

New genera and species of aphids (Hemiptera, Aphidomorpha, Burmitaphididae) in mid-Cretaceous Burmese amber



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ABSTRACT

In this paper new aphid genera and species, *Echinoaphis penalverii* gen. et sp. nov. and *Vasteantenatus hukawngi* gen. et sp. nov. in the fossil family Burmitaphididae are described and illustrated; these aphids are from the mid-Cretaceous Burmese amber of northern Myanmar.

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1. Introduction

The Late Cretaceous is a very important period for aphid phylogeny. All recent aphid families originated at that time (Heie, 1987; von Dohlen et al., 2006; Nováková et al., 2013). Only several aphids have been described from the Late Cretaceous on the basis of rock impressions, but they are very rare (Shaposhnikov, 1979; Heie and Wegierek, 2011; Kania and Wegierek, 2013). Therefore, our understanding of the Late Cretaceous fauna is mainly based on the genera and species preserved as amber inclusions.

The oldest Cretaceous aphid containing amber (Heie and Azar, 2000) comes from Lebanon (ca. 130 Mya; Hauterivian/Barremian; Maksoud et al., 2016) and the youngest is Canadian (73–74 Mya Campanian; McKellar and Wolfe, 2010; Rasnitsyn et al., 2016). Most Late Cretaceous fossil species have been described from Canadian and Taimyr amber (20 and 17 species respectively) (Heie and

Wegierek, 2011). “Taimyr amber” is composed of variedly aged resins (Albian–Santonian) and all its sites in the Cretaceous were located near the Arctic Circle (Rasnitsyn et al., 2016). Thanks to Canadian and Taimyr amber inclusions, it is possible to study the Cretaceous aphid fauna of the Far North.

In the tropics, the Cretaceous biocenoses have yielded Lower Cretaceous Lebanese amber (4 species) and Burmese amber, which is dated from the turn of Early and Late Cretaceous (Grimaldi et al., 2002; Ross et al., 2010; Rasnitsyn et al., 2016). The Burmese assemblage is the richest Cretaceous fossil resin arthropod assemblage known to date (Rasnitsyn et al., 2016). Only 7 aphid species have been described from that amber so far (Poinar and Brown, 2005, 2006; Wegierek et al., 2017; Poinar, 2017, 2018; Liu et al., 2018).

2. Material and methods

Aphid inclusions originated from deposits in Hukawng Valley of northern Myanmar, are currently considered to be of Albian (Ross et al., 2010), late Albian (Zheng et al., 2018), Albian–Cenomanian boundary (Rasnitsyn et al., 2016) or earliest Cenomanian age (Shi et al., 2012). Mining took place at a hill called 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

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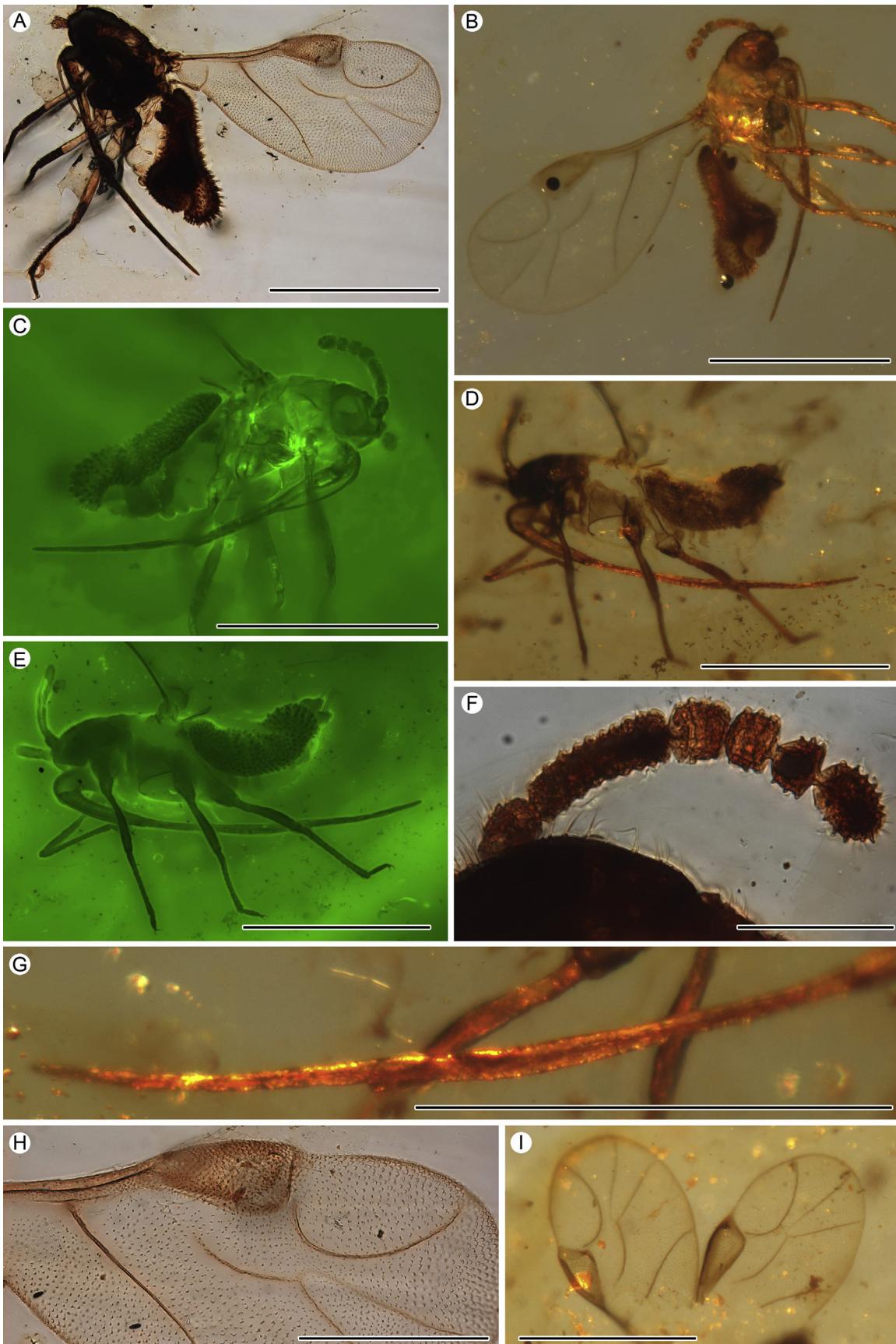


Fig. 1. *Echinoaphis penalverii* sp. nov. Holotype, NIGP167702 A-C. A. Lateral view, left side, under Zeiss Axio Imager 2 compound microscope. B. Lateral view, right side. C. Lateral view, right side, under Zeiss Axio Imager 2 compound microscope using fluorescence as light source; Paratype, NIGP167703 D-E. D. Lateral view, left side. E. Lateral view, left side, under Zeiss Axio Imager 2 compound microscope using fluorescence as light source; F. Holotype, Right antenna, under Zeiss Axio Imager 2 compound microscope; G. Paratype, Rostrum; E. Holotype, Forewing; pterostigma, veins Rs, M; I. Paratype, Forewings. Scale bar in picture A-E, G, I = 0.5 mm, F = 0.1 mm, H = 0.25 mm.

razor blade, polished with emery papers with different grain sizes and finally illustrated with diatomite mud. The specimens are deposited in Nanjing Institute of Geology and Palaeontology CAS, Nanjing, China [NIGP]. The photographs were taken using the Zeiss Discovery V20 stereo microscope and the Zeiss Axio Imager 2 compound microscope with a digital camera attached, respectively. The photographs with green background (Figs. 1C, D, 2D and 7E) were taken using fluorescence as light source attached to the 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 Burmitaphididae Poinar and Brown, 2005

Genus *Echinoaphis* gen. nov.

urn:lsid:zoobank.org:act:815C22C8-D07C-4587-A9F6-

FDDFF2CF07AC

Type species: *Echinoaphis penalverii* sp. nov., by present designation.

