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Detailed descriptions of a female and male of the aphids family Parvaverrucosidae (Hemiptera: Aphidomorpha) from mid-Cretaceous amber of Myanmar revealed their new systematic position



CRETACEO

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1. Introduction

The extinct aphid family Parvaverrucosidae Poinar and Brown, 2006 is known only from the mid-Cretaceous Burmese amber. Originally it was described as Verrucosidae Poinar and Brown, 2005. Having realized that the genus name was preoccupied (MacCook, 1888), the authors changed it from Verrucosa Poinar and Brown, 2005 to Parvaverrucosa Poinar and Brown, 2006; consequently, the family name has been altered as well (Poinar and Brown, 2005, 2006).

Besides the above mentioned family, Burmese amber has yielded aphids representing the families of Burmitaphidididae Poinar

ABSTRACT

Basing on new materials from Burmese amber, the paper presents a redescription of a female and a description of a male of Parvaverrucosa annulata Poinar and Brown, 2006. Up till now the family Parvaverrucosidae has been included into the "Aphidina vivipara" group. However, new, well-preserved inclusions of this species testify to transferring the family to "Aphidina vivipara". The structure of apical parts of abdomen suggests that pre-adaptations to subsequent mutualistic relationships between aphids and ants might have developed in early Cenomanian.

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and Brown, 2005; Isolitaphidae, Poinar 2017 (Poinar and Brown, 2005; Poinar, 2017, 2018; Liu et al., 2018; Wegierek et al., 2018) and Szelegiewicziidae Wegierek, 1989 (Wegierek et al., 2017). Within this insect group only Isolitaphidae have 10-segmented antennae and differently built wings where CuA veins have a common stem. Unlike Isolitaphidae, in wings of Burmitaphididae, Szelegiewicziidae and Parvaverrucosidae veins CuA1 and CuA2 are widely separated and hind wings are considerably reduced. The antennae in Burmitaphididae and Szelegiewicziidae are 7- and in Parvaverrucosidae only 3-segmented (Poinar and Brown, 2005).

The presence of siphunculi is regarded as one of the diagnostic characters decisive for dividing aphids into two groups: Aphidina vivipara and Aphidina ovipara (Börner, 1952; Heie, 1987; Wojciechowski, 1992; Heie and Wegierek, 2009). The division seems so important for contemporary aphidologists that some researchers refer to them as independent taxa using the terms "nonaphidid aphids" (nonaphidines) and "true aphids" (aphidines). Siphunculi are absent in Burmitaphidididae and present in Isolitaphidae. Although siphunculi were described in Parvaverrucosidae (Poinar and Brown, 2005, 2006), their occurrence seems



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questionable so the systematic status of the family is still not fully resolved.

2. Material and methods

Aphid inclusions from Hukawng Valley of northern Myanmar, currently considered to be of early Cenomanian in age (Smith and Ross, 2018). Mining took place at a hill named Noije Bum, near Tanai Village (26° 21′ 33.41″ N, 96° 43′ 11.88″ E) (Kania et al., 2015, Fig. 1). The inclusions were prepared using a razor blade, polished with emery papers with different grain sizes and finally lustrated with diatomite mud. The specimens (additional material) are housed in Nanjing Institute of Geology and Palaeontology, Chinese Academia of Sciences, 210008 Nanjing, China [**NIGP**]. Photographs were taken using a Zeiss Discovery V20 stereo microscope and Zeiss Axio Imager 2 compound microscope with a digital camera attached, respectively. Photographs with green background were taken using fluorescence as light source attached to a Zeiss Axio Imager 2 compound microscope. All measurements are given in mm.

3. Systematic palaeontology

Order Hemiptera Linnaeus, 1758. Suborder Sternorrhyncha Amyot - Serville, 1843. Infraorder Aphidomorpha Becker-Migdisova and Aizenberg, 1962. Superfamily Palaeoaphidoidea Richards, 1966. Family Parvaverrucosidae Poinar and Brown, 2006. Type genus. *Parvaverrucosa* Poinar and Brown, 2006.

