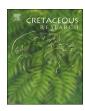
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Short communication

New fossil Juraphididae (Hemiptera: Aphidomorpha) from Burmese amber, with phylogeny of the family



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ABSTRACT

A new aphid genus and species, *Prolavexillaphis munditia* Liu, Qiao and Yao gen. et sp. nov., is assigned to Juraphididae (Aphidomorpha). The specimen is described from Upper Cretaceous amber from Myanmar. In this study the phylogeny of the extinct family Juraphididae based on 33 morphological characters detailed the status of the new fossil and the relationships within the family Juraphididae. *Isolitaphis prolatantennus* Poinar, 2017 (Isolitaphidae) from the same deposit was also included in this phylogenetic analysis due to the similarities between two families. Two main clades within Juraphididae are recognized from our cladistic analysis: *Prolavexillaphis* Liu, Yao and Qiao gen. nov. and *Isolitaphis* (Poinar, 2017) form a monophyletic lineage; *Aphaorus* (Wegierek, 1991), *Pterotella* (Wegierek, 1991), *Juraphis* (Shaposhnikov, 1979) form a monophyletic lineage. These results indicate that *Isolitaphis* (Poinar, 2017) belongs to Juraphididae. Therefore, we propose a synonymy of Isolitaphidae with Juraphididae and the type species, *Isolitaphis prolatantennus* Poinar, 2017, is transferred to the Mesozoic family Juraphididae. A key to all species of Juraphididae is provided.

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1. Introduction

Juraphididae, an extinct Mesozoic family of aphids, was erected by Żyła et al. and are included in the superfamily Palaeoaphidoidea based on cubitus veins CuA₁ and CuA₂ branching off from a common stem (Żyła et al., 2014). The differences between Juraphididae and all other families of Palaeoaphidoidea consist in cubital veins. Juraphididae have short and not thickened common stem of CuA₁ and CuA₂ (Żyła et al., 2014). Only three genera and five species of the family have been reported prior to this study: *Pterotella formosa* Wegierek, 1991, from Upper Jurassic deposit (Khotont, Mongolia) and *Pterotella shartegensis* Żyła, Blagoderov and Wegierek, 2014, from Upper Jurassic deposit (Shar Teg, Mongolia); *Aphaorus curtipes* Wegierek, 1991, from Lower Cretaceous deposit (Khutel Khara, Mongolia); *Juraphis crassipes* Shaposhnikov, 1979 and *Juraphis karataviensis* Żyła, Blagoderov and Wegierek, 2014, from Upper Jurassic deposit (Karatau, Kazakhstan). Here it is described an

amber specimen of juraphidids, *Prolavexillaphis munditia* Liu, Qiao and Yao gen. et sp. nov., from the Hukawang Valley, Myitkyina District of Kachin State in Myanmar. The age of this deposit has been confirmed at 98.8 \pm 0.6 Ma. (Cenomanian) (Shi et al., 2012). And this is the third report of the aphids known from Burmese amber (Poinar and Brown, 2005, 2006; Poinar, 2017).

2. Materials and methods

2.1. Examined taxa and terminology

Specimen of extinct juraphidids described in this paper is partially melted and damaged and is deposited in the Key Lab of Insect Evolution and Environmental Changes, at the College of Life Sciences, Capital Normal University, in Beijing, China. Morphological terminology in this paper mainly follows Zyla et al. (2014).

The photographs and magnified details of the specimen were taken with the Nikon SMZ 18 dissecting microscope and a Leica DFC500 digital camera system. Line drawings were based on the multi-angle sight and were prepared by using Adobe Photoshop CC2017 and Adobe illustrator CC2017 graphics software.

