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ORIGINAL ARTICLE

First fossil representative of the tribe Amphignomini (Hemiptera: Fulgoromorpha: Achilidae) from mid-Cretaceous Kachin amber and its significance

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Key words. *Amphignokachinia* gen. n., *Amphignokachinia subversa* sp. n., *Amphignoma*, Burmese amber, inclusion, planthopper, taxonomy

Abstract. A new genus *Amphignokachinia* Brysz & Szwedo, gen. n. and species *Amphignokachinia subversa* Brysz & Szwedo, sp. n. of Achilidae (Hemiptera) planthoppers of the tribe Amphignomini are described. It is the second genus and first fossil representative of the tribe Amphignomini coming from the Cenomanian amber in Kachin State, Myanmar. Diagnosis of the tribe is revised and its position in respect of fossils in the family Achilidae is discussed.

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INTRODUCTION

Planthoppers of the family Achilidae Stål, 1866 are commonly present in a variety of fossilized material, but remain predominantly undescribed and unexplored. Most specimens originate from amber inclusions (e.g., Miocene Dominican amber, Eocene Baltic amber, Early Upper Cretaceous Kachin amber) and a few adpression fossils (e.g. Crato Formation of Brazil, Bembridge Marls of Bouldnor Formation, Isle of Wight, U.K.). New fossil findings have elucidated the evolutionary history of this family and a revision of its classification is due.

One such discovery is the first occurrence of a representative of the tribe Amphignomini Emeljanov, 1991, belonging to the subfamily Myconinae Fennah, 1950. This tribe includes the monotypic Asian *Amphignoma* Emeljanov, 1991, containing only *A. corybas* Emeljanov, 1991, an extremely rare species recorded only from Mai Chou, Hòa Bình district, Ha Son Binh province in northern Vietnam, which has not been recorded again since its original description. A representative of Amphignomini found in the mid-Cretaceous period is significant because it is the first record of fossil Achilidae from that period that also represents an extant tribe being present in such an old period of time as Achilidae fossils are typically recovered from the Eocene.

MATERIAL AND METHODS

Fossil material examined in this study is in the museum collection Bayerische Staatssammlung für Paläontologie in Munich. Comparative material was loaned from the Zoological Institute, Russian Academy of Sciences, St. Petersburg. No changes were made to the material without the approval of the collections' curators. To avoid any confusion and misunderstanding, all authors declare that the fossil reported in this study was not involved in armed conflict and ethnic strife in Myanmar. The fossil specimen is deposited permanently in a public collection, in full compliance with the International Code of Zoological Nomenclature (ICZN, 1999), the Statement of the International Palaeoentomological Society (Szwedo et al., 2020) and policies presented by Haug et al. (2020). Although Kachin amber has been mined and traded for thousand years (Laufer, 1906; Zherikhin & Ross, 2000; So, 2013), most organismal inclusions of valuable scientific significance have only been described in recent years (Ross, 2022). The amber from Kachin is giving new insights into the complex development of modern fauna during mid-Cretaceous biotic re-