Etymology. Derived from *echinus* = hedgehog and Latin *aphis*, aphid. The name is feminine.

Diagnosis. Very tiny aphids (body length less than 1). Antennae short, not reaching the base of forewing. Rostrum long, extending beyond the body. Posterior pterostigma margin directed towards the anterior wing margin at an almost right angle at the level of vein M branching. Vein Rs arising from the perpendicular margin of pterostigma. Vein M_{1+2} sharply turning towards Rs at the level of branching then turning back towards wing apex halfway between the apexes of M and Rs. Hindwings reaching CuA₂ apex. Abdomen is unique in structure among aphids, covered with bottle-shaped setae on the dorsal side and in apical part laterally.

***Echinoaphis penalverii* sp. nov.**

urn:lsid:zoobank.org:act:1CDE32F7-0740-4EBD-B153-

A5FE7151BDB4

(Figs. 1 and 2)

Etymology. This species is named in honor of Dr. Enrique Peñalver (Mollá Museo Geominero Instituto Geológico y Minero de España; Madrid Spain).

Type material. Holotype, NIGP167702 (alate female). Paratype, NIGP167703 (alate female);

Type locality and horizon. Hukawng Valley of northern Myanmar. mid-Cretaceous, probably uppermost Albian–lowermost Cenomanian.

Diagnosis. As for the genus.

Description. Alate female (Fig. 1A–E). Body length 0.75 (holotype 0.85). Head as long as wide (0.14). Compound eyes very large (Fig. 1C), occupying all lateral surface of head, adjoining posterior head margin. Paired ocelli situated at half length of the head, unpaired ocellus on anterior head margin, below antennal bases. Antennal bases on anterior margin of head (Fig. 1C). Antennal segment III (0.10) as long as the cumulative length of the following three segments (Fig. 1F); antennal segments lengths: I 0.05, II 0.02, IV 0.03, V 0.03, VI 0.03, VII 0.05. Flagellar segments with fine, ellipsoidal rhinaria arranged in rows: segment III with 10 rows, segments IV to VI with 3 rows and the last segment with 5–6 rows. Rostrum longer than the body (Fig. 1A–E) last

rostral segment gradually tapering towards a sharp apex (Fig. 1G).

Thorax stumpy, about 0.25 long, prothorax as long as the head. Pronotum in form of a broad plate approximating mesothorax in length. Anterior margin of pronotum slightly convex, lateral margins slanting (originating at half height of the head, then running towards forewing base).

Forewings 0.71, (0.87 in holotype, Fig. 1H and I). Narrow at base, abruptly broadening at the level of pterostigma (at most 0.43 in width). Apical part wider, semicircular. Pterostigma short and broad (Fig. 1H and I), broadest in apical part with the margin running almost perpendicularly to the main vein stem. Vein Rs strongly arcuate, separating at the distal corner of pterostigma, running towards posterior wing margin in its distal part (Fig. 1A, H and I). Vein CuA₂ lying near the wing base, at a distance equal to its length. CuA₁ slightly sinusoidal in shape, in apical part reaching posterior wing margin at the pterostigma level. Vein M at base weakly sclerotised, articulate. Vein M_{1+2} separating from the main M stem at level of Rs base, running towards Rs for a short distance, then abruptly turning back towards the apical part of the wing. Vein M_{2+3} almost straight, branching from the main stem towards postero-apical wing margin. Hindwings 0.10 in length (Fig. 2A and B).

Legs of approximately the same length (Fig. 1A, D and E). Fore coxae set at posterior margin of prothorax: coxa I 0.06, trochanter I 0.04, femur I 0.016 (holotype), 0.22, tibia I 0.23, tarsus I 0.01 I 0.06, trochanter I 0.04, femur I 0.016 (holotype), 0.22, tibia I 0.23, tarsus I 0.01, segment II 0.07. The distance between fore and middle coxae comparable to the length of middle femur. Legs II and III in the posterior part of thorax close to each other (at coxa length). Coxa II 0.07, trochanter II 0.02, femur II 0.19, tibia II 0.21 (holotype), 0.29, tarsus I 0.03, II segment 0.09. Hind legs: coxa III 0.07, trochanter III 0.04, femur III 0.20, tibia III 0.23, tarsus segment I 0.03, segment II 0.09.

Abdomen 0.44, 0.42 (holotype) about as long as the remaining part of the body (Fig. 1A, B, D and E). Dorsal side of abdomen covered with very dense setae, which form an enveloping compact structure (Figs. 1C and 2C–E). At half abdomen length the setae descend also to the sides forming a capsule which encloses the genital block. Apical part of abdomen without setae, strongly sclerotized. Both, the tergite and sternite with long bristles: four dorsal ones straight and long (0.06), six ventral ones hooked, 0.10 in length (Fig. 2F). Ventral side at base of abdomen membranous, abdominal sternites in form of weakly sclerotised shields.

Genus *Vasteantenatus* gen. nov.

urn:lsid:zoobank.org:act:BED05DD3-FF9B-4746-BBC6-

AC6964BC34FD

Type species: *Vasteantenatus hukawngi* sp. nov., by present designation.

Etymology. The genus name is composed of the prefix vast – enormous, huge and antennae. The name is feminine.

Diagnosis. Aphids 2.0 in length.: Antennae characteristically extremely long, almost as long as the body. Pterostigma lenticular, terminating in a sharp tip which is extended as an enforced anterior wing margin. Vein M forked, with almost straight branches arising at the base of pterostigma. Vein Rs separating from Pt behind halfway of its length. Hindwings not reaching apical part of vein CuA₂. Abdominal tergites weakly sclerotised, with no processes.

Vasteantenatus hukawngi sp. nov.

urn:lsid:zoobank.org:act:B38D1365-D7B1-400C-BBD4-227CA93C663A
(Figs. 3, 4, 5 and 7)

Etymology. Derived from the name of Hukawng Valley of northern Myanmar, where the examined amber originated.

Type material. Holotype, **NIGP167704** (alate female). Paratypes, **NIGP167705** (alate female), **NIGP167706** (alate male), and **NIGP167707** (alate male).

Type locality and horizon. Hukawng Valley of northern Myanmar, mid-Cretaceous, probably uppermost Albian–lowermost Cenomanian.

Diagnosis. As for the genus.

Description. Body slender, spindle-shaped in shape (Fig. 3A and B). Head as long as wide, with the suture running in the middle along the body axis. Anterior margin concave, with the ocellus visible in the middle. Compound eyes well visible dorsally, large, occupying almost all lateral surface of the head, as wide as half head width. Ommatidia very numerous, fine. Paired ocelli large, set behind antennal bases, at half-length of the compound eyes. Antennal bases on lateral head margin (Fig. 3A and C). Last antennal segment VII terminating in a short (1/10 of the segment length), almost blunt tip covered with short setae (Fig. 3D). All flagellar segments (except the tip of segment VII) with transverse rows of rhinaria lying close to each other (Fig. 3E).

Prothorax narrow. Pronotum trapezoid in shape, slightly wider than head, anterior margin slightly concave, posterior margin almost straight. Corners of pronotum rounded. Mesothoracic tergite nearly as wide as pronotum. Praescutum reaching one-fourth the length of mesothorax. Mesoscutum plates twice as long as wide, covered with setae. Similar setae on prothorax. Metanotum in form of a broad plate, crescent in shape. Meso-sternum as long as wide.