Emended diagnosis. Extremely short thick antennae, composed of deep ring-like structures. Rostrum very long with extremely long apical segment. Forewings with strongly tapering base. Cubital veins distinctly separated. Distance between bases of CuA₁ and CuA₂ almost equal to length of CuA₂. Vein Rs separating distally from the middle of pterostigma. Vein M arising from the base of pterostigma or close to it, bifurcated. Hind wing reduced to hamulhalter. Siphunculi absent.

Genus Parvaverrucosa Poinar and Brown, 2006

Type species. Parvaverrucosa annulata Poinar and Brown (2006) by original designation and monotypy *Diagnosis.* As for the family.

Parvaverrucosa annulata Poinar and Brown (2006). (Figs. 1–3).

Type material. Holotype: B-He-13A¹(female), Paratype: B-He-13B¹ (female). The additional material: B-He-13C¹(female), NIGP167771 (female), NIGP167772 (male).

Type locality and horizon. Hukawng Valley of northern Myanmar. Cretaceous, lower Cenomanian.

Redescription. Female. An alate morph (Fig. 1A, B). Head small, wedge-shaped, 0.12 long, with apex extending beyond the bases of antennae. Antennnae located close to each other on ventro-lateral margin of head (Fig. 1C, D). Flagella 5-segmented (Fig. 1C), length 0.15–0.17; antennal segments not clearly out-lined, segments IV-VI very short, the ultimate one longer, apically pointed. Rhinaria absent. Compound eyes on sides of the head, overlapping the ventral side of head, adhering closely to the base of rostrum (Fig. 1D). Rostrum extending distinctly beyond the body, at most for as long as body length (Fig. 1A). Segment III

short (0.08), 4x shorter than the ultimate, needle-like one (0.33) (Fig. 1E, F).

Thorax as long (0.25) as it is wide (Fig. 1A). Pronotum trapezoid, with a broad base, anterior margin with a concavity, only slightly wider than head. Mesothorax longer than prothorax (app. 1.5 times). Mesothoracic sclerites poorly outlined. Mesoscutellum rectangular, narrow, contained within the concavity of mesoscutum. Mesothoracic sternite short (0.15) and wide, with antero-lateral fragments strongly expanded. Fore coxae (0.06) lying close to each other right behind head on the ventral side (Fig. 1D). Fore femur (0.23) and fore tibia (0.23) of similar length. The distance between fore and middle coxae 2-3 times longer than that between middle and hind coxae. Middle coxa 0.08 and hind coxa (0.08) of similar length. Hind legs longer than fore and middle ones (middle femur 0.18, middle tibia 0.26; trochanter 0.05, hind femur 0.28, hind tibia 0.40). Tarsi of all legs of similar length; segment II of fore tarsus 0.08, middle tarsus 0.08 and hind tarsus segment I 0.02; II 0.08.

Forewings (Fig. 1A, G): length holotype 0.87 (damaged), additional material 1.25–1.28; width holotype 0.41, additional material 0.51. M brached behind Rs base. Rs arcuate. Hind wings length 0.12 (Fig. 1H, I).

Abdomen broadly set, about as long as thorax, widening gradually to a broad base up to the last three tergites. The fore three tergites of abdomen slightly bent backward, short and wide, segment IV almost rectangular, the following ones bent forward, tergite VII bent most intesively, only half as wide as abdomen (Fig. 1A). Abdomen terminating in a rounded anal plate. Abdomen termination with a group of bristles (0.10 in length), the tips of which are turned inwards.