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2.2. Phylogenetic analysis

A cladistic analysis is performed based on 33 morphological characters in order to detail the phylogenetic status of Prolavexillaphis munditia Liu, Qiao and Yao gen. et sp. nov. and assess the relationship within the family Juraphididae. According to Zyła et al. (2014), the clade of Ellinaphididae + Palaeoaphididae has been regarded as the sister group of Juraphididae. Following previous studies (Żyła et al., 2014; Zyła and Wegierek, 2015), we chose type species of the genera of the family Palaeoaphididae (Palaeoaphis archimedia Richards, 1966), Ellinaphididae (Ellinaphis sensoriata Shaposhnikov, 1979) and Greenideidae (Quisqueyaaphis heiei Wegierek, 2001) as our out-group taxa. The six in-group terminal taxa include all juraphidids species except poorly preserved Pterotella shartegensis Zyła, Blagoderov and Wegierek, 2014, which has only a distinct imprint of forewing and was not available for study. Isolitaphidae Poinar, 2017 is one such family, known only from one specimens collected also in Myanmar, based on antennae with ten segments, short and broad pterostigma, rostrum reaching hind coxae, base of vein Rs before midpoint of pterostigma, the presence of ovipositor and siphunculi, vein M with three branches and a forked cubitus vein (Poinar, 2017). Isolitaphis prolatantennus Poinar, 2017 shares many similarities with Prolavexillaphis munditia Liu, Qiao and Yao sp. nov., such as slender body, body length (close to and less than 2.0 mm), antenna length almost equal to or slightly shorter than body length, processus terminalis faintly developed. What's more, Isolitaphis prolatantennus also strongly resembles other members of the Iuraphididae in vein M with three branches (Pterotella Wegierek, 1991: Aphaorus Wegierek, 1991 and Juraphis Shaposhnikov, 1979), short and broad pterostigma (Pterotella shartegensis Żyła, Blagoderov and Wegierek, 2014), common stem of cubital veins manifestly shorter than CuA2, with its width as thin as vein M (all juraphidids), vein M arising from base of pterostigma (all juraphidids) and ovipositor present (all juraphidids). Therefore, we consider that the diagnosis of the Isolitaphidae is in keeping with the characteristics of Juraphididae and Isolitaphis prolatantennus Poinar, 2017 was also included in in-group taxa. In the analysis, 33 adult morphological characters were used: all are unordered and equal weight. A complete list of the taxa and the data matrix used in this phylogenetic analysis are provided in the Appendix. Inapplicable states were assigned a gap value ('-') and treated equivalent to missing data ('?'). Analysis of this character matrix was conducted with PAUP* 4.0b10 (Swofford, 2002) using maximum parsimony (MP). Heuristic searches were performed with 1000 random-taxa-addition replicates and tree bisection and reconnection (TBR) branch swapping. The calculation of Bremer supports was computed with the function implemented in PAUP* 4.0b10 and TreeRot.v3 (Sorenson and Franzosa, 2007). Unambiguous characters were viewed with WinClada v1.00.08 (Nixon, 2002).

3. Results and discussion

3.1. Systematic paleontology

Order Hemiptera Linnaeus, 1758 Suborder Sternorrhyncha Amyot and Serville, 1843. Infraorder Aphidomorpha Becker-Migdisova and Aizenberg, 1962. Superfamily Palaeoaphidoidea Richards, 1966. Family Juraphididae Żyła, Blagoderov and Wegierek, 2014.

Genus **Prolavexillaphis** Liu, Qiao and Yao gen. nov. (urn:lsid:zoobank.org/NomenclaturalActs/0215AC5D-532F-43DC-AD7B-BFEF8E8E7478)

Type species. Prolavexillaphis munditia Liu, Oiao and Yao sp. nov.

Etymology. The new generic name is taken from the Latin "prolatus" = elongated, "vexillum" = flag, derived from the elongated wings.

Diagnosis. Antennae with nine segments, measuring longer than half of length of body. Base of vein Rs faintly curved at base, leaving at a point closer to base of pterostigma. Pterostigma narrow and long, at least four times as long as wide.

