (Fig. 14G) and part of leg (Fig. 15A) of *Sylvicola* (*S.*) *cinctus* is given. Allula (Fig. 14B) and sensilla on halter of new species (Fig. 14H) are comparable to those of *Sylvicola* (*S.*) *cinctus.*

4. Discussion

The taxonomic system of the family is still under current discussion but it is widely acknowledged that extant wood gnats "can be partitioned into three primary subgroups as follows: (1) a widespread group of *Sylvicola* only, (2) a pantropical group of *Olbiogaster* and some smaller genera, and (3) a widespread group of *Mycetobia* and some smaller genera" (Michelsen, 1999). Edwards (1930: 115) had already proposed a possibility of division of the family into three parts *Anisopus* (now–*Sylvicola*)/*Mycetobia* and *Mesochria*/*Olbiogaster* and *Lobogaster* (*Carreraia* wasn't described yet) but he did not discuss the characters. He wrote: "The five known genera of the family may be arranged in three groups, which are so distinct in various ways as almost to be deserve sub-family rank". Hennig (1954) supported only the erection of Olbiogastrinae and later (1973) suggested several diagnostic features: lateral position of spiracles on segment VIII and absence of torma in larva, absence of macrotrichia on wing membrane and apical comb on hind tibia in imago. The latter was shown to be of little value in classification because this character appears in most, if not all, species of the family and differs only in the degree of development of the pectinate bristles (Peterson, 1981).

Edwards (1928) considered that members of the genus *Olbiogaster,* or at least flies with a practically identical venation, are known from as far back as the Early Jurassic. Kovalev (1990) followed this opinion and included all Mesozoic members of Anisopodidae into Olbiogastrinae thought their shorter antennae (unknown in extant members) had been described long time ago. Probably the main reason for such consideration is the absence of macrotrichia on the wing membrane of Cretaceous anisopodids.

The species of the extant genera are distinguished mainly by color pattern of wing and body (Edwards, 1928; Tozoni, 1993) hence at the first glance, the significant differences of three new species worth to be erected up to a generic rank. Moreover, if we follow Kovalev (1990) and consider the short Sc as a genus level character, then *Cretolbia hukawnga* sp. nov. should probably be separated into its own genus (Sc is the shortest among species described herein ending in proximal part of the wing).

However, as one can see in Table and, for example in the two species of *Mesochria* from Fiji (Thompson, 2006), the intraspecific variation is considerable and male eyes may be holoptic or dichoptic, bristles on scutum weak or distinct, tibial spurs on hind tibia one or two and vein M_4 setose or bare. Unfortunately, nobody paid attention on the length of Sc in extant species, but we can estimate a variation of the character based on published figures of wings. This character varies significantly among Palearctic species of one subgenus of *Sylvicola*: in *S.* (*S.*) *cinctus* Sc ends just before r-m level, in *S.* (*S.*) *oceanicus* Frey, 1949 beyond r-m level, in *S.* (*S.*) *zetterstedti* (Edwards, 1923) Sc ends much more distally, level with M_{1+2} bifurcation (Krivosheina, 1998). Therefore, the recent variation of this character is comparable with the one discovered in anisopodids from Burmese amber, described herein. Therefore we prefer to include all species under discussion in one genus, in spite of the differences in pilosity of body, shape of terminal flagellomere, structure of pubescence and size of empodium in male and females. Some of these differences can be sexual, others – specific peculiarities and only