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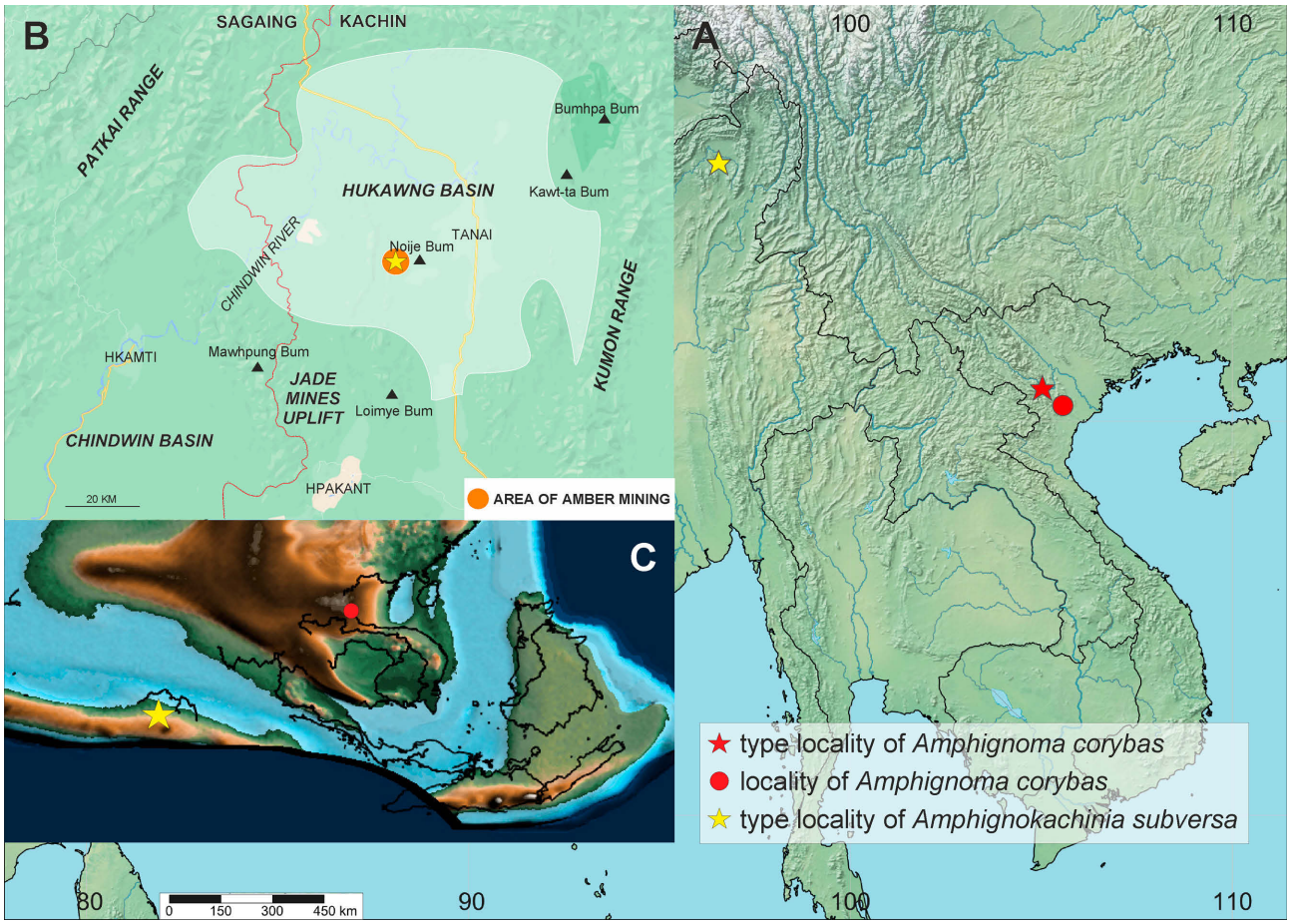

Fig. 1. Maps showing the localities of where *Amphignoma corybas* and *Amphignokachinia subversa* gen. et sp. n. were collected. A – map of S–E Asia with localities marked (generated by https://www.simplemappr.net/, Projection: World Mercator, modified); B – map of Hukawng Valley in N. Myanmar (after Ridd et al., 2018, based on Google Maps, modified); C – map of S–E Asia in Early Cretaceous 101.8 Ma. (after Scotese, 2013, modified).

organization (Szwedo & Nel, 2015), as this amber preserves the most diverse Cretaceous biota, including plants, arthropods, bivalves, ammonites, reptiles, plus even birds and dinosaurs and provides significant material for understanding the Cretaceous Terrestrial Revolution (Jiang et al., 2018).