Forewings elongated, narrow in basal part up to the point where CuA₂ joins posterior wing margin (Fig. 3A and B). From there the wings become broader towards pterostigma and then start tapering again; this part of wing (up to the rounded apex) is one-third the length of wing. Pterostigma 3x as long as wide (Fig. 3F). The distance between CuA₁ and CuA₂ bases equals to CuA₂ length. Vein M branching at the level of the tip. Hind wing represented by narrow stub (Fig. 3G). Fore coxae adjoined, lying quite far from middle coxae. Hind tarsi long, especially segment II (Fig. 3H). Tarsi terminating in long claws (Fig. 3I).

Alate female (Figs. 3A, B and 4A). Body 1.70, 2.10 (holotype). At bases of antennae and on anterior part of the head setae equal in length to at least half width of antennal segment II. Antennal segment III longest (0.67) (Figs. 3C and 4B, C), IV (0.40) (Fig. 4D). The subsequent two antennal segments V and VI similar in length (0.32–0.33). Antennal segment VII 0.32–0.42. Forewings (Figs. 3A, B, and 4E): length 2.5, 2.9 (holotype), width 0.87, 1.2. Fore tibia (0.67, 0.71 (holotype), covered with setae (at most as long as tibia width) (Fig. 3D). Tarsal segment II 0.15 in length. Middle and fore legs situated quite apart, twice further than hind legs. Middle tibia 0.80 (holotype), hind tibia 0.91 (holotype). Both tibiae covered with dense short setae, at most one-third the width of tibia. Hind tarsus: segment I 0.04; segment II 0.20; claws 0.04 (Fig. 3H). Abdominal tergites broad (segments 3–5 broadest; 0.80) in the middle part weakly sclerotised making tergite margins poorly visible (Figs. 3H and 4A). Laterally tergites broadened and rounded. Penultimate abdominal tergite much narrower, curved forward in a crescent-like manner, a half of the previous tergite. Abdomen termination blunt, last tergite small, with a convex anterior and a straight posterior margin.

Alate male (Fig. 5A–C). Body length 2.0–2.1. Head covered with fine setae, their length at most half width of antennal segment III. Antennal segment (Fig. 5D–F) III longest (0.50, 0.60), IV 0.34, 0.40, V 0.28–0.30, IV 0.25, 0.28, VII 0.32. In NIGP167707 last segment with a rounded apex. Prothorax covered with setae, which are similar to but not as dense as those on the head. The distance between the bases of middle and hind legs comparable to coxa length (Fig. 5A). Hind legs apart by at least the width of femur at base. All tibiae covered with dense setae. The setae not longer than half tibia width. Fore tibia 0.63, tarsal segment II 0.16, claws 0.06. Middle legs: coxa 0.16, femur 0.60, tibia 0.70, tarsal segment I 0.02; segment II 0.13. Hind coxa 0.21, trochanter 0.07, tibia 0.90, 0.75; tarsal segment II 0.19, 0.15; claws 0.06, 0.04. Forewings (Fig. 5G): length 2.70, width 1.00. Abdomen slender, evenly broad practically from base to penultimate segment, dorso-ventrally flattened especially in apical part. Abdominal tergites long, about one-third the width, on posterior margin slightly rounded. Last abdominal segment trapezoid in shape. Phallus located ventrally (Fig. 6A and C) with a short, broad base extending into a block-like process (total length 0.21, 0.23).

4. Discussion

The family Burmitaphididae includes four genera described so far, *Burmitaphis* Poinar and Brown, 2005, *Caulinus* Poinar and Brown, 2005, *Alavesiaphis* Peñalver and Wegierek, 2008 and *Tanyaulus* Poinar, 2018 (Heie and Wegierek, 2011; Poinar, 2018). The first two were described from Burmese amber (Poinar and Brown, 2005). The third one originated from Spanish amber (Peñacerrada I deposit; Peñalver and Wegierek, 2008). The new inclusions have been preserved so well that it has been possible to extend the diagnosis of the family presented by Poinar and Brown (2005). As in other aphid families, antennae vary in length (not only short), all flagellar segments have secondary rhinaria, which are tiny, ellipsoidal in shape and arranged in transverse rows encircling the segments. On forewings the distance between veins CuA₁ and CuA₂ is comparable to Cu₂ length. Hindwings lack transverse veins and are transformed into hamulohalters, which is another characteristic feature of the family.

The new species *Echinoaphis penalverii* gen. et sp. nov. differs from all aphids known so far in a specific structure of the abdomen. In none is the abdomen covered with so numerous setae, which form a compact structure similar to a “saddle” or a “duvet” on the dorsal side (Figs. 1C and 2A, C, D, E). Much longer setae a similar type were reported in the Cretaceous Lebanese *Gondwanaphis estephani* Wegierek and Grimaldi, 2010 (Fig. 6A), Burmese amber *Tanyaulus caudisetula* Poinar, 2018 and some recent species (Fig. 6B–H). However, in these taxa if the setae are abundant, they are arranged in (at most) 6 rows along the abdomen. The new species also possesses characteristic forewings. Pterostigma, which is short, broad and blunt, is not lenticular in shape as in *Burmitaphis* and *Caulinus*, neither do veins Rs and M run in a typical way. The structural outline of forewings in *Echinoaphis penalverii* is most reminiscent of that in *Alavesiaphis*, where pterostigma is similarly shaped with apical margin running across the main wing axis (Peñalver and Wegierek, 2008). Nevertheless, there are several differences between these genera reflected by the way particular veins run and branch. In the new species vein CuA₂ is shorter, only one-fifth CuA₁ length; in *Alavesiaphis* it is one-third CuA₁ length; vein M in *Alavesiaphis* is straight and long whereas in *Echinoaphis* it is short and articulate, which makes veins M branch at Rs. Moreover, vein M₁₊₂ runs differently. In the representatives of both species M₁₊₂ runs towards Rs but in *Echinoaphis* it does so for a very short distance, only one-ninth the vein length, whereas in the Spanish species it follows that course for one third of the vein