Remarks. The new genus can be attributed to Juraphididae by the following diagnostic characters: cubitus veins CuA_1 and CuA_2 separating from a common stem; common stem of cubital veins manifestly shorter than CuA_2 , with its width as thin as vein M, leaving from main vein Sc + R + M; vein M with four branches; hindwing with separate CuA_1 and CuA_2 veins. The new genus can be distinguished from the other four genera by the following key.

Prolavexillaphis munditia Liu, Qiao and Yao sp. nov. (urn:lsid:zoobank.org/NomenclaturalActs/0D4EA194-27A6-4CE4-952D-7D85E9742B8D)

Figs. 1-3

Etymology. Species name is taken from the Latin "munditia" = elegance.

Diagnosis. See Diagnosis for the genus above. *Description.* Body elongate, approximately 2 mm.

Head with compound eyes rather prominent, length ca. 0.11 mm. Antennae with nine segments, measuring longer than half of length of body, ca. 1.10 mm, longer than tibiae of all legs; segment III nine to ten times as long as wide, markedly longer than other segments; segment IV slightly longer than segment V; terminal of segment VI swells, its widest part about 1.5 times longer than basal portion; segments VI, VII, VIII and IX longer than wide and decreasing in size posteriorly; a short, convex processus terminalis visible on terminal segment; segment III—IX covered with short weak hair; ellipsoidal secondary rhinaria arranged in transverse rows, densely and distributed equally. Rostrum shorter than body, extend to hind coxae; base of rostrum difficult to see as head turned downwards.

Forewing 1.06 mm greatest wide, 4.01 mm long, longer than twice as long as body; pterostigma spindle-shaped, sharp and long, 0.84 mm in length, four times as long as wide; main vein (Sc + Rs + M) thicker than the other veins; common stem of cubital veins manifestly shorter than CuA2, 0.20 mm long; distance from base of wing to base of cubitus longer than half of main vein length; vein CuA₁ two to three times longer than CuA₂; vein M directed towards base of pterostigma, not connected with main vein, with four branches; common stem of vein M almost equal to lengths of M_{1+2+3} ; lengths of $M_{1+2}+M_{1+2+3}$ almost equal to that of M_1 ; vein Rs only slightly curved at base, leaving at a point closer to base of pterostigma and reaching edge of the wings. Hindwing 2.16 mm long, slightly longer than half of forewing, with separate CuA₁ and CuA₂ veins. Femur slender; hind femur longer than half of the hind tibia length. Tarsi two-segmented; tarsi 2 five times as long as tarsi 1, with two developed tarsal claws; length of fore claws 0.09 mm, middle 0.10 mm, hind 0.07 mm; the ratio of fore tarsi to its claws 5:3, middle 7:3, hind 3:1.

Abdomen slender. Ovipositor and siphunculi invisible.

Type material. Holotype, CNU-APD-MA2017001, adult, relatively well preserved with partial dissolution.

Locality and horizon. Hukawng Valley, Kachin State, Northern Myanmar; lowermost Cenomanian, Upper Cretaceous.

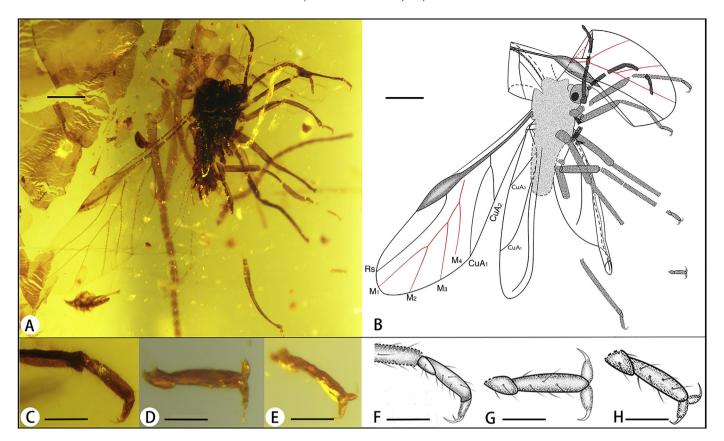


Fig. 1. Prolavezillaphis munditia Liu, Qiao and Yao sp. nov., photograph and outline, holotype, CNU-APD- MA2017001; A, B lateral view; C, F fore tarsus; D, G middle tarsus; E, H hind tarsus. Scale bar for $A-B=0.5\,$ mm; $C-H=0.1\,$ mm.

