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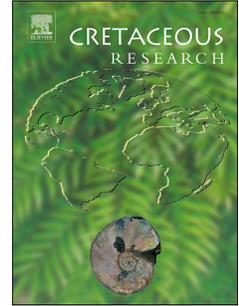
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The aphid *Hormatalis lancigerens* gen. et sp. nov. from Burmese amber sheds new light on the phylogenetic position of the Cretaceous family Isolitaphidae (Hemiptera: Aphidomorpha)

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Abstract:

In this paper a new genus and species of the female aphid *Hormatalis lancigerens* Wegierek and Wang, gen. et sp. nov., in the fossil family Isolitaphidae are described and illustrated, from the mid-Cretaceous Burmese amber of northern Myanmar. Based on a cladistic analysis

the Cretaceous aphid family Isolitaphidae, including *Hormatalis* Wegierek and Wang, gen. nov. and *Isolitaphis* Poinar, 2017, is recognized as monophyletic and sister to siphunculi aphids.

Keywords Burmese amber, Myanmar, mid-Cretaceous

1. Introduction

The Late Cretaceous constitutes a crucial period in aphid history. It has been suggested that this was the time when recent aphid groups originated (Heie, 1987; von Dohlen et al., 2006; Nováková et al., 2013; Perkovski and Wegierek, 2017b). Several aphids have been described from the Late Cretaceous based on rock impressions (Shaposhnikov, 1979; Heie and Wegierek, 2011; Kania and Wegierek, 2013) but they are very rare. Our understanding of the Late Cretaceous fauna mainly relies on amber inclusions. Cretaceous aphids have been described from Lower Cretaceous Lebanese amber, (Heie and Azar, 2000; 130 Mya; Hauterivian/Barremian; Maksoud et al., 2016) and Upper Cretaceous Canadian amber, (Rasnitsyn et al., 2016; 73-74 Mya, Campanian). Most Late Cretaceous species were described from Canadian amber (20 species) and Taimyr amber (18 species) (Heie and Wegierek, 2011; Perkovski and Wegierek, 2017a). The latter amber is composed of variedly aged resins (from Early Cretaceous: Albian to Late Cretaceous: Santonian), each of the collection sites for the Taimyr species were located near the Arctic circle in the Cretaceous (Rasnitsyn et al., 2016). Thanks to the inclusions from Canadian and Taimyr amber, we can reconstruct the Late Cretaceous aphid fauna of the Northern Hemisphere.

In the tropics, there were Cretaceous biocenoses which have yielded the Lower Cretaceous Lebanese amber (4 species) and Burmese amber dated from the beginning of the Late Cretaceous (Grimaldi et al., 2002; Ross et al., 2010; Rasnitsyn et al., 2016). Burmese amber

has yielded the richest Cretaceous fossil resin arthropod assemblage known to date (Rasnitsyn et al., 2016), however, aphids are very rare. Prior to this study, only six aphid species representing three endemic families were described from that amber (Poinar and Brown, 2005, 2006; Poinar, 2017a, b).

2. Material and methods

2.1. Specimen examination

The aphid inclusion in Burmese amber is from Hukawng Valley of northern Myanmar, currently considered to be of the earliest Cenomanian age (Shi et al., 2012) or Albian-Cenomanian boundary (Rasnitsyn et al., 2016). Mining took place at a hill named Noiye Bum, near Tanai Village (26°15'N, 96°33'E) (Kania et al., 2015, fig. 1). The inclusion was prepared using a razor blade, polished with emery paper with different grain sizes and finally lustrated with diatomite mud. The specimen is housed in Nanjing Institute of Geology and Palaeontology, State Key Laboratory of Palaeobiology and Stratigraphy, Chinese Academy of Sciences, China (NIGP).

Detailed examination was undertaken with a Nikon MZ1500 stereoscopic microscope and a Nikon Microphot-FX equipped with changeable direct and transmitted light. Measurements are approximate because of inclusion shrivelling and possible optical deformations. The photographs were taken using the Nikon Microphot-FX with a Nikon Eclipse E 600 digital camera and Lucia® software, and adjusted using Adobe® Photoshop Elements 6.0. All measurements are given in mm.

2.2. Phylogenetic analysis– maximum parsimony (MP)

The data matrix was constructed using mesquite v2.71 (Maddison and Maddison, 2015). The matrix includes 33 characters scored for ten taxa. Unknown character states were

coded with '?' and inapplicable ones with '-'. The cladistic analysis was carried out with the program TNT version 1.1 (Goloboff et al., 2008a), using maximum parsimony (traditional search) as the optimality criterion. Parsimonious tree searches were conducted using equal weight (EW) and implied weight (IW) of characters (Goloboff, et al., 2008b) with concavity indices (K) ranging from 3 to 10. The results of both analyses presented in topology of the trees were the same. All obtained trees were scanned and analysed using WinClada v1.00.08 (Nixon, 2002) and the shortest three trees were chosen. The nonhomoplasies and homoplasies on cladograms were searched for using slow optimization allowed to map all characters and states simultaneously. As it allows to map all characters and states simultaneously, Winclada was used in this study to indicate apomorphies which supported the nodes.