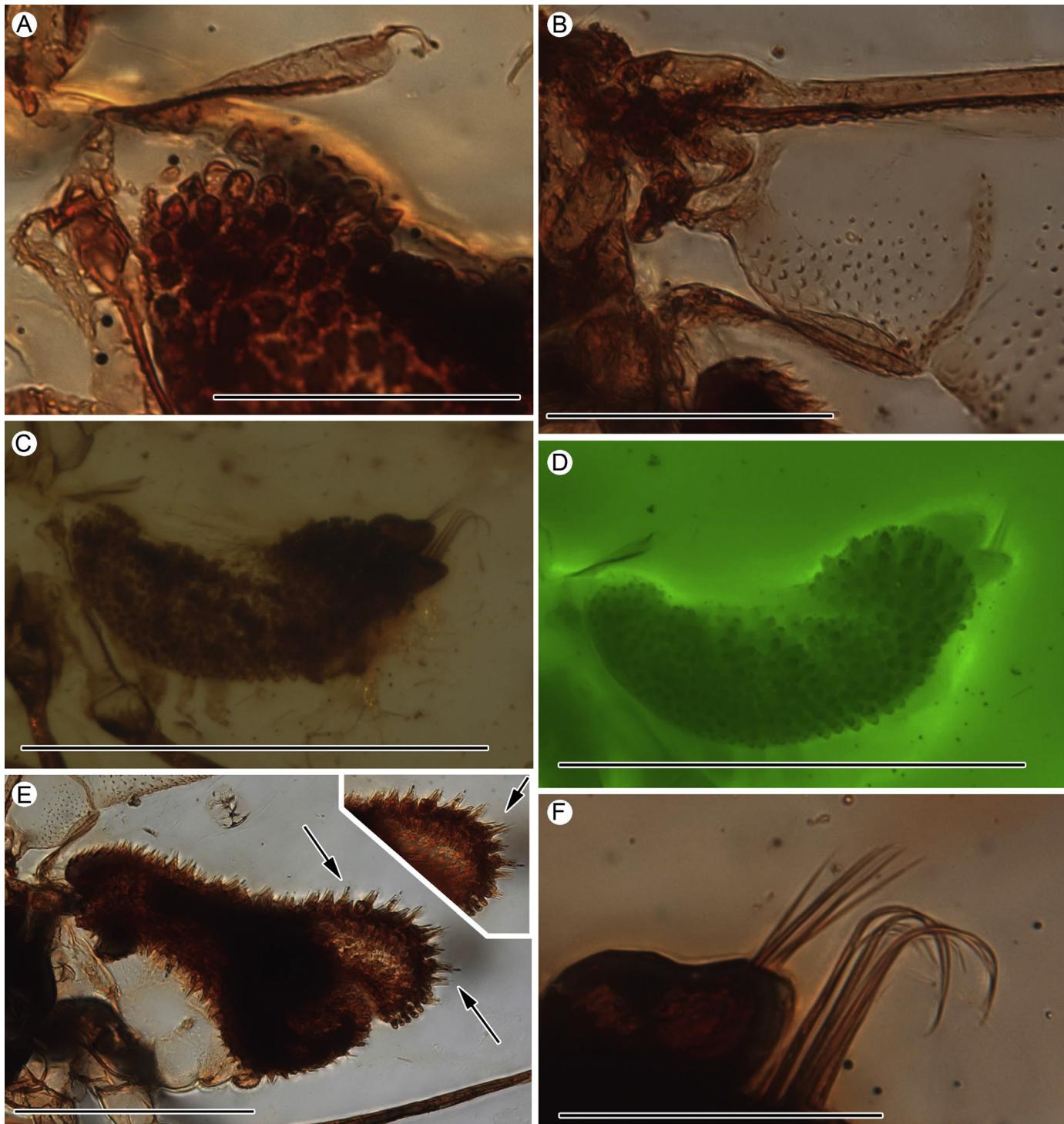


Fig. 2. *Echinoaphis penalverii* sp. nov. A. Paratype, NIGP167703 – hindwing, setae, under Zeiss Axio Imager 2 compound microscope. B. Holotype, under Zeiss Axio Imager 2 compound microscope. C. Abdomen, left side. D. Abdomen, left side, under Zeiss Axio Imager 2 compound microscope using fluorescence as light source. E. *Echinoaphis penalverii* sp. nov. abdomen setae. F. Apical part of abdomen, under Zeiss Axio Imager 2 compound microscope. Scale bar in picture A-B, F = 0.1 mm, C-D = 0.5 mm, E = 0.25 mm.

length. In spite of venation affinities, no other aphid except for *Echinoaphis penalverii*, shows such chaetotaxy on the abdomen.

The genus *Vasteantenatus* gen. et sp. nov. differ from other aphids known from Burmese amber in very long antennae. In spite of their length, they are 7 – segmented as in other Burmitaphididae representative (Figs. 3A, C and 5B, D). In *Vasteantenatus hukawngi* gen. et sp. nov. two morphs have been described – a female and a

male. Most fossil species have been described on the basis of females only (where the sex can be determined) (Heie and Wegierek, 2011). The sole species described on the basis of males is *Burmitaphis prolatum* Pionar and Brown, 2005 (Pionar and Brown, 2005). Although the authors illustrated and described the copulatory organ, they did not compare it to that in recent species. The structure has been analysed in details detail recently regarding different

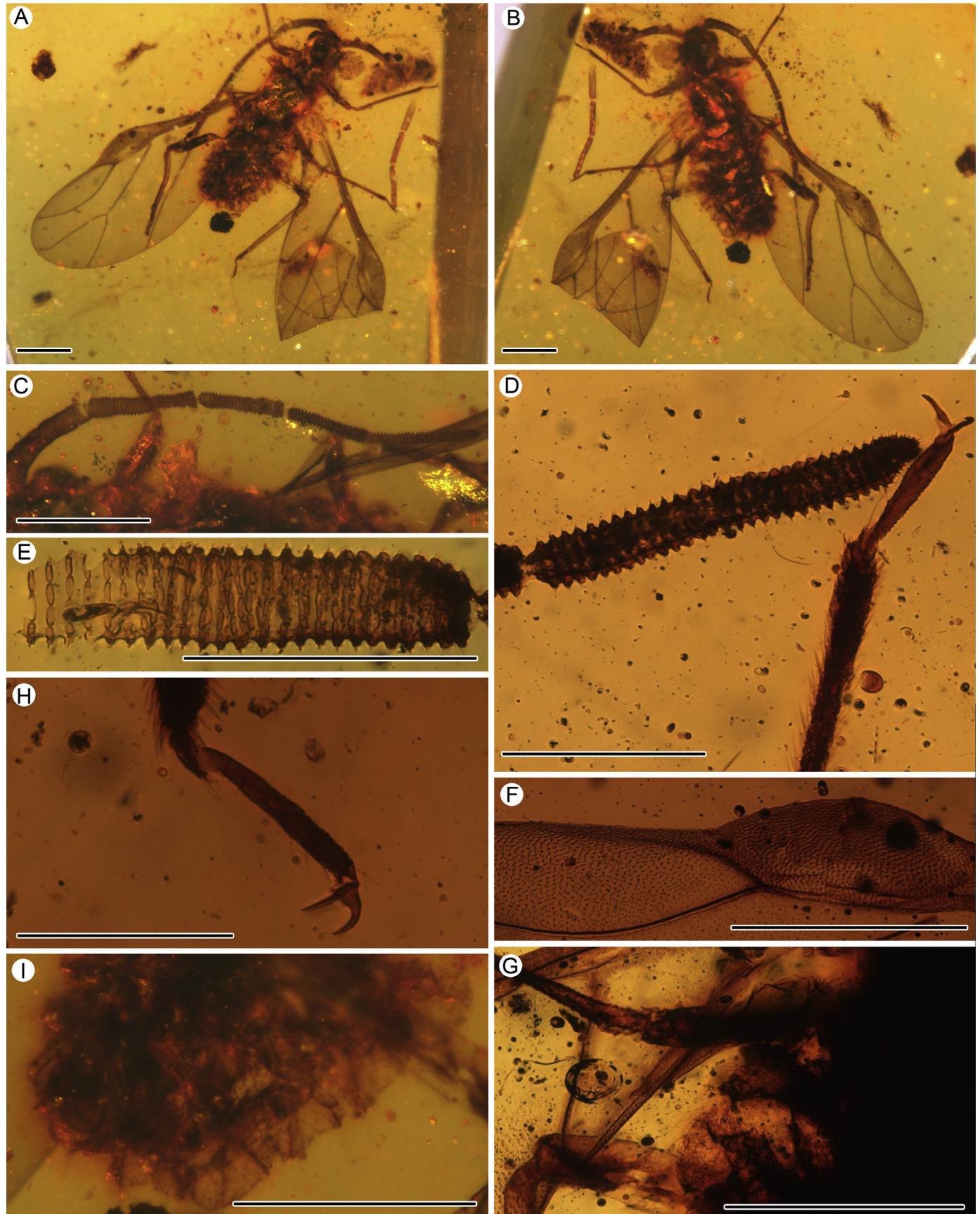


Fig. 3. *Vasteantenatus hukawngi* sp. nov. Holotype, NIGP167704 female. A. Ventral view. B. Dorsal view. C. Right antenna. D. Antennal segment V with transverse rows of rhinaria. E. Last antennal segment, middle left tarsus. F. Pterostigma. G. Hindwing. H. Hind left tarsus. I. Apical part of abdomen. Scale bar in picture A-C, F-H = 0.5 mm, E, D, I = 0.2 mm.