The fossil studied comes from a mid-Cretaceous (Cenomanian, Upper Cretaceous) amber mine, near the town of Danai (Tanai) (26°21′33.41″N, 96°43′11.88″E; palaeolatitude 5.0 ± 4.7°S) in the Hukawng Valley of Myanmar (Fig. 1B–C) (Kania et al., 2015; Thu & Zaw, 2017; Jiang et al., 2019; Westerweel et al., 2019), which was the main source of amber in the country until 2017. The age of Kachin amber has been established as early Cenomanian (98.79 ± 0.62 Ma) based on radiometric U-Pb analyses of zircons from volcanoclastic amber-bearing sediments (Shi et al., 2012). Some ammonites found within in these sediments indicate a Late Albian-Early Cenomanian age (Cruickshank & Ko, 2003; Yu et al., 2019). As it appears mineralogically distinct from other types of amber, that from Kachin was named burmite by Helm (1892, 1893).

Extant material consists of two specimens from the collection of Zoological Institute, Russian Academy of Sciences, St. Petersburg:

Holotype female: White label [Vietnam, Mai Chou / prov. Ha Son Binh / forest, 1.11.1990 / Belokobylskij]; red label, handwritten [Amphignoma / corybas gen. sp. nov. / Emeljanov det.]; red label [printed: Holotypus / handwritten: Amphignoma corybas / Emeljanov 1991].

Additional specimen (sex not determined): White labels [handwritten: Vietnam, Hoa Binh prov. / Yen Thuy distr. Da Phoc / 100 m / 3–4.5.2002 Belokobylsky]; [handwritten: Amphignoma / corybas / printed: Emeljanov det.].

Material was examined using standard entomological and palaeoentomological methods using a stereoscopic microscope. For more precise observations, the amber piece was placed under a thin layer of resin-friendly sugar solution and covered with a microscope slide. Observations were made in the Laboratory of Evolutionary Entomology and Museum of Amber Inclusions, Department of Invertebrate Zoology and Parasitology, University of Gdańsk, using Olympus SZ61 and SZX10 stereoscopic microscopes. Photographs were taken using an Olympus EP50 camera attached to an Olympus SZ61 microscope with EPview Version 3.7.2 (Olympus Soft Imaging Solutions GmbH freeware). Photographs were readjusted using CorelDRAW X7 software (Corel Corporation). Drawings were made with the aid of a camera lucida attached to the Olympus SZH10 microscope.

General morphological terminology used herein follows Anufriev & Emeljanov (1988) and Asche (2015), while the venation terminology follows Nel et al. (2012) and Bourgoin et al. (2015). Differences in terminology used in the Emeljanov's descriptions (Emeljanov, 1991, 1992) are as follows: corypha = vertex; metopa = frons.