Outgroup Selection. In the current study, the outgroup *Rasnitsynaphis* Homan and Wegierek, 2011 (*Rasnitsynaphididae* Homan and Wegierek, 2011) was accepted as the most phylogenetically remote taxon in relation to the studied aphid taxa. The second outgroup was *Archeoviparosiphum* Żyła et al., 2015 (*Oviparosiphidae* Shaposhnikov, 1979), which, unlike *Rasnitsynaphis* (Homan and Wegierek, 2011; Żyła et al., 2017), does not have the common stem of CuA. The set of morphological characters was compiled for particular in-groups taxa. If there were enough features available, the typical genera of families were analysed: *Aphididae* Latreille, 1802; *Aphis* Linnaeus, 1758. *Isolitaphidae* Poinar, 2017; *Isolitaphis* Poinar, 2017. *Hormaphididae* Mordvilko, 1908: *Hormaphis* Osten-Sacken, 1861. *Juraphididae* Żyła, Blagoderov and Wegierek, 2014; *Juraphis* Shaposhnikov, 1979; *Phylloxeridae* Herrich-Schaeffer in Koch, 1854; *Phylloxera* Boyer de, 1834.

In other cases the best preserved characters in non-typical genera of families were selected: *Elektraphididae* Steffan, 1968; *Schizoneurites* Cockerell, 1915; *Palaeoaphididae* Richards, 1966; *Ellinaphis* Shaposhnikov, 1979).

All characters were coded based on first hand examination of specimens or from information derived from the literature. This provided improved feature characteristics which could be combined to achieve a more precise coding of the outgroup to be analysed from the phylogenetic perspective.

3. Results

3.1. Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Suborder Sternorrhyncha Amyot and Serville, 1843

Infraorder Aphidomorpha Becker-Midisoava and Aizenberg, 1962

Family Isolitaphidae Poinar, 2017

Type genus *Isolitaphis* Poinar, 2017

Genus *Hormatalis* Wegierek and Wang, gen. nov.

(urn:lsid:zoobank.org:act:188F7410-5BD3-4CFD-A7F9-F4DC2B7D13FE)

Type species: *Hormatalis lancigerens* Wegierek and Wang, sp. nov., by present designation.

Etymology. Derived from the name of Horm (aphis) and the Latin *talis* = such, the like, in kind. The name is feminine.

Diagnosis. Antennae 10- segmented. Rhinaria annular. Veins CuA₁ and CuA₂ with a short common stem, which is as thick as the remaining veins on the wing. Abdomen covered with wax plates.

Hormatalis lancigerens Wegierek and Wang, sp. nov.

(urn:lsid:zoobank.org:act:D5E4010F-C704-4674-97C3-4FE4022C31E5)

(Fig. 1)

Etymology. Latin: lanx, lancis – “scale, plate” and gero, gerens (participium praesentis) – “wearing”

Holotype. NIGP167953 (alate female).

Type locality. Hukawng Valley of northern Myanmar.

Stratigraphic horizon. Mid-Cretaceous Burmese amber.

Diagnosis. As for the genus.

Description. Female. Body length 2.42 (Figs 1A, B). Head short (0.23), almost twice as wide as long (the width between eyes 0.42) (Fig. 1B). Anterior head margin concave in middle, with an unpaired ocellus located in immersion. A distinct suture running from ocellus towards posterior head margin present. Compound eyes on lateral surfaces of head, composed of tiny ommatidia. Postero-lateral margin of compound eyes bearing distinct protuberances with a triommatidium. Paired ocelli located on dorsal side between compound eye and the base of antennae (Fig. 1B). Antennal base on antero-lateral margin of head (not on ventral side). Antenna 10-segmented, slender, covered irregularly with short setae (Fig. 1F). Setae not longer than half of segment diameter. Antennal segment III of the same width along its length (0.54), antennal segment IV (0.16, 0.17), V (0.11), VI (0.14, 0.15) VII (0.18), VIII (0.13, 0.14), IX (0.12) narrower at base and broader apically. On antennal segments III to IX rhinaria in form of closed or partly open rings (Figs 1F, J). Ultimate segment X without rhinaria (Fig. 1H), distinctly narrower than remaining ones, gradually tapering from base to rounded apex and covered with setae along its length. Setae not longer than half width of flagellomere. Rostrum blunt, not extending beyond hind coxae; segment lengths: III (0.06), IV (0.09) (Fig. 1I).

Pronotum clearly outlined (Fig. 1D), rectangular in shape, wider (0.67) than long (0.33) with anterior margin straight and anterior corners rounded; posterior margin arcuate, concave. In the middle part pronotum becomes convex. This prominence forms a "triangle" with the base overlapping posterior tergite margin and the tip directed towards the base of head. Mesothorax not compact in structure (Fig. 1D). Prescutum (prsc) triangular in shape, distinctly shifted towards pronotum. In the middle part mesothorax connected with

sclerotized, paired plates of mesosternum, which are also triangular in shape (stn₂). Between anterior margins of stn₂ and lateral margins of prsc on mesothorax membranous fragments. A similar large membranous structure occurs between the inner margins of stn₂ sclerite.

Forewings elongate (length: left 3.05, right 3.14; width: 1.15, 1.05) (Fig. 1E). Pterostigma (Pt.) long, lenticular, 4 times as long as wide. All veins of the same width. Main stem of CuA very short, only one-sixth the length of CuA₂. Vein M arising at Pt base, not reaching the main stem, broadly branched, with the first fork at about the level Rs separates from Pt and the second fork just apical of Pt tip. M₁₊₂ two-thirds the length of M. Rs broadly arcuate, separating from Pt almost halfway along its length. Hind wings long (left 1.75, right 1.83) (Fig. 1E), reaching the point at which CuA₁ terminates on the posterior margin in the forewings. Double transverse veins are present separated by a distance half the length of the basal vein.