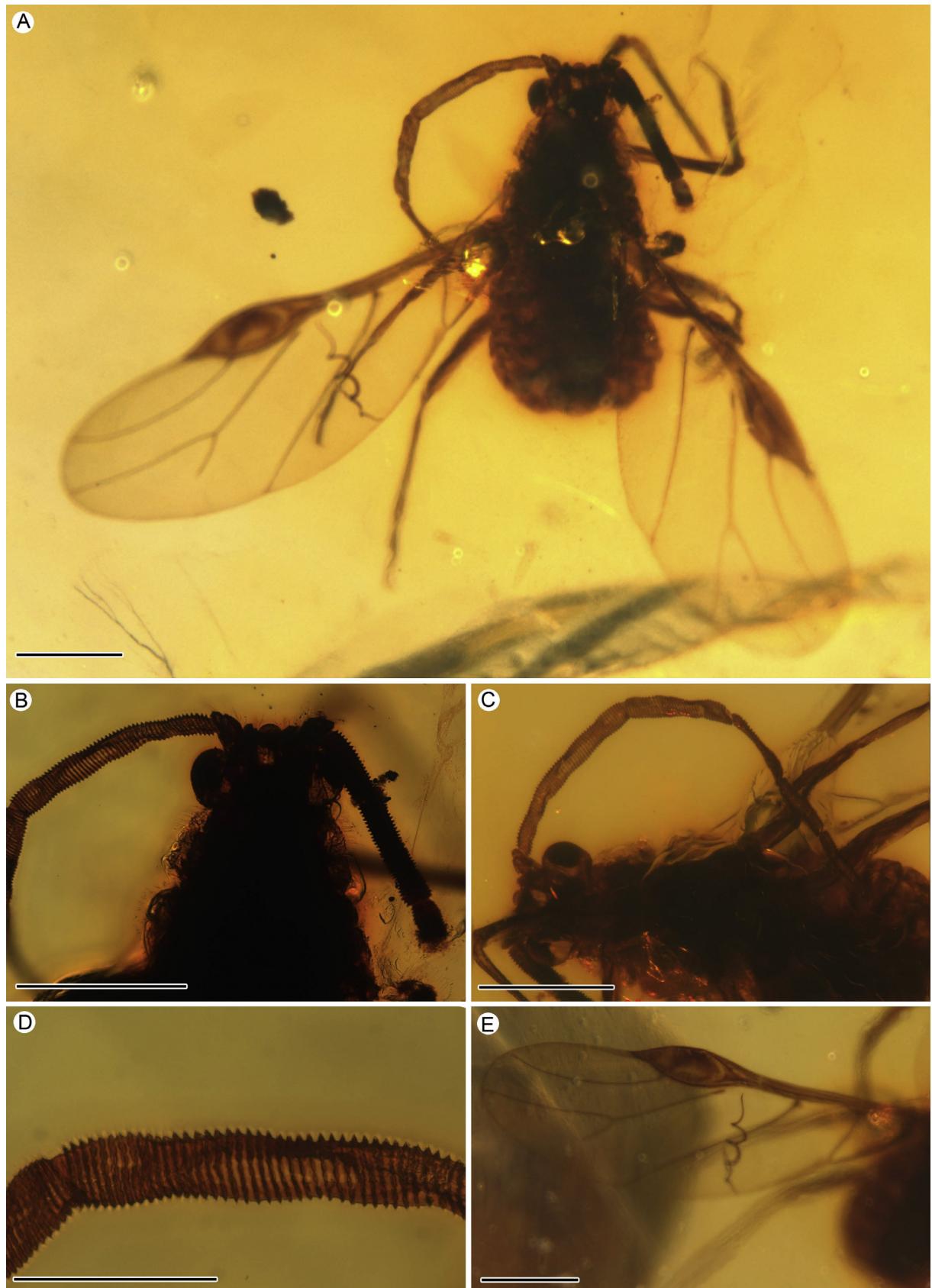


Fig. 4. *Vasteantenatus hukawngi* sp. nov. Paratypes, NIGP167705, female. A. Dorsal view. B. Head and antennae, dorsal view, under Zeiss Axio Imager 2 compound microscope. C. Left antenna. D. Antennal segment IV with transverse rows of rhinaria, under Zeiss Axio Imager 2 compound microscope. E. Forewing. Scale bar in picture A-C, E = 0.5 mm, D = 0.2 mm.