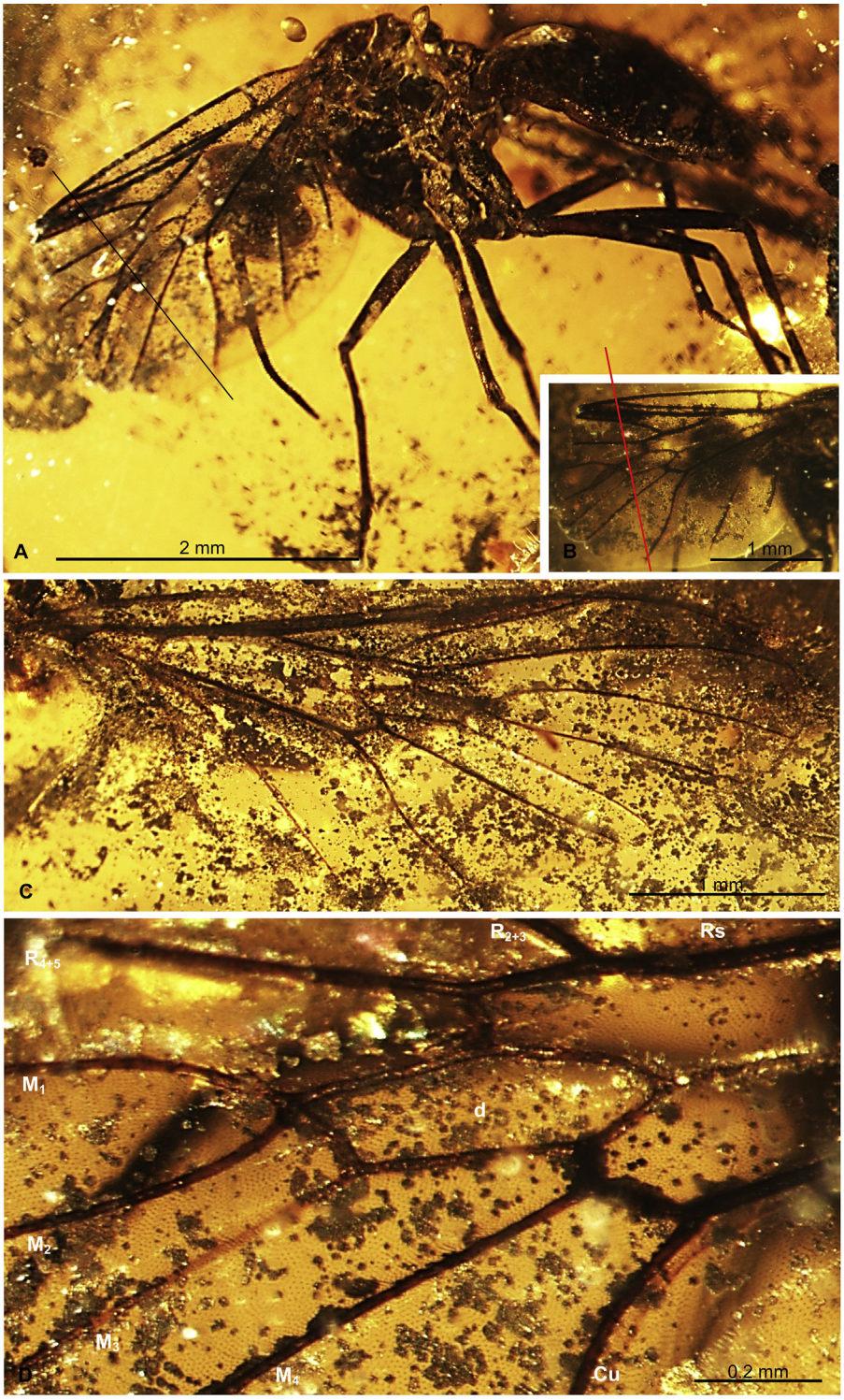

Fig. 13. *Cretolbia zhuodei* sp. nov., holotype No. NIGP168839: A. habitus, latero-dorsal view; B. wing venation with Sc long, ending just behind M_{1+2} bifurcation level, pointed by red line; C. right wing; D. part of left wing. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

new data (and new anisopodid males) can elucidate the problem.

It is worth to mention that plesiomorphic (shorter antenna) as well as apomorphic (holoptic eyes of male) characters distinguish the new genus from extant Olbiogastrinae. Both characters (and large empodium) are known in *Sylvicola* but the new genus differs from the latter also in the absence of macrotrichia and color pattern on the wing membrane and R_{2+3} not curved (all probably plesiomorphic states) as well as M_3 weaker than other medial veins (an undobtely apomorhic state) which are typical olbiogastrine