3.2. Phylogenetic analysis

The heuristic analysis resulted in a single most parsimonious tree (tree length = 55 steps; consistency index (CI) = 0.70 and retention index (RI) = 0.57), presented in Fig. 4, with unambiguous characters mapped. The major consequences of our phylogenetic analysis are as follows: Juraphididae is a monophyletic group; both *Isolitaphis prolatantennus Poinar*, 2017 and our new fossil belong to Juraphididae, they are sister groups; *Juraphis* and *Pterotella* form a sister group; *Aphaorus* and *Juraphis* + *Pterotella* form a sister group. This can be simplified to: Juraphididae = (*Isolitaphis* + *Prolavexillaphis* gen. nov.) + (*Aphaorus* + (*Juraphis* + *Pterotella*)).

3.2.1. Juraphididae

The monophyly of Juraphididae is well supported by four synapomorphies (characters 20, 21, 24, 28; Fig. 4): common stem of cubital veins shorter than half of CuA₂ and not thickened (characters 20, 21) are exclusive to the family Juraphididae; vein M directed towards base of pterostigma (character 24); vein Rs weakly curved at base (character 28). The analysis has demonstrated that Juraphididae is composed of two main lineages. Our results reaffirm that Juraphididae is a monophyletic group as indicated in previous study (Żyła et al., 2014).

3.2.2. (Aphaorus + (Juraphis + Pterotella))

According to the present result, the monophyly of this branch is confirmed by a single character states, namely hind tibia short, not longer than one-third of body length (character 16, state 0). *Aphaorus* is designated by three autapomorphies: antennae 8-segmented (character 3, state 1); femur thick (character 14, state 0); sternite of ovipositor square (character 32, state 1).

Antennal segment III short, only as long as half of sum of following segments (character 5, state 0); last antennal segment taper apically (character 10, state 1); hind femur short, not longer than half of the hind tibia length (character 15, state 0); tarsal segment I approximately one fourth of segment II (character 18, state 0); pterostigma short, at most three times longer than wide (character 31, state 0) support the monophyly of *Juraphis* and *Pterotella*.

3.2.3. Isolitaphis + Prolavexillaphis gen. nov.

Based on the original description and drawing (Poinar, 2017), some of the points in this article is pending further discussion. First of all, claval suture marked on the drawing of forewing seems to be misinterpreted, since no corresponding structure on the other forewing (see fig. 1 in Poinar, 2017). In addition, it's improper to compare Isolitaphidae with Oviparosiphidae just based on the presence of the ovipositor and to distinguish Isolitaphidae by their difference. Ovipositor is not particular in the Mesozoic aphids and many families bear this structure (Fu et al., 2017) such as Bajsaphididae (Homan et al., 2015), Palaeoaphididae (Kania and Wegierek, 2005), Ellinaphididae (Kania and Wegierek, 2008) and also Juraphididae (Żyła et al., 2014). Besides, the presence of siphunculi is not sufficiently great to support the Isolitaphidae as an independent family of aphids. Due to the limitations of fossils juraphidids, the presence of siphunculi was uncertain before. However, well-preserved characters in amber can provide a better understanding of morphological and supply details for Juraphididae, such as siphunculi present (Isolitaphis prolatantennus Poinar, 2017), the new type of rhinaria (Prolavexillaphis munditia Liu, Qiao and Yao sp. nov.). What's more, 10-segmented antennae are indeed unique (Poinar, 2017), but they are not enough as a basis for a new