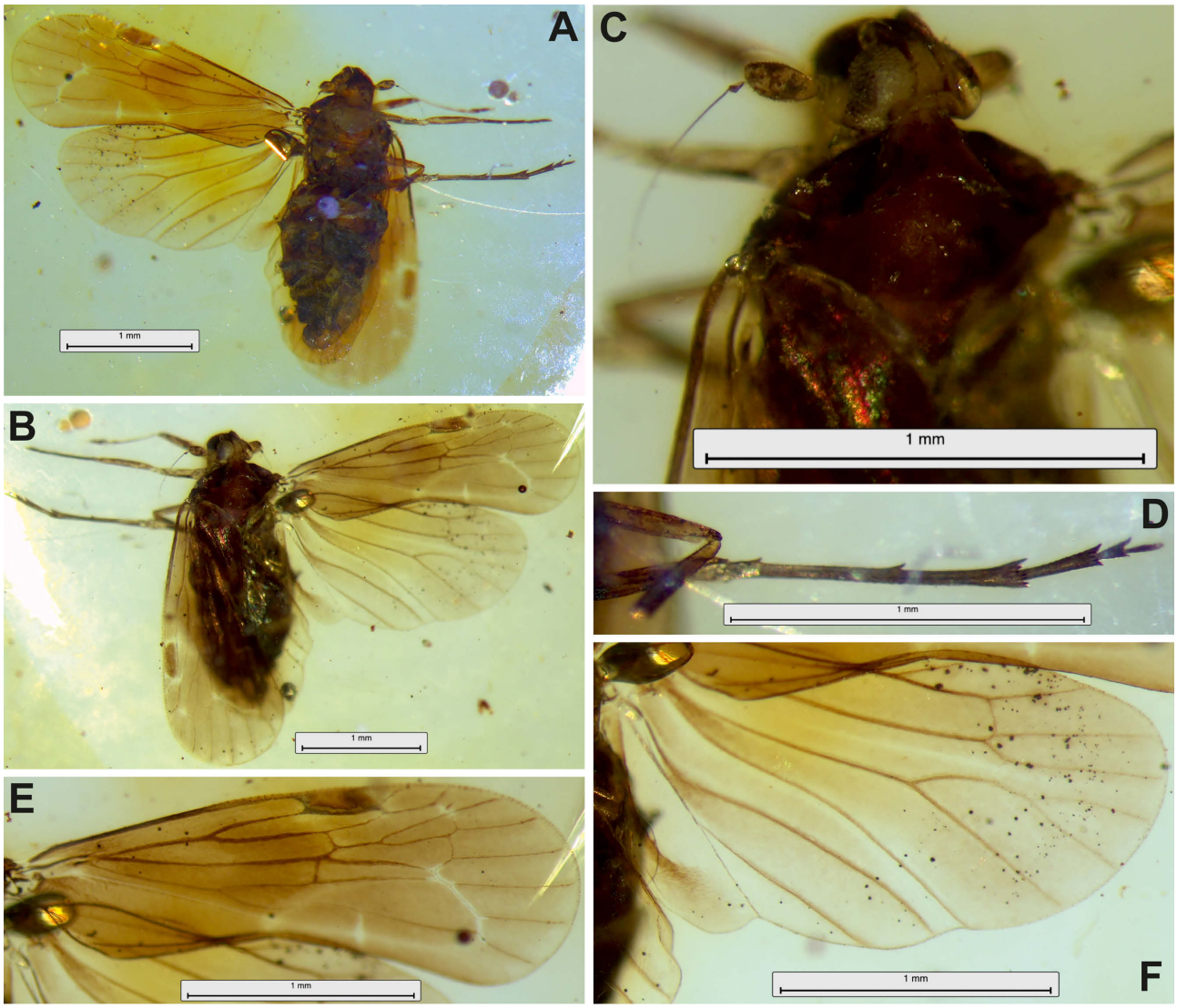

Fig. 2. *Amphignokachinia subversa* gen. et sp. n. A – body in ventral view; B – body in dorsal view; C – anterior portion of body in dorsal view; D – right metaleg; E – right forewing; F – right hind wing.

SYSTEMATICS

Order Hemiptera Linnaeus, 1758

Suborder Fulgoromorpha Evans, 1946

Superfamily Fulgoroidea Latreille, 1807

Family Achilidae Stål, 1866

Subfamily Myconinae Fennah, 1950

Tribe Amphignomini Emeljanov, 1991

Type genus. *Amphignoma* Emeljanov, 1991; by original designation and monotypy.

Original diagnosis (after Emeljanov, 1991, not the imprecise 1992 English translation in *Entomol. Rev*. **71**: 53–73): Genae with subantennal carinae; postclypeus broad, slightly offset from lora, in the same line as lateral carinae of frons (metopa). Mesonotum with median carina only, lateral carinae absent. Metatibia with 2 lateral spines [including femorotibial (subgenual) one], metatarsi with apical teeth without subapical setae. Both pairs of wings with nodal fracture. Hind wings with arculus, but without basal cell, with unique uninterrupted line of veins running across wing in nodal region including crossveins and sections of longitudinal veins from nodus to fork in CuA.

Revised diagnosis. Head capsule with genae with subantennal carina developed; suture between gena and loral plate fully developed. Rostrum short, not reaching metacoxae. Pronotum with triangular disc prolonged and reaching vertex. Mesonotum without lateral carinae. Tegmen with well-developed tornus, with sclerotization in area of pterostigma; branch CuA_1 forked on membrane. Hind wing with thickened vein A_2 not reaching wing margin and curving arcuately medially; median fold not reaching margin of hind wing, not crossing line of transverse veinlets. Metatibia with 2 lateral teeth (including subgenual one); metatarsomeres without subapical setae.