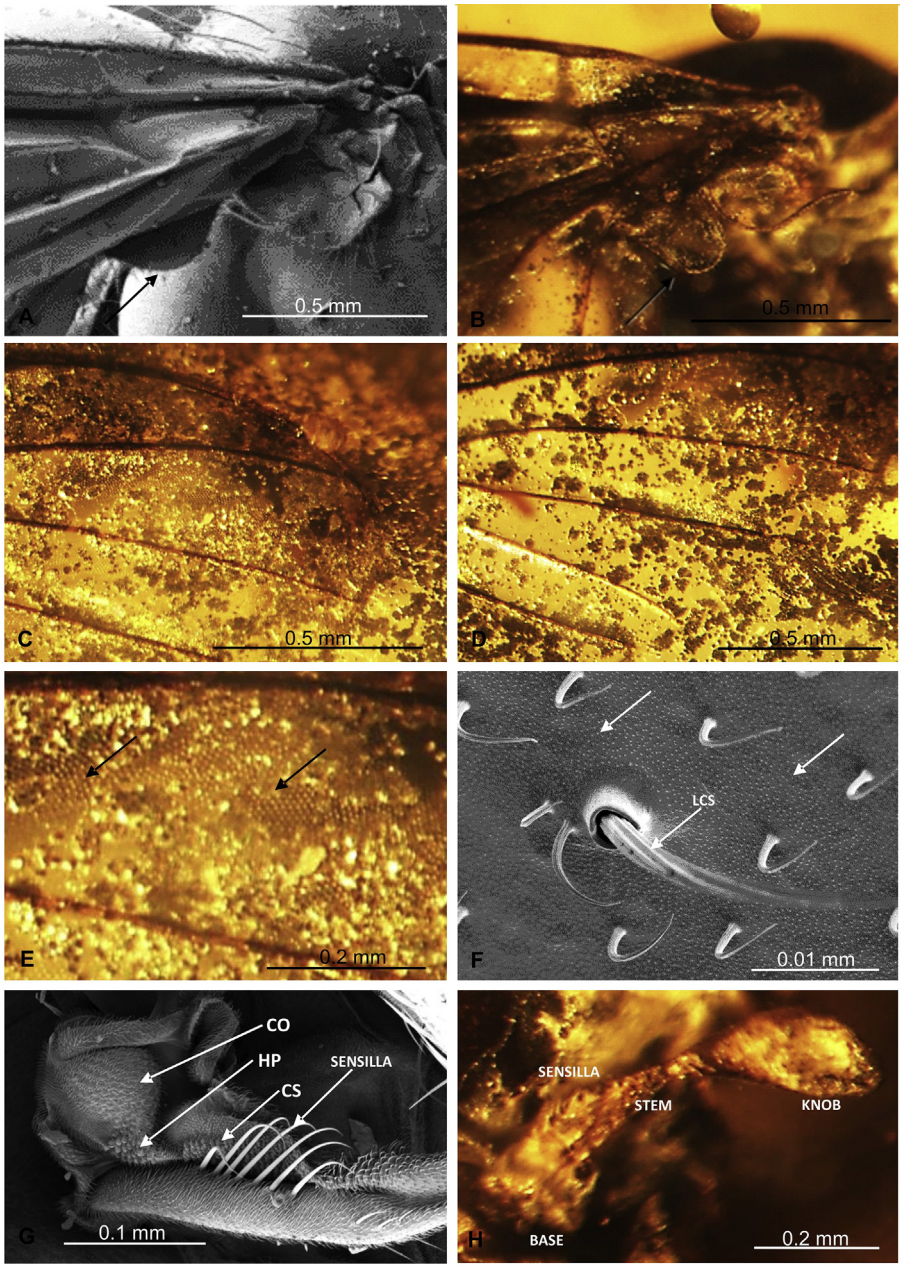

Fig. 14. Morphology of wings. A, F, G: *Sylvicola* (*S.*) *cinctus* (Fabricius, 1787), SEM: A. base of wing with strongly differentiated alula (pointed by arrow), F. membrane of wing; G. base and stem of halter with differentiated sensilla visible; B – E, H: *Cretolbia zhuodei* sp. nov., holotype, No. NIGP168839: B. – base of wing with strongly differentiated alula (pointed by arrow); C. apex of wing; D. edge of wing; E. microstructure of wing membrane (pointed by arrows); H. halter with differentiated sensilla visible. Abbreviations: CO – chordotonal organ; CS – campaniform sensilla; HP – Hicks' palpillae; LCS – long chaetic sensilla (long grooved setae).

peculiarities. The only undoubted apomorphic state (holoptic eyes) which connected the new genus with Anisopodinae (and Mycetobiinae) is so common in numerous nematocerous families that it is of little value for the understanding of relationships.