Legs slender (Figs 1A, C). Length: middle femur 0.45, hind femur 0.62; middle tibia 0.75, hind tibia 0.94; hind tarsus I 0.04, II 0.17; claws 0.09 (Fig. 1G).

Abdomen with 6 rows of wax plates dorsally (Fig. 1A) Wax plates located at the sides of abdomen (on margins, Figs 5E, F), app. 0.30 in length, in apical part of abdomen 0.25 in length.

3.2. Cladistic analysis

3.2.1. The list of the characters for the data set.

1. Body: (0) thick (*Archeoviparosiphum*, *Ellinaphis*, *Hormaphis*, *Hormatalis*, *Juraphis*, *Phylloxera*, *Rasnitsynaphis*, *Schizoneurites*); (1) slender (*Aphis*, *Isolitaphis*).
2. Epicranial suture on head: (0) present (*Archeoviparosiphum*, *Ellinaphis*, *Hormatalis*, *Isolitaphis*, *Juraphis*, *Rasnitsynaphis*); (1) absent (*Aphis*, *Hormaphis*, *Phylloxera*, *Schizoneurites*).

3. Lateral sutures on head: (0) present (*Archeoviparosiphum*, *Ellinaphis*, *Juraphis*, *Rasnitsynaphis*); (1) absent (*Aphis*, *Hormaphis*, *Hormatalis*, *Isolitaphis*, *Phylloxera*, *Schizoneurites*).
4. Triommatidium: (0) absent (*Archeoviparosiphum*, *Ellinaphis*, *Juraphis*, *Rasnitsynaphis*); (1) present (*Aphis*, *Hormaphis*, *Hormatalis*, *Isolitaphis*, *Phylloxera*, *Schizoneurites*).
5. Antennal segments: (0) ten (*Hormatalis*, *Isolitaphis*); (1) seven to nine (*Archeoviparosiphum*, *Ellinaphis*, *Juraphis*, *Rasnitsynaphis*); (2) six (*Aphis*); (3) five (*Hormaphis*, *Schizoneurites*); (4) three (*Phylloxera*).
6. Length of antenna: (0) longer than one-third but only slightly as long as half body length (*Archeoviparosiphum*, *Ellinaphis*, *Hormatalis*, *Hormaphis*, *Juraphis*, *Rasnitsynaphis*); (1) shorter or equal to one-third of the body length (*Phylloxera*, *Schizoneurites*); (2) almost as long as the body (*Aphis*, *Isolitaphis*).
7. Segment III of antenna: (0) shorter than subsequent segments (*Archeoviparosiphum*, *Aphis*, *Ellinaphis*, *Hormatalis*, *Isolitaphis*, *Juraphis*, *Phylloxera*, *Rasnitsynaphis*, *Schizoneurites*); (1) equal or longer than subsequent segments (*Hormaphis*).
8. Segments of flagellum except III: (0) the same length (*Hormaphis*, *Isolitaphis*, *Rasnitsynaphis*); (1) various lengths (*Archeoviparosiphum*, *Aphis*, *Juraphis*, *Ellinaphis*, *Hormatalis*, *Phylloxera*, *Schizoneurites*).
9. Last antennal segment: (0) several times shorter than segment III (*Hormatalis*, *Isolitaphis*, *Rasnitsynaphis*); (1) shorter than half of segment III (*Archeoviparosiphum*, *Juraphis*); (2) longer than half of segment III (*Ellinaphis*, *Hormaphis*); (3) slightly longer than segment III (*Schizoneurites*); (4) several times longer than segment III (*Aphis*); (?) *Phylloxera* proportion unknown, segment III is the last one.
10. Last antennal segment: (0) slender (*Aphis*, *Hormatalis*, *Isolitaphis*, *Rasnitsynaphis*); (1) stout (*Archeoviparosiphum*, *Ellinaphis*, *Hormaphis*, *Juraphis*, *Phylloxera*, *Schizoneurites*).