Composition. *Amphignoma* Emeljanov, 1991 [Extant; Vietnam] (Figs 1A and C, 3C–F, 4C, D, 5A), *Amphignokachinia* Brysz et Szwedo, gen. n. [Cenomanian, Upper Cretaceous; Kachin amber, Myanmar] (Figs 1, 2, 3A, B, 4A, B, 5B).

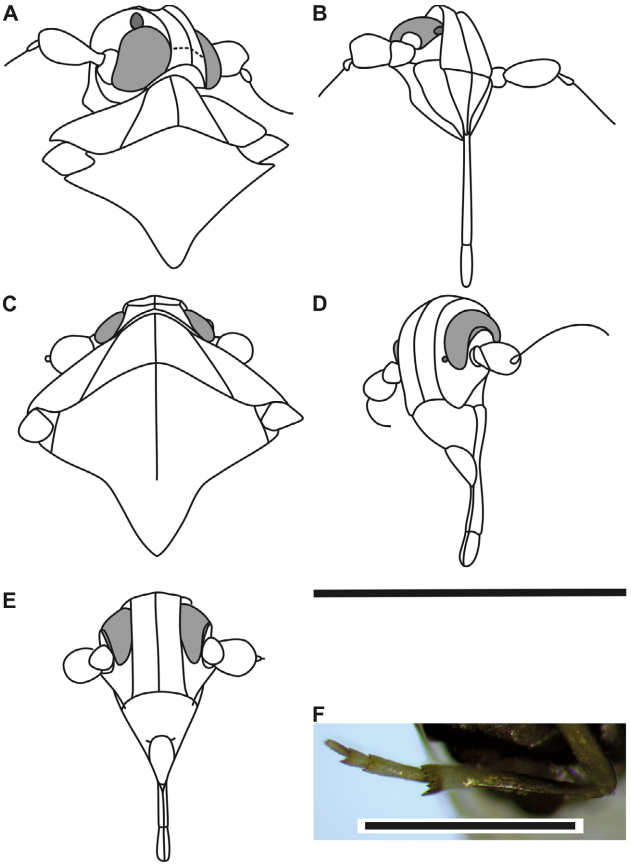

Fig. 3. Species of Amphignomini. A – *Amphignokachinia subversa* gen. et sp. n., anterior part of body in dorsal view; B – *A. subversa*, head capsule in frontolateral view; C – *Amphignoma corybas*, anterior portion of body in dorsal view; D–E – *A. corybas*, head capsule in frontolateral and frontal view; F – *A. corybas*, metaleg. C–E – after Emeljanov, 1991, modified. Scale 1 mm.