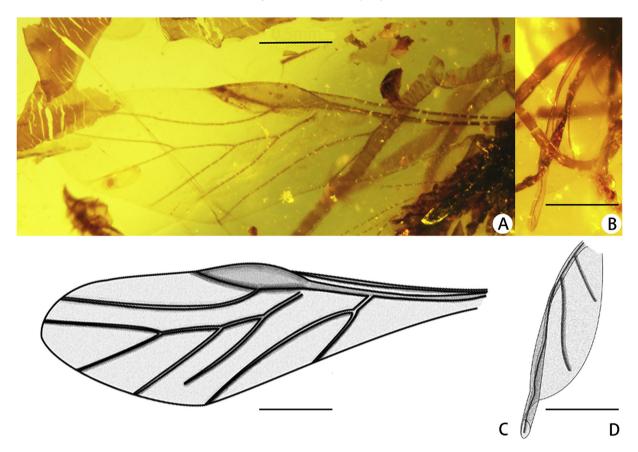


Fig. 2. Prolavexillaphis munditia Liu, Qiao and Yao sp. nov., photograph and outline, holotype, CNU-APD- MA2017001; A, C fore wing; B, D hind wing. Scale bar = 0.5 mm.

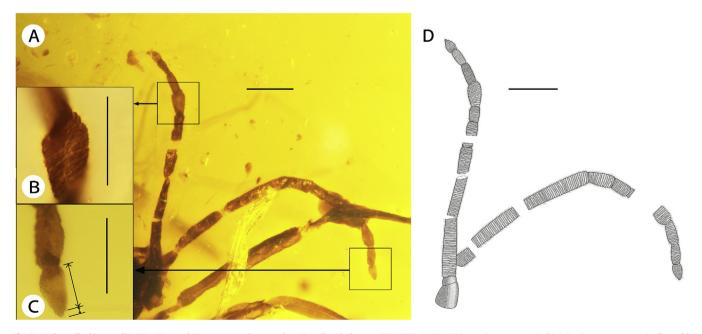


Fig. 3. Prolavexillaphis munditia Liu, Qiao and Yao sp. nov., photograph and outline, holotype, CNU-APD- MA2017001; A, D antennae; B rhinaria; C processus terminalis and basal part. Scale bar for A, D = 0.2 mm; B, C = 0.1 mm.

family considering the diversity of the number of antennal segments within many families of aphids. In the family Juraphididae, 7- or 8-segmented antennae have already come to light (Żyła et al., 2014). Among the sister groups of the family Juraphididae,

Palaeoaphidoidae have antennae with 6- or 7-segments (Richards, 1966; Wegierek, 1993; Heie, 1996). It also occurs in other families in Palaeoaphidoidea, such as Szelegiewicziidae with 5- or 7-segmented antennae in the fossil records (Wegierek, 1989). As

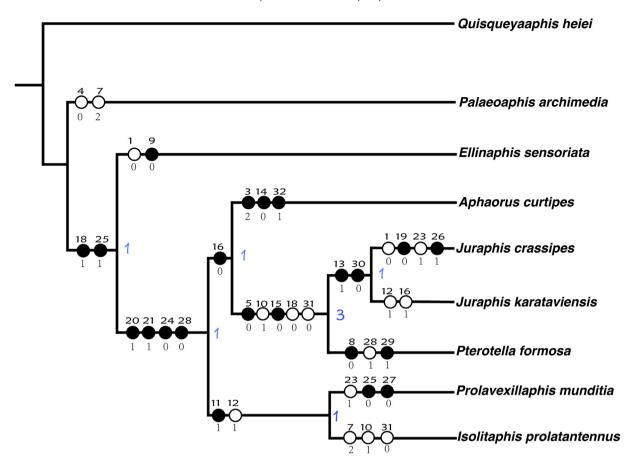


Fig. 4. Phylogeny of Juraphididae, Topology represents the single most parsimonious tree with a black circle as the nonhomoplasious state and a white circle as the homoplasious state; Bremer support values are shown at relevant nodes.

stated above, the diagnosis of the family Isolitaphidae is scientifically seen as untenable.