- 11.** Processus terminalis: (0) absent (*Archeoviparosiphum*, *Ellinaphis*, *Hormaphis*, *Hormatalis*, *Isolitaphis*, *Juraphis*, *Rasnitsynaphis*); (1) weakly developed (*Phylloxera*, *Schizoneurites*); (2) distinct (*Aphis*).
- 12.** Primary rhinaria: (0) absent (*Archeoviparosiphum*, *Ellinaphis*, *Hormaphis*, *Hormatalis*, *Isolitaphis*, *Juraphis*, *Rasnitsynaphis*); (1) present (*Aphis*, *Phylloxera*, *Schizoneurites*).
- 13.** Secondary rhinaria: (0) more or less ellipsoidal, arranged in dense rows, which encircle antennal segments (*Archeoviparosiphum*, *Ellinaphis*, *Juraphis*); (1) annular, occurring on all flagellar segments (*Hormaphis*); (2) the last segment without secondary rhinaria (*Aphis*, *Hormatalis*, *Isolitaphis*, *Rasnitsynaphis*); (3) absent (*Phylloxera*, *Schizoneurites*).
- 14.** Primary and secondary rhinaria occur together on antenna or separately: (0) only secondary rhinaria separate (*Archeoviparosiphum*, *Ellinaphis*, *Hormaphis*, *Hormatalis*, *Isolitaphis*, *Juraphis*, *Rasnitsynaphis*); (1) together (*Aphis*); (2) only primary rhinaria separate (*Phylloxera*, *Schizoneurites*).
- 15.** Rostrum: (0) relatively long, reaching the hind coxa or longer (*Archeoviparosiphum*, *Aphis*, *Hormatalis*, *Isolitaphis*, *Rasnitsynaphis*); (1) reaching behind posterior margin of mesosternum (*Juraphis*); (2) reaching middle part of mesosternum (*Phylloxera*, *Schizoneurites*); (3) short, reaching anterior margin of mesosternum (*Ellinaphis*, *Hormaphis*).
- 16.** Hind tibia: (0) longer than half of the body length (*Archeoviparosiphum*, *Aphis*, *Rasnitsynaphis*); (1) longer or equal to one-third of the body length (*Ellinaphis*, *Hormatalis*, *Isolitaphis*); (2) shorter than one-third of the body length (*Hormaphis*, *Juraphis*, *Phylloxera*, *Schizoneurites*).
- 17.** Hind tarsus: (0) short, less than one-fourth of hind tibia length; (*Archeoviparosiphum*, *Aphis*, *Ellinaphis*, *Hormatalis*, *Rasnitsynaphis*); (1) long, more than one-fourth of hind tibia length (*Hormaphis*, *Isolitaphis*, *Juraphis*, *Phylloxera*, *Schizoneurites*).

18. Cubital veins: (0) as thick as the remaining veins on the wing (*Archeoviparosiphum*, *Aphis*, *Hormaphis*, *Hormatalis*, *Isolitaphis*, *Juraphis*, *Phylloxera*, *Schizoneurites*, *Rasnitsynaphis*); (1) thickened (*Ellinaphis*).

19. Cubital veins: (0) common stem CuA equal or shorter than half CuA₂ (*Hormaphis*, *Hormatalis*, *Isolitaphis*, *Juraphis*, *Phylloxera*, *Schizoneurites*); (1) common stem of cubital veins equal to CuA₂ length (*Ellinaphis*); (2) CuA₁ and CuA₂ leave the main vein at one-point (*Archeoviparosiphum*); (3) bases of veins separate and far apart (*Aphis*, *Rasnitsynaphis*).

20. Common stem of cubital veins or base of CuA₂ and CuA₁: (0) mid-distance between the base of wing and the base of vein Rs (*Archeoviparosiphum*, *Juraphis*); (1) shifted to the base of wing (*Aphis*, *Ellinaphis*, *Hormaphis*, *Schizoneurites*, *Rasnitsynaphis*); (2) shifted to the base of Rs (*Hormatalis*, *Isolitaphis*); (3) the distance from Rs is reduced (*Phylloxera*).

21. Base of vein M: (0) close to the base of pterostigma (*Archeoviparosiphum*, *Aphis*, *Hormatalis*, *Isolitaphis*, *Juraphis*, *Rasnitsynaphis*); (1) mid distance between the base of pterostigma and common stem of cubital veins or base of CuA₁ (*Ellinaphis*); (2) running towards CuA base (*Hormaphis*); (3) leaving pterostigma (*Phylloxera*, *Schizoneurites*).

22. Branches of vein M: (0) three branches (*Archeoviparosiphum*, *Aphis*, *Ellinaphis*, *Hormatalis*, *Isolitaphis*, *Juraphis*, *Rasnitsynaphis*); (1) unbranched (*Hormaphis*, *Phylloxera*, *Schizoneurites*).

23. Common stem of M: (0) longer or equal to M₁₊₂ (*Archeoviparosiphum*, *Aphis*, *Hormatalis*, *Isolitaphis*, *Juraphis*, *Rasnitsynaphis*); (1) shorter than M₁₊₂ (*Ellinaphis*); (2) only common stem (*Hormaphis*, *Phylloxera*, *Schizoneurites*).

24. M₃₊₄: (0) as long as common stem of M (*Aphis*, *Rasnitsynaphis*); (1) slightly longer than common stem (*Archeoviparosiphum*, *Hormatalis*); (2) at least 2x as long as common stem of M (*Ellinaphis*, *Isolitaphis*, *Juraphis*); (3) only common stem (*Hormaphis*, *Phylloxera*, *Schizoneurites*).