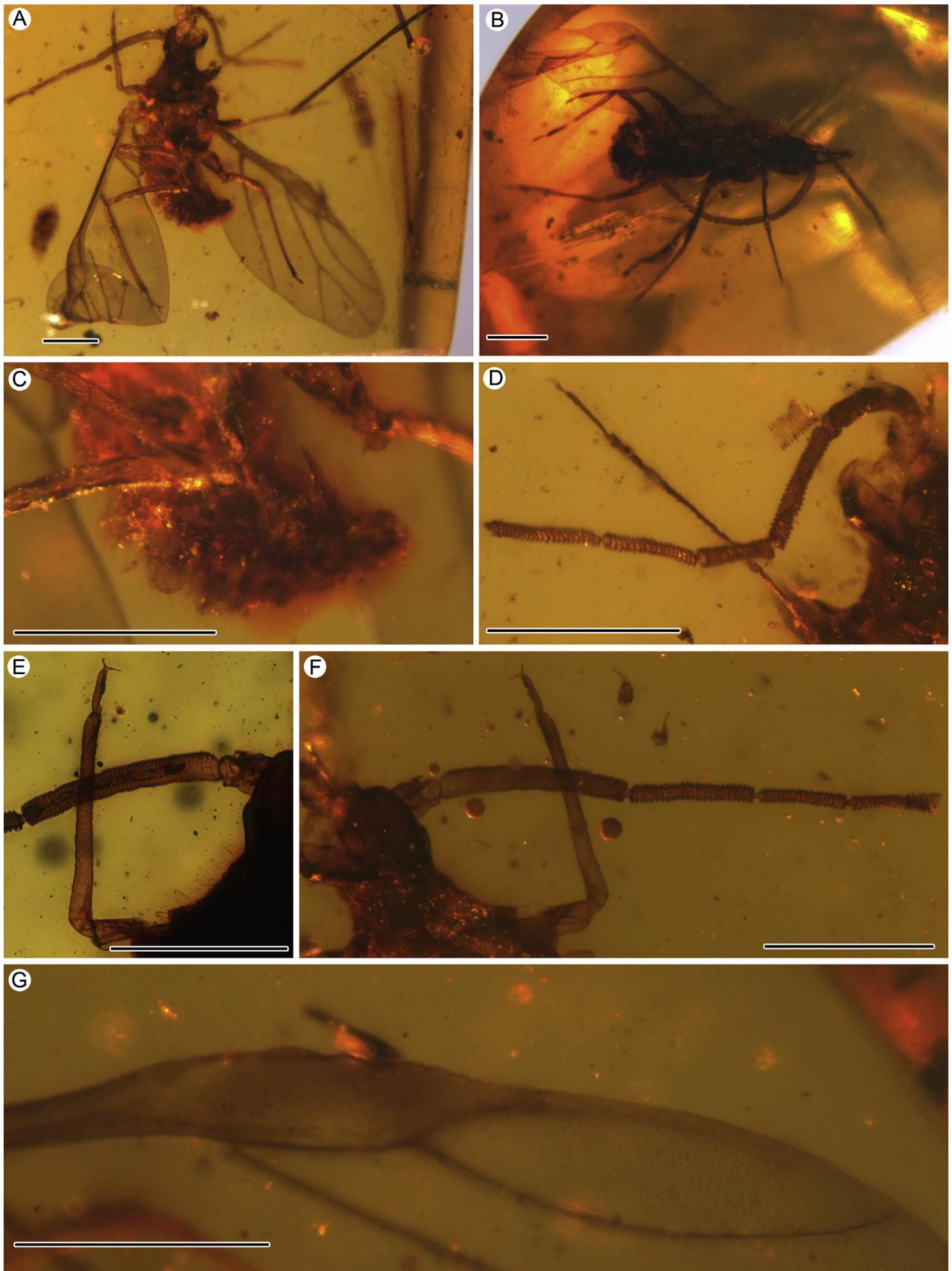


Fig. 5. *Vasteantenatus hukawngi* sp. nov. A. Paratype, NIGP167706, male, ventral view. B Paratype, NIGP167707, male, ventral view. NIGP167706. C. Apical part of abdomen, phallus. D. Left antenna. E. Antennal segment III with transverse rows of rhinaria. F. Right antenna. G. Forewing: pterostigma, veins Rs, M. Scale bar in picture A-G 0.5 mm.

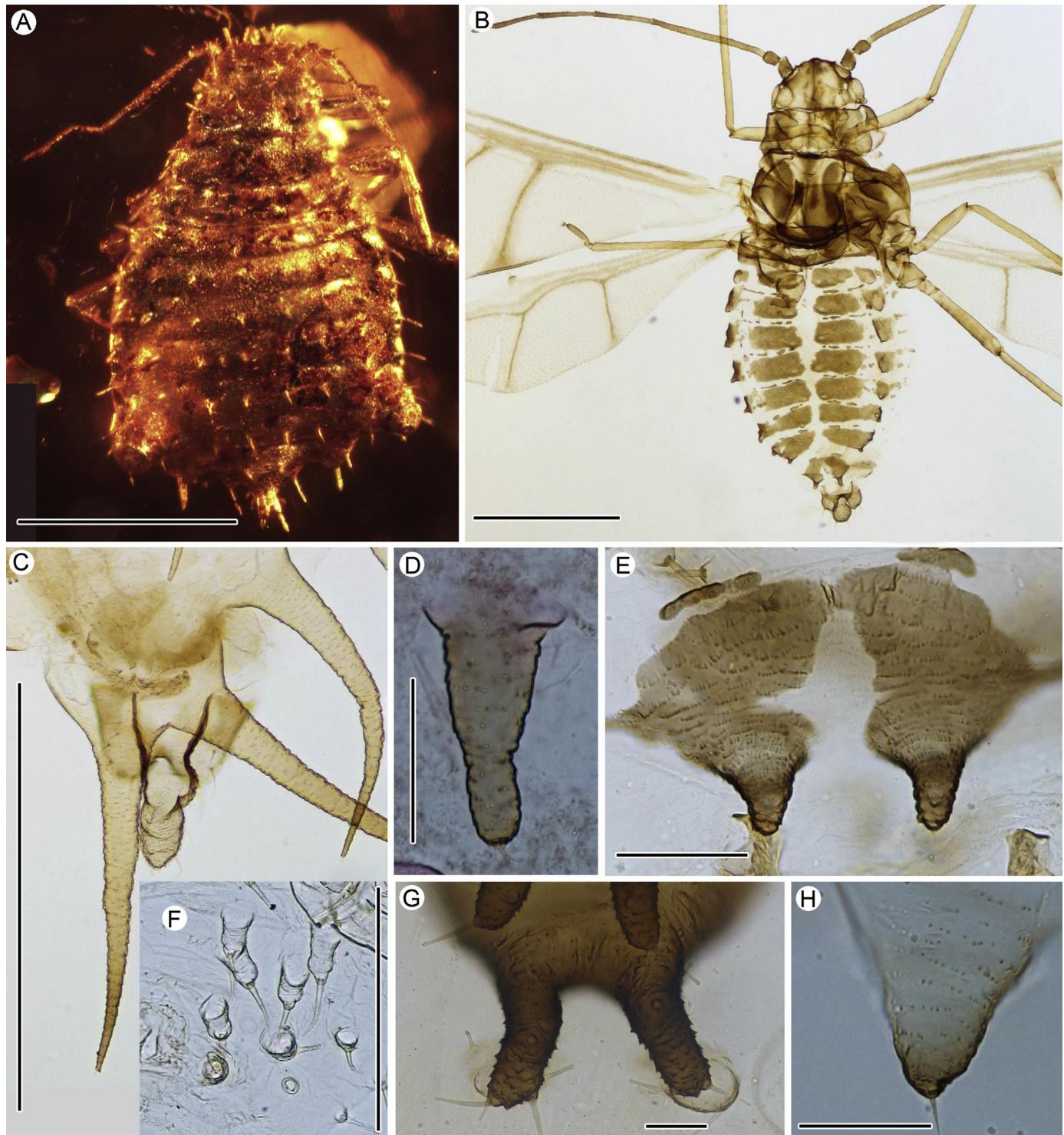


Fig. 6. A. *Gondvanaphis estephani* aptera dorsal view, setae. B. *Ctenocallis israelica* Hille Ris Lambers, 1954; alate, dorsal view, projections. C. *Lizerus cermelii* Quednau, 1974; aptera, apical part of abdomen, projections. D. *Pterocallis nigrirostrata* (Shinji 1941); alata, projection. E. *Ctenocallis izralica*; alata, projections. F. *Dasyaphis rhusae* (Shinji 1922); nymph, setae. G. *Tuberculatus quercicola* (Matsumura, 1917): alata, projections. H. *Tinocallis ulmifolii* (Monell, 1879) alata, projection. Scale bar in picture A-C = 0.5 mm, D-E, G-H = 0.5 mm, F 0.25 mm.

aphid groups with the usage of various microscopy techniques (Wieczorek et al., 2011, 2012; Depa et al., 2015). In recent aphids phallus is situated ventrally on the abdominal sternite IX and is composed of a sclerotized basal part and a membranous apical

part—aedeagus (usually not visible in slide-mounted specimens). The basal part is composed of a pair of various-shaped, partially sclerotized lobes (Fig. 7A). Laterally of the phallus, there is a pair of setose parameres (Wieczorek et al., 2011; Kanturski et al., 2015). In