Addition to the synapomorphies of Juraphididae previously mentioned, Isolitaphis Poinar, 2017 also share many similarities with other genera, such as segment III of antennae markedly longer than other segments, almost as long as sum of following segments (Aphaorus Wegierek, 1991; Prolavexillaphis Liu, Qiao and Yao gen. nov.); last antennal segment taper apically (Juraphis crassipes Shaposhnikov, 1979; Pterotella formosa Wegierek, 1991); forewing not shorter than body length (Aphaorus curtipes Wegierek, 1991; Juraphis karataviensis Żyła, Blagoderov and Wegierek, 2014; Prolavexillaphis munditia Liu, Qiao and Yao gen. nov.); vein Rs leaving at a point closer to base of pterostigma, faintly curved at base (Juraphis Shaposhnikov, 1979; Aphaorus Wegierek, 1991; Prolavexillaphis Liu, Qiao and Yao gen. nov); pterostigma broad and short, its length at most three times as long as wide (Juraphis Shaposhnikov, 1979; Pterotella Wegierek, 1991), with a sharp termination (Aphaorus Wegierek, 1991; Pterotella Wegierek, 1991). Furthermore, the following characters of the family Isolitaphidae can also be found in genera of the family Juraphididae: rostrum shorter than body but extend to hind coxae (Juraphis Shaposhnikov, 1979); vein M threebranched, originating from base of pterostigma (Aphaorus Wegierek, 1991); forked cubitus vein (all Juraphidids). As stated above, the structures of *Isolitaphis* are rarely sufficient to support the establishment of the family Isolitaphidae.

Based on the phylogenetic results, *Isolitaphis* is recognized as a sister group to *Prolavexillaphis* gen. nov., supported by two characters: processus terminalis on terminal segment faintly developed (character 11, state 1); rostrum longer than one-third of body

length (character 12, state 1). *Prolavexillaphis* gen. nov. has two autapomorphies [vein M with four branches (character 25, state 0); common stem of vein M_{1+2} short, shorter than half of M_1 (character 27, state 0)] and a synapomorphic character [Vein CuA₁ longer than two times of CuA₂ (character 23, state 1)]. Hence we believe that *Prolavexillaphis* gen. nov. should be recognized as a new genus and decide to transfer the *Isolitaphis* to the family Juraphididae.

3.3. Key to the species of the family Juraphididae

4. Vein Rs strongly curved, leaving at midpoint of pterostigma; pterostigma with sharp termination.....**Pterotella** Wegierek, 1991......5 Vein Rs weakly curved, leaving at a point closer to base of pterostigma; pterostigma with rounded termination..... 5. Vein M with four branches; vein M_{1+2} short, shorter than half of the length of M₁ shorter than common stem of vein M... Vein M with three branches; vein M_{1+2} long, nearly equal to M₁, longer than common stem of vein M..... 6. Rostrum long, reaching hind coxae; forewings almost as long as body; hind tibia length shorter than one-third of body Rostrum short, far from hind coxae; forewings manifestly longer than body; hind tibia length equal to half of the body length.....

4. Conclusion

Based on both the morphological characteristics of the specimen and the results of phylogenetic analysis, the new genus and species, *Prolavexillaphis munditia* Liu, Qiao and Yao gen. et sp. nov., should be assigned to Juraphididae and *Isolitaphis prolatantennus* Poinar, 2017 should be considered as a member of juraphidids. Consequently, we decide to transfer *Isolitaphis* to the family Juraphididae and propose a synonymy of Isolitaphidae with Juraphididae.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.cretres.2017.11.009.

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