- 25.** Base of vein Rs: (0) close to the base of pterostigma (*Archeoviparosiphum*, *Ellinaphis*, *Hormaphis*, *Hormatalis*, *Juraphis*, *Rasnitsynaphis*); (1) in the middle of pterostigma (*Isolitaphis*); (2) closer to the distal part of pterostigma (*Aphis*, *Schizoneurites*); (3) outside pterostigma (*Phylloxera*).
- 26.** Pterostigma, length: (0) average (*Rasnitsynaphis*); (1) long, at least 4 times longer than wide (*Archeoviparosiphum*, *Aphis*, *Ellinaphis*, *Hormaphis*, *Phylloxera*); (2) short, at most 3 times longer than wide (*Hormatalis*, *Isolitaphis*, *Juraphis*, *Schizoneurites*).
- 27.** Hind wing: (0) apex between CuA₁ and CuA₂ (*Aphis*, *Ellinaphis*, *Hormaphis*, *Phylloxera*, *Schizoneurites*); (1) reach the apex of CuA₁ (*Hormatalis*, *Isolitaphis*, *Juraphis*); (?) (*Archeoviparosiphum*, *Rasnitsynaphis*).
- 28.** Hind wing: (0) two cubital veins (*Aphis*, *Ellinaphis*, *Hormatalis*, *Isolitaphis*, *Juraphis*); (1) a single cubital vein or two veins having a common stem (*Hormaphis*); (2) without cubital vein (*Phylloxera*, *Schizoneurites*); (?) (*Archeoviparosiphum*, *Rasnitsynaphis*).
- 29.** Siphunculus: (0) absent (*Ellinaphis*, *Juraphis*, *Phylloxera*, *Rasnitsynaphis*, *Schizoneurites*); (1) present (*Archeoviparosiphum*, *Aphis*, *Isolitaphis*) or secondarily lost (*Hormaphis*); (-) (*Hormatalis*).
- 30.** Wax gland plates on abdomen: (0) absent (*Archeoviparosiphum*, *Ellinaphis*, *Isolitaphis*, *Juraphis*, *Rasnitsynaphis*); (1) produce powder or filaments (*Aphis*, *Hormaphis*, *Phylloxera*); (2) produce wax plates (*Hormatalis*); (-) (*Schizoneurites*).
- 31.** Ovipositor: (0) typical (*Archeoviparosiphum*, *Ellinaphis*, *Isolitaphis*, *Juraphis*, *Rasnitsynaphis*, *Schizoneurites*); (1) internal sclerotized rudiments (*Phylloxera*); (2) rudimentary gonapophyses (*Aphis*, *Hormaphis*); (-) (*Hormatalis*).
- 32.** Cauda: (0) absent (*Archeoviparosiphum*, *Ellinaphis*, *Juraphis*, *Rasnitsynaphis*, *Schizoneurites*); (1) small, short (*Isolitaphis*, *Phylloxera*); (2) knobbed (*Hormaphis*); (3) elongate, longer than its basal width (*Aphis*); (-) (*Hormatalis*).

33. Oviparous: (0) (*Archeoviparosiphum*, *Ellinaphis*, *Juraphis*, *Isolitaphis*, *Phylloxera*, *Rasnitsynaphis*, *Schizoneurites*); viviparous: (1) (*Aphis*, *Hormaphis*); (-) (*Hormatalis*).

3.2.2. The character state matrix (Table 1).

3.2.3. Cladistics

The analysis of morphological data under the equal weight (EW) criterion with the use of TNT (2008), produced 80 trees of different lengths. The topology of the most parsimonious trees (the shortest trees) is shown in Figs 2, 3 and 4. Character data were plotted on the tree using slow optimization in Winclada (Nixon, 2002). The main difference in the topology of all trees consisted of substantially different positions for *Juraphis*, *Ellinaphis*, *Archeoviparosiphum* and *Hormaphis*, as clearly shown in the trees.

The analysis revealed that *Hormatalis* Wegierek and Wang, gen. nov., together with *Isolitaphis* constitute a monophyletic family, Isolitaphidae, which is supported by two synapomorphies (5-0; 20-2) and can be observed in the presented trees (Figs 2 and 4). However, the relationships among ingroups show two paraphyletic lines of aphids. One of them includes all aphid taxa with siphunculi (synapomorphy 29-1) and the other clade (*Phylloxera* + *Schizoneurites*) representing aphids without siphunculi (Fig. 2). The other branch of the same tree is formed by the clade *Ellinaphis* + *Juraphis*, which does not have siphunculi, and does not include *Phylloxera* + *Schizoneurites*. Several other characters (four synapomorphies: 5-3; 22-1; 23-2; 24-3) indicate the close relationship of the clade *Phylloxera* + *Schizoneurites* with *Hormaphis*; the latter taxon belonging to the line endowed with siphunculi (Figs 2 and 4). This condition has caused some confusion while placing *Phylloxera* + *Schizoneurites* on the tree (Fig. 2). It is primarily the clade formed by so-called spurious or unstable associations, because it was shifted to the group of taxa with siphunculi

(Fig. 2). Morphological data of clade *Phylloxera* + *Schizoneurites* strongly supports their relationship based on several shared synapomorphies (6-1;11-1;13-3; 14-2; 15-2; 21-3; 28-2).

A different situation is observed in Fig. 3, where the clade of siphunculi aphids is grouped based on symplesiomorphic characters (29-1) and *Hormaphis* is not included. This genus with five autapomorphic characters (7-1; 13-1; 21-1; 28-1; 32-2; 32-2) is a sister group to *Phylloxera* + *Schizoneurites* and it is also nested in the line of aphids without siphunculi (*Juraphis*, *Elinaphis*, *Phylloxera* + *Schizoneurites*) making the line paraphyletic.

Morphological data provide important evidence for the relationship between *Phylloxera* + *Schizoneurites* and *Juraphis* and *Ellisaphis* by the absence of siphunculi (Fig. 4). However, *Archeoviparosiphum* (the line of siphunculi aphids) has two other synapomorphies (9-1;13-0) and on cladogram (Fig. 4) is placed as sister taxon to the clade (*Juraphis* + *Elinaphis*) and (*Phylloxera* + *Schizoneurites*). It has proved difficult to account for the relationships between taxa based on these morphological data. Particularly referring to the position of *Phylloxera* + *Schizoneurites* (Fig. 2), *Hormaphis* (Fig. 3) and *Archeoviparosiphum* (Fig. 4). *Archeoviparosiphum* is placed in a common clade in the siphunculi aphid line on the basis of the synapomorphy ((29-1), Fig. 2) and this same character is presented as symplesiomorphy (Fig. 3) due to the absence of *Hormaphis* in this clade.