The general morphology of Anisopodidae has not changed since Cretaceous and *Cretolbia* gen. nov. is distinguished by the unique combination of known characters. The system of very differentiated microtrichia or sensory organs in these insects is quite complicated, it is especially obvious in morphology of antenna or palpi. Many differentiated structures are better visible under scanning electron microscope, but sometimes we can observe these details on amber inclusions and even on compressions (Kania and Wegierek, 2008). For example, very similar elongated sensilla are visible on stem of halter of *Sylvicola* (Fig. 14G) and *Cretolbia zhuodei* gen. et sp. nov. (Fig. 14H). There is a strong possibility that this is the same type of sensilla. Long sensilla also occur on legs of *Sylvicola* (Fig. 15A) but they are probably absent on *Cretolbia zhuodei* gen. et sp. nov. (Fig. 15B). This kind of comparison is the base for further studies of fossil and recent Anisopodidae for a better understanding of the morphology of these insects.

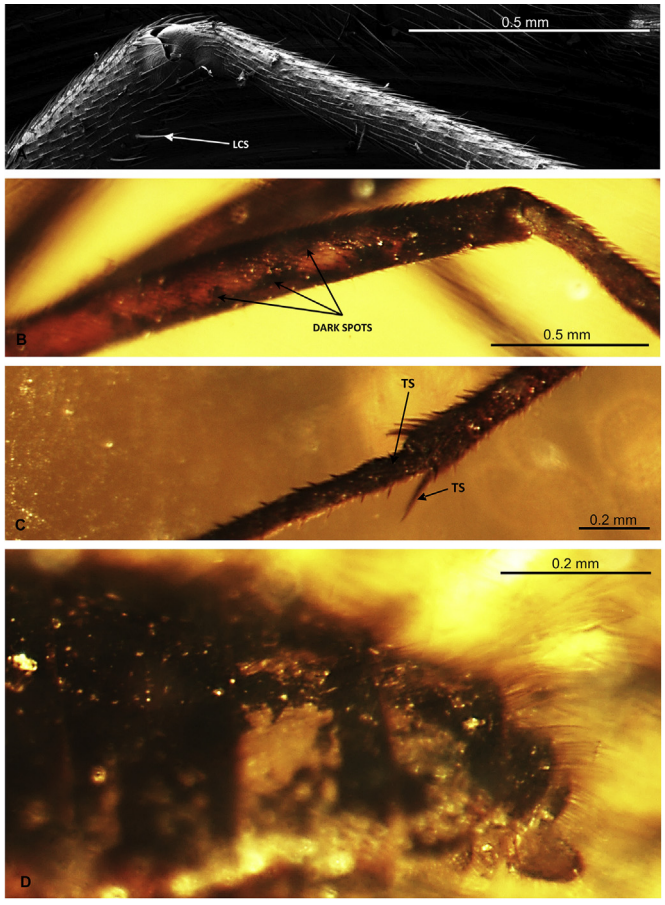

Fig. 15. A. *Sylvicola* (*S.*) *cinctus* (Fabricius, 1787), SEM, femur and tibia with long chaetic sensilla; B. – D. *Cretolbia zhuodei* sp. nov., holotype, No. NIGP168839: B. femur and tibia without long chaetic sensilla; C. tibial spurs of fore leg; D. female terminalia. Abbreviations: LCS – long chaetic sensilla (long grooved setae); TS – tibial spurs.

5. Conclusions

The study of inclusions in Burmese amber gives us the inside view of life in the Cretaceous, an epoch when the dinosaurs existed with many groups of insects. This is a very important period to study the evolution of many groups of animals, also the insects. The discovery of the new genus of Anisopodoidea which existed about 140 million years ago provides us with new information about this group of insects.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2018.10.013.