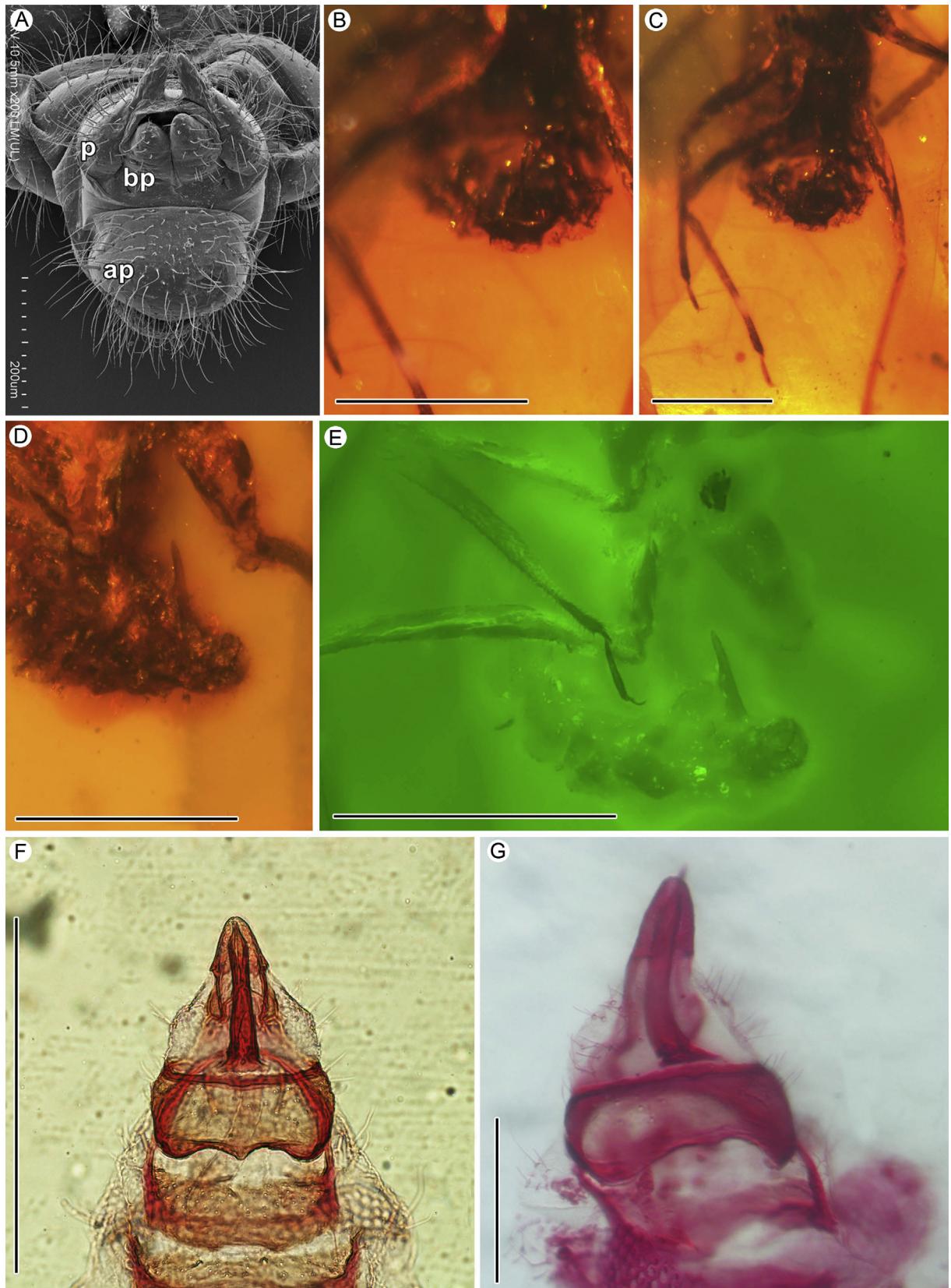


Fig. 7. Apical ventral parts of male abdomen. A. *Stomaphis quercus* (Linnaeus, 1758), SEM Dr. M. Kanturski. B-C *Vasteantenenus hukawngi* sp. nov. NIGP167707. D. *Vasteantenenus hukawngi* sp. nov. NIGP167706. E. NIGP167706 under Zeiss Axio Imager 2 compound microscope using fluorescence as light source. F-G *Orthezia urticae* (Linnaeus, 1758). Scale bar in picture B-F = 0.5 mm, G = 0.1 mm.

the new species, as in *Burmitaphis prolatum*, only the sclerotized basal phallus part is present (aedeagus invisible). Contrary to recent males, that part is very long, tubular in shape and paired basal parts adhere to each other. It is evident in *Burmitaphis prolatum*, but in *Vasteantenatus hukawngi* these structures seem to have fused together (Fig. 7B–E). Such phallus base is more reminiscent of the structure in coccids (Coccoidea) (Fig. 7F and G) than in recent aphids, where they are short, usually spade-like in shape and loosely connected (Fig. 7E). A copulatory organ also includes parameres. In *Vasteantenatus hukawngi* parameres are invisible, most likely strongly reduced and in *Burmitaphis prolatum* they are well-developed, 4x shorter than the basal part.

5. Concluding remarks

Although aphids from Burmese amber represent only three families [Burmaphididae (most of the described taxa), Isolitaphidae and Parvaverrucosidae], they are endowed with specific morphological characters which are not found in other members of the group either in fossil or recent forms: untypical antennae in *Parvaverrucosa annulata* (Poinar and Brown, 2005) and *Isolaphis prolatantennus* Poinar, 2017; very abundant club-shaped setae in *Echinoaphis penalverii* gen. et sp. nov.; lack of rostrum in many examined insects. Alike male coccids (Gullan and Kosztarab, 1997), some aphid morphs may not feed. Moreover, in inclusions from Burmese amber males occurred more frequently than in recent aphid populations, where they are only seasonal (usually at the end of summer and the beginning of autumn in temperate zone; the production of sexual forms is related to the drop of temperature and the photoperiod; Kawada, 1987). It relates a group-specific life cycle and holocyclic mode dominating in recent aphids. From the ancestral cyclically parthenogenetic life cycle, ~3% of aphid species have become secondarily entirely asexual, whereas numerous species (>30% of a sample of 270) show coexistence of cyclical parthenogens (Simon et al., 2002).

Accordingly, there seem to be two ways to explain the phenomenon. It can be assumed that alate males occurred throughout vegetation season in the Burmese Cretaceous forest. This however, would stand in stark contrast to our understanding of the biology of recent aphids in the tropics. Most aphid species there are anholocyclic (have no sex generation). Also in the families which became adapted to this climatic zone (Hormaphididae, Greenideidae), males occur seasonally (Ghosh, 1987; Ghosh and Agarwala, 1993; Chena et al., 2014). On the other hand, this phenomenon may be interpreted in a taphonomic way: it seems possible that there was a correlation between the occurrence of a sex generation in Burmaphididae and the seasonal abundance of the resin which would favour aphid inclusions. This would also confirm the thesis that the Burmese Cretaceous forest was unique as in no other amber has such a phenomenon been observed (Heie and Wegierek, 2011).

Both, the reported morphological characters, as well as the bionomy suggest that the Burmese aphid fauna is quite unique, which may be connected with specific adaptations to warm, tropical forest situated very close to the equator (paleolatitude 12°; Zherikhin and Ross, 2000; Grimaldi et al., 2002). According to Grimaldi et al. (2002) this amber was formed under conditions that were probably more tropical than any other major deposit of Cretaceous amber.