Fig.2

Fig.3

Fig.4

3.2.4. Phylogenetic position of *Hormatalis* Wegierek and Wang, gen. nov.

The presence of wax plates (autapomorphy (30-2)) is a diagnostic character of *Hormatalis*. This genus is clearly separated from *Isolitaphis*, also with one autapomorphy (25-1). Both terminal taxa are placed in a siphunculi line of aphids based on other common

characters (3-1; 4-1). The topologies of two trees presented Isolitaphidae as a monophyletic family, including *Hormatalis* and *Isolitaphis*. The relationship between these genera is supported by two synapomorphies (5-0; 22-2) (Figs 2 and 4). Since the position of the taxon seems clear, we consider *Hormatalis* to have the rank of genus, and to be a sister group to *Isolitaphis*.

It has been determined that *Archeoviparosiphum* (Oviparasiphidae; siphunculi line of aphids, character 29-1) is a sister taxon to the clade (3-1; 4-1) including siphunculi taxa Isolitaphidae (*Hormatalis* and *Isolitaphis*) + Aphididae (*Aphis*) + Hormaphididae (*Hormaphis*) + non siphunculi families Phylloxeridae (*Phylloxera*) and Elektraphididae (*Schizoneurites*) (Fig. 2). However there is a possibility to exclude these two families Phylloxeridae (*Phylloxera*) + Elektraphididae (*Schizoneurites*) from siphunculi clade and move them to clade *Ellinaphis* + *Juraphis* (Fig. 2) in which an ancestor did not have siphunculi.

4. Discussion

It is generally assumed that Sternorrhyncha, the group comprising Aphidomorpha Becker-Migdisova and Aizenberg, 1962; Coccidomorpha Heslop-Harrison, 1952; Naibiomorpha Szwed, 2017; Pincombeomorpha Shcherbakov, 1990; Aleyrodomorpha Chou, 1963; and Psyllaeformia Verhoeff, 1893; originated from Archescytinoidea Tillyard, 1926 (Shcherbakov and Popov, 2002; Grimaldi and Engel, 2005). Such a conclusion has been drawn because the group is regarded as plesiomorphic when bases of CuA₁ and CuA₂ form a common stem. Accordingly, the feature is typical of the ancestors of all Sternorrhyncha groups including aphids. Additionally, this discussion is mostly based on three parsimonious trees (Figs 2, 3 and 4) and it clearly defines the position of Isolitaphidae.

4.1. Important characters

4.1.1. Wings

It is interesting to note that the common stem of CuA is relatively rare in both the fossil and recent aphids. The plesiomorphy of that condition is confirmed first of all by the Triassic wing imprints of *Triasoaphis* Evans, 1956; *Creaphisi* Shcherbakov and Wegierek, 1991 and *Leaphis* Shcherbakov, 2010. The oldest aphids which show this character are in the family Juraphididae (Żyła et al., 2014) for which whole body structures are also known. In Juraphididae the common stem of CuA was short and the cubital veins did not differ in width from other veins in the forewing; similar to the condition in Isolitaphidae, these data indicate plesiomorphies or homoplasies (18-0, 19-0). The present analysis has shown an evident autapomorphy (20-2) (Figs 2, 3 and 4) of the cubital veins in Isolitaphidae (*Hormatalis* and *Isolitaphis*), because the CuA₁ and CuA₂ base is shifted towards the base of Rs. Isolitaphidae share a only one character (common stem CuA equal or shorter than half CuA₂) (—with the recent aphid family Hormaphididae, whose oldest representatives are known from Baltic amber (Heie and Wegierek, 2011; Wegierek and Żyła, 2011). The CuA common stem (19-0 plesiomorphy) is present in Hormaphididae (it is sometimes significantly reduced, in this case CuA₁ and CuA₂ separate at the same point), and the pterostigma is similarly lenticular in shape. There are, however, some differences in venation —M is not branched (22-1, plesiomorphy) but it is sometimes bifurcated. Also, in Hormaphididae M does not usually arise from the common stem and, contrary to the condition in Isolitaphidae, is not directed towards the Pt base but runs towards the base of CuA. In Palaeoaphididae (Żyła and Wegierek, 2015) the cubital veins were similarly structured but the common stem was longer (equal to at least half the length of CuA₂) and the cubital veins were much thicker than M and Rs, which is regarded as an autapomorphy (18-1, 19-1). The Elektraphididae family (Heie and Wegierek, 2011, Perkovski and Wegierek, 2017) is known from the turn of the Cenozoic era. In the forewings of that family, as in recent Phylloxeridae, Rs is extremely reduced [an autapomorphy (20-3) and unbranched M (22-1, homoplasy Fig. 4)]. The common stem of

CuA (if present) is relatively short (19-0, plesiomorphy), approximately half the length of CuA₂.