Description. Male. An alate morph (Fig. 2A). Body flattened dorsoventrally (length 0.88), only mesothrorax arched. Head elongated (0.14) twice as long as wide. Antennal bases on ventral side of head at antero lateral margin (Fig. 2B). The distance between bases of antennae not longer than antennal width. Flagellum (0.16 in length) 5-segmented (Fig. 2B), with the boundaries between segments illformed. Segment III the longest. Segments V-VI very short. Segment VII as long as segments V+VI. Rhinaria not visible. Compound eyes located on sides of the head, expanding to the ventral side of head. Large paired ocelli on the inner antero lateral edge of compound eyes. Rostrum absent.

Thorax length 0.35 (Fig. 2C). Pronotum narrow, indented in the middle part, forming a rim tightly adhering to head. Mesothorax strongly arched, praescutum not clearly outlined. Mesoscutellum rectangular in shape, 5-6 times wider than long. Mesothoracic sternite strongly expanded (0.19), with the anterior edge convex in the middle. Metathorax well developed, about as long as mesothorax. Fore coxae lying right behind head, tightly adhering to each other (Fig. 2D). Femur (0.21) and tibia (0.28) of similar length. Middle and hind femora set wide apart, lying close behind each other in a distance approximating their length. Middle coxa shorter (0.08) than the hind one (0.10). Length: middle femur 0.20; hind femur 0.28; middle tibia 0.26; hind tibia 0.38. Apical part of tibia with numerous setae (Figs. 2E, F). Tarsus short, middle 0.08, hind 0.10 (segment I 0.02, segment II 0.07), claws long (0.04) (Fig. 2E).

Forewings elongated (1.36) (Fig. 2A). M running almost parallel to Rs. Common stem of M very long branching as far as in the apical part of the wing. Rs evenly curved a little. Hind wings 0.21.

Abdominal segments clearly outlined (Fig. 2C). The first six tergites in form of trapezoid shields, with a concavity in the middle part. Tergite VII visible from the dorsal side is narrow, only 1/3 of the width of previous sclerites. Phallus located ventrally in apical part of abdomen with two parameres (0.03) on sides (Fig. 2E, F).

¹ Deposited in the Poinar amber collection at Oregon State University.



Fig. 1. Parvaverrucosa annulata Poinar and Brown (2006) (female). A. Habitus (NIGP167771), dorsal view; B. Habitus (holotype) lateral view (fot. G. Poinar); C-I specimen NIGP167771. C. Antennae, ventral view; D. Head and thorax ventral view; E. III + IV rostral segments; F. Rostrum, ventral view; G. Right forewing, dorsal view; H. Left hindwing, dorsal view; I right hindwing, dorsal view. A scale bars 0.5; B-I scale bars 0.2. Detailed descriptions of a female and male of the extinct aphids Parvaverrucosidae (Hemiptera: Aphidomorpha) revealed their new systematic position.



Fig. 2. *Parvaverrucosa annulata* Poinar and Brown (2006) (male NIGP167772); A. Habitus; B. Head and antennae, ventral view; C. Body, dorsal view; D. Body, ventral view, arrows show apical part of abdomen with two parameres; E. Abdomen, ventral view; F. Apical part of abdomen, ventral view, arrows show phallus and paramere. A, D-F scale bars 0.2; B-C scale bars 0.1. Detailed descriptions of a female and male of the extinct aphids Parvaverrucosidae (Hemiptera: Aphidomorpha) revealed their new systematic position.





Fig. 3. Parvaverrucosa annulata Poinar and Brown (2006) (female). A, B, D specimen NIGP167771. A. Body, dorsal view, B. Abdomen, dorsal view; C. Apex of abdomen, arrow show ? siphunculus (holotypoe, fot. G. Poinar), lateral view; D. Abdomen apex with a group of bristles, dorsal view; E. Laingia psammae Theobald, 1922 abdomen termination with trophobiotic organ, lateral view (SEM M. Kanturski); F. Lachnus roboris (Linnaeus, 1758) abdomen termination with trophobiotic organ, dorsal view (SEM M. Kanturski). A-D scale bars 0.1; E-F scale bars 0.3. Detailed descriptions of a female and male of the extinct aphids Parvaverrucosidae (Hemiptera: Aphidomorpha) revealed their new systematic position.