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References

- Chena, J., Jiang, L.Y., Qiao, G.X., 2014. Hormaphidinae (Hemiptera: Aphididae), with comments on the evolution of galls. *Cladistics* 30, 26–66. <https://doi.org/10.1111/cla.12024>.
- Depa, Ł., Kanturski, M., Junkiert, Ł., Wieczorek, K., 2015. Giant females vs dwarfish males of the genus *Stomaphis* Walker (Hemiptera: Aphididae) – an aphid example of the ongoing course to permanent parthenogenesis? *Arthropod systematics & phylogeny* 73, 19–40.
- von Dohlen, C.D., Rowe, C.A., Heie, O.E., 2006. A test of morphological hypotheses for tribal and subtribal relationships of Aphidinae (Insecta: Hemiptera: Aphididae) using DNA sequences. *Molecular Phylogenetics and Evolution* 38, 316–329. <https://doi.org/10.1016/j.ympev.2005.04.035>.
- Ghosh, A.K., 1987. Biotaxonomy of Greenideinae (Homoptera: Aphidoidea). In: Holman, J., Pelikán, J., Dixon, A.F.G., Weismann, L. (Eds.), Population structure, genetics and taxonomy of aphids and thysanoptera. Proceedings of the International Symposia held at Smolenice Czechoslovakia 9–14 September 1985, pp. 273–292.
- Ghosh, A.K., Agarwala, B.K., 1993. The fauna of India and the adjacent countries. In: Homoptera: Aphidoidea – Part 6, subfamily Greenideinae. Survey of India, Calcutta, p. 330.
- Grimaldi, D.A., Engel, M.S., Nascimbene, P.C., 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates* 3361, 1–71. [https://doi.org/10.1206/0003-0082\(2002\)361<0001:FCAFMB>2.0.CO;2](https://doi.org/10.1206/0003-0082(2002)361<0001:FCAFMB>2.0.CO;2).
- Gullan, P.J., Kosztarab, M., 1997. Adaptations in scale insects. *Annual Review of Entomology* 42, 23–50.
- Heie, O.E., 1987. Palaeontology and phylogeny. In: Minks, A.K., Harrewijn, P. (Eds.), *Aphids: their biology, natural enemies and control*, vol. 2A. Elsevier Science Publishers, B.V., Amsterdam, pp. 367–391.
- Heie, O.E., Azar, D., 2000. Two new species of aphids found in Lebanese amber and a Revision of the family Tajmyraphididae Kononova, 1975 (Hemiptera: Sternorrhyncha). *Annals of the Entomological Society of America* 93, 1222–1225.
- Heie, O.E., Wegierek, P., 2011. A list of fossil aphids (Hemiptera, Sternorrhyncha, Aphidomorpha). *Monographs of the Upper Silesian Museum* 6, 1–82.
- Kania, I., Wang, B., Szwedo, J., 2015. *Dicranoptyla* Osten Sacken, 1860 (Diptera, Limoniidae) from the earliest Cenomanian Burmese amber. *Cretaceous Research* 52, 522–530.
- Kania, I., Wegierek, P., 2013. Evolution aspects of Ellinaphididae and phylogeny relationship of new Early Cretaceous aphids from Bon-Tsagaan locality (Mongolia). *Cretaceous Research* 44, 166–182. <https://doi.org/10.1016/j.cretres.2013.04.006>.
- Kanturski, M., Karcz, J., Wieczorek, K., 2015. Morphology of the European species of the aphid genus *Eulachnus* (Hemiptera: Aphididae: Lachninae) – a SEM comparative and integrative study. *Micron* 76, 23–36.
- Kawada, K., 1987. Polymorphism and morph determination. In: Minks, A.K., Harrewijn, P. (Eds.), *Aphids: their biology, natural enemies and control*, volume 2A. Elsevier Science Publishers, B.V., Amsterdam, pp. 255–268.
- Liu, X., Qiao, G., Yao, Y., Ren, D., 2018. New fossil Juraphididae (Hemiptera: Aphidomorpha) from Burmese amber with phylogeny of the family. *Cretaceous Research* 84, 420–425. <https://doi.org/10.1016/j.cretres.2017.11.009>.
- Maksoud, S., Azara, D., Graniere, B., Gézeba, R., 2016. New data on the age of the Lower Cretaceous amber outcrops of Lebanon. *Palaeoworld*. <https://doi.org/10.1016/j.palwor.2016.03.003>.
- McKellar, R., Wolfe, A.P., 2010. Canadian amber. In: Penney, D. (Ed.), *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, pp. 96–113.
- Nováková, E., Hypša, V., Klein, J., Footit, R.G., von Dohlen, C.D., Moran, N.A., 2013. Reconstructing the phylogeny of aphids (Hemiptera: Aphididae) using DNA of the obligate symbiont *Buchnera aphidicola*. *Molecular Phylogenetics and Evolution* 68, 42–54. <https://doi.org/10.1016/j.ympev.2013.03.016>.
- Peñalver, E., Wegierek, P., 2008. New Tajmyraphididae in Spanish amber. A new genus and species of the family Tajmyraphididae (Hemiptera: Sternorrhyncha) in Early Cretaceous amber from Peñacerrada I (Spain). *Alavesia* 2, 187–192.
- Poinar Jr., G., 2017. A new family of aphids (Hemiptera: Aphidoidea) in mid-Cretaceous Myanmar amber. *Cretaceous Research* 75, 7–10. <https://doi.org/10.1016/j.cretres.2017.03.013>.
- Poinar Jr., G., 2018. A new genus and species of aphids, *Tanyaulus caudisetula* gen. et sp. nov. (Hemiptera: Aphidoidea: Burmitaphididae) in mid-Cretaceous Myanmar amber. *Cretaceous Research* 82, 36–39. <https://doi.org/10.1016/j.cretres.2017.10.025>.
- Poinar Jr., G., Brown, A.E., 2005. New Aphidoidea (Hemiptera: Sternorrhyncha) in Burmese amber. *Proceedings of the Entomological Society of Washington* 107, 835–845.
- Poinar, G., Brown, A.E., 2006. Remarks on *Parvaverucosa annulata* (= *Verrucosa annulata* Poinar and Brown 2005) (Hemiptera: Sternorrhyncha: Aphidoidea). *Proceedings of the Entomological Society of Washington* 108 (3), 734–735.

- Rasnitsyn, A.P., Bashkuev, A.S., Kopylov, D.S., Lukashevich, E.D., Ponomarenko, A.G., Popov, YuA., Rasnitsyn, D.A., Ryzhkova, O.V., Sidorchuk, E.A., Sukatsheva, I.D., Vorontsov, D.D., 2016. Sequence and scale of changes in the terrestrial biota during the Cretaceous (based on materials from fossil resins). *Cretaceous Research* 61, 234–255.
- Ross, A.J., Mellish, C., York, P., Crigton, B., 2010. Burmese amber. In: Penney, D. (Ed.), *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, pp. 208–235.
- Simon, J.C., Rispe, C., Sunnucks, P., 2002. Ecology and evolution of sex in aphids. *Trends in Ecology & Evolution* 17, 34–39.
- Shaposhnikov, G.K., 1979. Oligomerization, polymerization and organization of morphological structures in the evolution of aphids (Homoptera, Aphidinea). *Entomologicheskoe Obozrenie* 58, 718–741 [in Russian].
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* 37, 155–163.
- Wegierek, P., Źyla, D., Homan, A., Cai, C.H., Huang, D., 2017. New genus and species of the extinct aphid family Szelegiewicziidae and their implications for aphid evolution. *The Science of Nature – Naturwissenschaften*. <https://doi.org/10.1007/s00114-017-1517-x>.
- Wieczorek, K., Piachno, B.J., Świątek, P., 2011. A comparative morphology of male genitalia of Aphidiidae (Insecta, Hemiptera): part 1. *Zoomorphology* 130, 289–303.
- Wieczorek, K., Piachno, B.J., Świątek, P., 2012. A comparative morphology of male genitalia of Aphidiidae (Insecta, Hemiptera): part 2. *Zoomorphology* 131, 303–324.
- Zheng, D., Nel, A., Chang, S.-C., Jarzembski, E.A., Zhuo, D., Wang, B., 2018. Paracoryphagrionidae fam. nov., a pseudostigmatoid damselfly from mid-Cretaceous Burmese amber showing regular series of triangular cells (Odonata: Zygoptera: Coenagrionidae). *Cretaceous Research* 81, 93–97. <https://doi.org/10.1016/j.cretres.2017.10.005>.
- Zherikhin, V.V., Ross, A.J., 2000. A review of the history, geology and age of Burmese amber (Burmite). *Bulletin of the Natural History Museum, Geology* 56, 3–10.