In Hormaphididae the wings are folded flat over the body. This form of wing folding is rare in aphids and seems possible due to a specially structured mesothorax where the prescutum (prsc) is reduced (Wegierek, 2002). In Isolitaphidae the prsc is still a large sclerite, but there are some characters which indicate that their wings might also have been, at least partly, folded in a similar manner over the body. They include forward shifted prsc (towards the head), broad spacing of paired sclerites of the mesosternum (stn2) and large membranous fragments in the structure of the mesonotum (Fig. 1d).

4.1.2. Antennae

Juraphididae and Palaeoaphididae differed considerably from Isolitaphidae in the structure of antennae. However, Isolitaphidae are the only family in this group to have ten segmented antennae (autapomorphy 5-0) (Figs 2, 3, and 4). Juraphididae lived around the Jurassic/Cretaceous boundary and Palaeoaphididae are known from the Cretaceous (Perkovski and Wegierek, 2017). Juraphididae and Palaeoaphididae had antennae with seven–nine segments (5-1, plesiomorphy) and more or less ellipsoidal secondary rhinaria arranged in dense rows, which encircled all flagellar segments (13-0, synapomorphy). Annular rhinaria occur on all flagellar segments, which is an autapomorphy (13-1) in Hormaphididae (Figs 3, 4, 5) (Fig. 5I). In both Hormaphididae and Isolitaphidae annular or semi-annular rhinaria are present on flagellar segments. It should be noted, however, that the antennae in recent and fossil Hormaphididae (alate morphs) are reduced to five segments only (three segments of flagellum) (5-3, synapomorphy, this character is shared with the *Schizoneurites*).

In most representatives of recent families there is a circular rhinarium, so called main rhinarium on the last antennal segment (Fig. 5G). The distal margin of this rhinarium is

considered to be a boundary between the basal part of the segment and a terminal process (processus terminalis) (Fig. 5G). In Isolitaphidae the last antennal segment is devoid of rhinaria (Fig. 5H) so it would be difficult to find a terminal process there, as mentioned by Poinar (2017a). Nevertheless, it must be emphasised that the last antennal segment differs from the other flagellar ones in structure (Fig. 1F) Thus, it may be demonstrated that in aphids the evolutionary process of reducing the number of flagellar segments (merging) has probably led to transformation of the last antennal segment into a terminal process. Both Elektraphididae and Phylloxeridae also reduced the number of antennal segments (3-5), five segments are considered to be synapomorphic (5-3) in *Hormaphis* + *Schizoneurites* and three segments to be autapomorphic in *Phylloxera* (5-4). Primary rhinaria are oval in shape or form elongated receptor plates (secondary rhinaria are absent in *Phylloxera* and *Schizoneurites*, 13-3; only primary rhinaria (*Phylloxera*, *Schizoneurites*, 14-2) arranged singly or by two on flagellar segments and occupying much of the segment area (Steffan and Schlüter, 1981; Wegierek, 1996; Huber et al., 2009).

4.1.3. Wax glands

Although most recent aphids (mostly apterous morphs) possess wax glands (Miyazaki, 1987), Eriosomatidae (Fig. 5B), and especially Hormaphididae, show a remarkable ability to produce large amounts of wax. In recent Hormaphididae this special ability is mainly found in apterous morphs (Figs 5D, C). Most aphids produce formless fluff (Fig. 5B) and only very few representatives are capable of producing wax plates e.g. *Hormatalis* (30-2) (Figs 2, 3 and 4), this being an automorphic state (Figs 5D,C). Wax plates resemble wax structures which were produced by fossil and recent coccid females (Fig. 5A). The new genus and species is unique among fossil and recent aphids because its wax glands produced wax plates in alate morphs (Figs 1A, B; 5E, F).

4.1.4. Siphunculi

The genera *Isolitaphis* and *Hormatalis* form a sister group in a siphunculi line of aphids, however, on the basis of the examined inclusion of *Hormatalis* it is impossible to determine the state of siphunculi. Siphunculi are typical of most recent aphids (Aphididae, secondarily lost in some Hormaphididae; synapomorphy (29-1)) and some extinct groups such as Oviparopsidae (*Archeoviparosiphum*), which were formed by least the Upper Cretaceous (Shaposhnikov, 1981). In *Archeoviparosiphum* the authors (Żyła et al., 2015) noted the presence of clearly porous siphunculi. In the present analysis this character occurs as synapomorphy (29-1) in the above mentioned taxa. Shaposhnikov (1981), and Żyła et al., (2017) considered longer siphunculi an apomorphic state. According to Shaposhnikov's hypothesis a common ancestor of aphids which had porous siphunculi was probably the oldest, and obviously there were several lineages in which this character evolved independently. Hence many aphids have different shapes of siphunculi. It should be emphasized that siphunculi in *Hormaphis* are secondarily reduced, however, it comes from a siphunculi line.

4.1.5. Biological factors

Most recent aphids are distributed in a temperate zone of the Northern Hemisphere, which is quite an exceptional phenomenon in insects. There are several theories which try to explain this (Perkovski and Wegierek, 2017). Among the recent families only Hormaphididae and Greenideidae are adapted to subtropical and tropical zones. Fossil Hormaphididae species have been described from amber inclusions (Baltic and Dominican amber; Heie and Wegierek, 2011) but fossil Greenideidae are known almost exclusively from Miocene rock imprints. As particular amber faunas represent mainly local faunas of forest biocenoses (Zherikhin, 2002), Hormaphididae (except for Hormaphidinae) were probably associated with forest habitats of warm climate zones. Recently, strong host specificity is well defined and shows different patterns of host association among the Hormaphididae family.