4. Discussion

Presently, there are several parallel systematic divisions of aphids, which deal with both fossil and recent families [for instance the classifications suggested by Remaudière, Stroyan and Quednau; Heie and Wegierek (Nieto et al., 2011); Favret, 2016]. The main difference between the classifications consists in the taxonomic ranks given to individual taxa by particular authors (family, subfamily, and tribe). However, all systems follow the concept of two developmental lines (i.e. viviparous and oviparous aphids), which was introduced by Börner in 1952. Both aphid lines have a complex life cycle with altering generations and are polymorphic (Moran, 1992). In viviparous aphids parthenogenetic females are viviparous. In oviparous aphids, which are considered a plesiomorphic group, all females are oviparous. Among extant aphids the latter group is represented by Adelgidae and Phylloxeridae; they typically lack siphunculi and are endowed with an ovipositor.

In addition to the wing structure, Poinar and Brown (2005, 2006) drew attention to two features characteristic of Parvaverrucosidae: "3-segmented extremely thick antennae composed of deep ring like structures; siphunculi well developed". New materials confirmed that antennae were unusually structured in females and males of Parvaverrucosidae (Figs. 1B, C; 2B; 3A). Rhinaria were not reported in this group although these sense organs are present in most extinct and extant alate morphs in aphids. In spite of a compact structure of flagella, in new materials it was possible to distinguish 5 segments of flagellum so antennae were 7-segmented in Parvaverrucosidae (Figs. 1C, 3A) as in most Jurassic and Cretaceous aphids.

Having examined new materials (Fig. 3B) and analysed the photos (Fig. 3C) of the structures interpreted as "siphunculi" in the type specimen, we firmly believe that there were no siphunculi in Parvaverrucosidae. The structures described as siphunculi in the holotype (Fig. 3C) are most probably the fragments of abdomen which were deformed in inclusion.

Siphunculi are specific abdominal structures responsible for pheromone release, but their occurrence or absence does not affect the reproductive mode of aphids. However, in extant aphids they are present only in viviparous aphids = true aphids. Accordingly, following the "Novacula Occami et Nominalium" principle, we assume that the aphids devoid of siphunculi are oviparous, so Parvaverrucosidae also belonged to this group. In spite of similarities in structure of fore and hind wings between Parvaverrucosidae and Burmitaphidididae, the former should retain their separate taxonomic status due to the specific shape and structure of antennae. In both Burmitaphidididae and Parvaverrucosidae, males did not develop rostrum (Figs. 2B, D). Seldom is such a condition observed in extant aphids (e.g. Stomaphis, Depa et al., 2015); it may occur in apterous morphs at most. Unlike aphids, in coccids (a sister group to aphids) rostrum is not developed in either apterous or alate males, they feed only as larvae (Kosztarab and Kozár, 1988; Gullan and Kosztarab, 1997).

Attention should also be drawn to a group of bristles at abdomen termination (Fig. 3D), which is not typical of Mesozoic aphids. The tips of the bristles are turned inwards along the middle line of the body. Such an arrangement of bristles is reminiscent of a so-called trophobiotic organ in many extant aphids (Fig. 3E, F). It is characteristic of the aphid species that live in trophobiosis with ants and helps to hold a drop of honeydew which ants feed on (Kanturski et al., 2017). PerkovskiParvaverrucosidae were among the first to have an abdominal "trophobiotic organ', which, together with a long rostrum (Shingleton et al., 2005), may be regarded as a pre-adaptation to subsequent mutualistic relations with ants. Such relations between aphids and ants started to flourish as late as near the Cretaceous–Paleogene boundary Perkovsky and Wegierek (2018).

5. Conclusions

As all Mesozoic extinct aphid families, Parvaverrucosidae were oviparous. The structure of apical part of abdomen (a trophobiotic organ) represents a pre-adaptation to subsequent mutualistic relationships between aphids and ants.

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