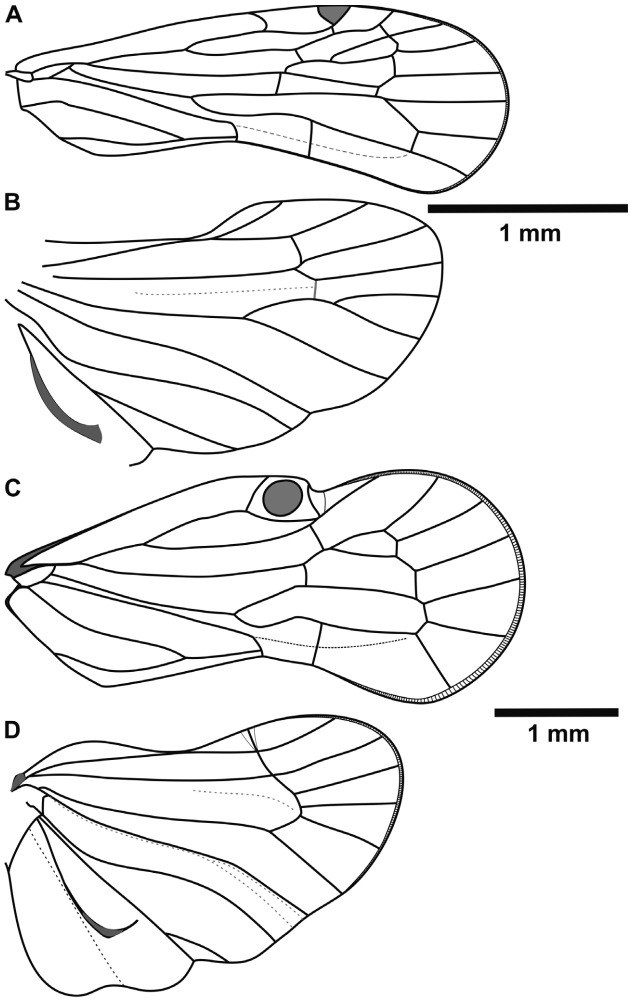

Fig. 4. Wing venation of Amphignomini: A – *Amphignokachinia subversa* gen. et sp. n., tegmen; B – *A. subversa*, hind wing; C – *Amphignoma corybas*, tegmen; D – *A. corybas*, hind wing.

Genus *Amphignokachinia* Brysz & Szwedo, gen. n.

ZooBank taxon LSID:
806246A0-C2BE-44C3-A379-D246DA089F4D

Type species. *Amphignokachinia subversa* sp. n.; here designated.

Etymology. Genus name derived from first genus of the tribe *Amphignoma* and Kachin – name of the region of origin of this type of amber. Gender: feminine.

Diagnosis. Vertex rectangular with anterior margin at ⅓ of length of the compound eye (vertex arcuate, with anterior margin in front of compound eye in *Amphignoma*). Frons subhexagonal, ellipsoid in shape (subquadrate, with straight lateral margins in *Amphignoma*), with widest part at level of antennae and frontoclypeal suture (margins subparallel, not widened in *Amphignoma*). Gena without elevated upper part (with elevated upper part bearing antennal fovea in *Amphignoma*). Postclypeus with both median and lateral carinae (median carina absent, lateral carinae curved outwardly in *Amphignoma*), narrower than frons (wider than frons in *Amphignoma*). Antenna with pedicel massive and elongated, subellipsoidal (massive and subglobose in *Amphignoma*). Width of pronotal disc ~⅔ of mesonotum width (more than ¾ in *Amphignoma*). Mesonotum not carinate (with median carina reaching scutellum in *Amphignoma*). Fore wing (tegmen) membranous, with sclerotization covering whole pterostigmal area (concave and round sclerotization in *Amphignoma*); C2 cell closed (open in *Amphignoma*); cell C5 lanceolate and enlarged apically (not lanceolate, with borders subparallel in *Amphignoma*); ScP+R and CuA fork at the same level (ScP+R fork very basal to CuA fork in *Amphignoma*); RA and RP connected apically by a short *ir* veinlet (RA with single terminal connected to single RP in *Amphignoma*). Hind wing with regular ScP+RA branch reaching margin well basal of hind wing apex (recurrent ScP+RA present as a part of continuous veins reaching across the wing from pterostigmal area to CuA vein in *Amphignoma*); fork in A_1 at half its length (fork at 4/5 of its length in *Amphignoma*). Legs elongated, slender (~20% longer than in *Amphignoma*).

Amphignokachinia subversa Brysz & Szwedo, sp. n.

ZooBank taxon LSID:
DF43BEC1-F75E-4775-9EAD-98676887C706

Figs 2A–F, 3A, B, 4A, B, 5B

Type specimen. Holotype, male. SNSB-BSPG 2021 XII 9 [BUB423], coll. Patrick Müller, Germany, deposited in Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany.

Etymology. Species name derived from Latin subversus, which means overturned, upset, overthrown. Specific epithet refers to the first incorrect identification of this specimen, which was deemed to represent another tribe of Achilidae.

Description

Habitus and coloration. Body flattened dorsoventrally, dark brown. Tegmen brown: darker in basal part, light-brown in apical part. Hind wings light-brown.