Cerataphidinae are primarily associated with *Styrax* (Styracaceae), and Hormaphidinae and Nipponaphidinae occupy *Hamamelis* and *Distylium* (Hamamelidaceae) as their primary hosts respectively. Secondary host association is more flexible, with Cerataphidini on Compositae, Gramineae, Loranthaceae, Palmaceae, and Zingiberaceae; Hormaphidini on *Betula* (Betulaceae) and *Picea* (Pinaceae); and Nipponaphidini on Fagaceae, Lauraceae, and Moraceae (Jiang et al., 2011, Chen et al., 2014). According to Huang et al., (2012), Hormaphidinae and Nipponaphidinae are expected to have been associated with *Hamamelis* and *Distylium* respectively around the Cretaceous–Paleogene boundary, accompanying the origins of these two plant genera. Cerataphidinae are believed to have colonized *Styrax* during the Late Cretaceous to Eocene. Living mostly in tropical conditions, each subfamily started to produce galls independently. Given all of the above, we hypothesize that galls in the three tribes of Hormaphidinae might have evolved along separate paths (Chen et al., 2014). Relatively closed true galls are believed to have more adaptive advantages in comparison to gallers. They serve as better shelters than opened leaf pseudogalls, providing more protection to the inducer and its offspring from natural enemies and adverse abiotic factors (e.g. rainwater, aridity, and high temperature) (Zhang and Qiao, 2007; Sano and Akimoto, 2011; Chen et al., 2014).

5. Conclusions

- The newly described genus *Hormatalis* Wegierek and Wang, gen. nov., has 10-segmented antennae and CuA veins with a short common stem shifted to base of Rs, similar to *Isolitaphis*. Cladistic analysis defined these features as synapomorphic, which grouped both genera in one family. In these analyses the Isolitaphidae family was recognized as monophyletic and it has a stable position in the cladograms.

- The main difference in the topology of trees obtained under EW searching strategies referred to the position of four taxa (Figs 2, 3, 4) *Juraphis*, *Ellinaphis*, *Hormaphis* and *Archeoviparosiphum*.
- Unlike *Isolitaphis*, the abdomen in *Hormatalis* is covered with wax plates, which testifies to its autapomorphic character (30-2). As demonstrated, this is a new characteristic feature of this genus.

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Fig. 1. *Hormatalis lancigerens* Wegierek and Wang, sp. nov. Holotype NIGP167953. A. Habitus, dorsal view. B. Head. C. Habitus, ventral view. D. Thorax, dorsal view. E. Left forewing and hindwing. F. Antennae, dorsal view. G. Hind tarsus. H. Apical part of antenna. I. Apical part of rostrum. J. Fragment of antennal segment III with rhinaria. Scale bar in picture A,C,E = 1 mm, in B,D,F = 0.5 mm, in G,H,I,J = 0.1 mm.

Fig. 2. Result of relationships deduced from an equal weight (EW). Characters are plotted showing slow optimization in Winclada: tree (L= 91, CI =70, RI= 58). Filled circles represent non-homoplastic characters, open circles homoplastic characters.

Fig. 3. Most parsimonious tree obtained using an equal weight (EW). Characters are plotted showing slow optimization: tree (L= 92, CI = 69, RI = 56).

Fig 4. Results of Maximum Parsimony (MP) analyses obtained using equal weights (EW). Characters are plotted showing slow optimization in Winclada: tree (L=95, CI = 67, RI = 52).

Fig. 5. A *Wathondara kotejai* Simon, Szwedó and Xia, 2015, dorsal view. B. woolly aphid (Phot. D. Race). C. *Ceratovacuna japonica* (Takahashi, 1924) (Phot. Yerim Lee). D. *Aleurodaphis blume* van der Goot, 1917 (Phot. Yerim Lee). E, F. Wax plates *Hormatalis lancigerens* Wegierek and Wang, sp. nov. G. *Lachnus roboris* (Linnaeus, 1758) ultimate segment VI with rhinaria (SEM M. Kanturski). H. *Hormatalis lancigerens* Wegierek and Wang, sp. nov. ultimate segment X without rhinaria. I. Hormaphididae indetermined ultimate segment V with rhinaria. Scale bar in picture E,F,H,I = 0.1 mm

3.2.2. The character state matrix (Table 1).

<i>Family</i>	<i>Genus</i>	<i>Character 1-33</i>
Rasnitsynaphididae	<i>Rasnitsynaphis</i>	00001000000020000031000000??00000
Oviparosiphidae	<i>Archeoviparosiphum</i>	00001001110000000020000101??10000
Palaeoaphididae	<i>Ellinaphis</i>	000010012100003101111012010000000
Isolitaphidae	<i>Hormatalis</i>	011130102100103210012123010111221
Isolitaphidae	<i>Isolitaphis</i>	101102000000200110020002121010010
Hormaphididae	<i>Hormaphis</i>	0011000100002001000200010210-2---
Juraphididae	<i>Juraphis</i>	000010011100001210000002021000000
Phylloxeridae	<i>Phylloxera</i>	01114101?111322210033123310201110
Elektraphididae	<i>Schizoneurites</i>	01113101311132221001312322020-000
Aphididae	<i>Aphis</i>	111122014021210000310000210011231