Measurements. Length 2.4 mm, length with wings 2.7 mm.

Head (Figs 2A–C, 3A, B) with compound eyes distinctly narrower than pronotum. Vertex with anterior margin barely distinguishable, at about ⅓ of the length of compound eyes, evenly becoming the frons, lateral margins elevated, subparallel, posterior margin shallowly arcuate, not elevated, reaching posterior ¼ of compound eyes; disc of vertex flat. Vertex measurements: median length 0.07 mm, lateral length 0.08 mm, width 0.09 mm, width with compound eyes 0.31 mm. Frons in mid line longer than clypeus, subhexagonally ellipsoidal, widest at the level of antennal bases, lateral margins carinately elevated, median carina present, elevated; disc on frons convex. Frons measurements: length 0.2 mm, maximum width 0.15 mm, width at vertex 0.08 mm, width at clypeus 0.13 mm. Frontoclypeal suture straight, concave relative to surfaces of frons and clypeus. Postclypeus convex; median and medio-lateral carinae present, the latter as a prolongation of lateral margins of frons; anteclypeus about twice as long as wide at base. Clypeus measurements: length 0.14 mm, width 0.11 mm.

Rostrum short, with apex slightly exceeding midcoxae; apical segment about 4× as long as wide; penultimate one twice as long as apical. Rostrum measurements: total length 0.47 mm, subapical segment length 0.32 mm, apical segment length 0.14 mm, apical segment width 0.03 mm. Suture between gena and loral plate fully developed. Compound eye large, convex, with antennal (subocular) indentation lacking ocelli, without subocular callosity; lateral ocellus at ½ of the height of compound eye. Antennal fovea slightly elevated, base of antenna below compound eye, at about half of its length; scapus short and annular; pedicel large and subovate, with rounded, convex sensory plates. Pedicel measurements: length 0.17 mm, width 0.09 mm. Flagellum with enlarged base, in total about 3 times as long as pedicel.

Thorax (Figs 2B, C, 3A). Pronotum narrow, with distinct median disc, delimited by lateromedian carinae diverging posteriad; median carina present, postocular carinae indistinct, pectoral area distinct, directed anteriorly; disc of pronotum subtriangular, with rounded anterior margin and concave, posterior margin not elevated, flat; anterior margin of pronotum reaching posterior ¼ of compound eye. Pronotum measurements: length 0.23 mm, width 0.6 mm, disc length 0.18 mm, disc width 0.33 mm. Mesonotum wider than long in mid line, without carinae; disc slightly convex, scutellum flat. Mesonotum measurements: length 0.44 mm, width 0.54 mm. Metanotum length 0.13 mm.

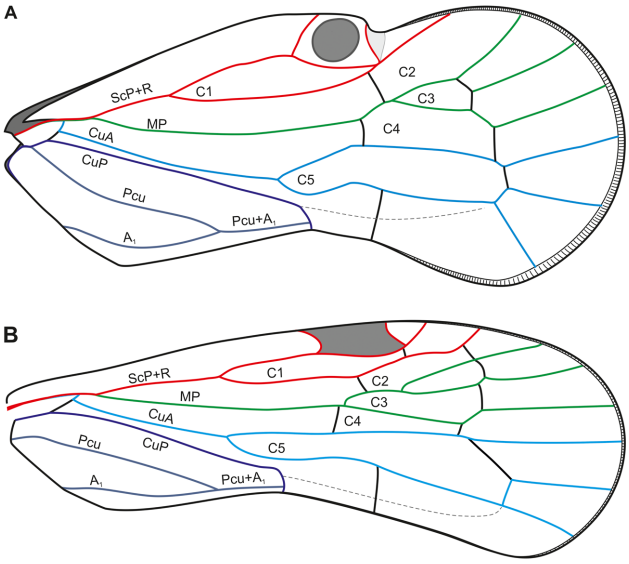

Fig. 5. Tegmen of Amphignomini with coloured veins and noted cells. A – *Amphignoma corybas*; B – *Amphignokachinia subversa* gen. et sp. n.

Legs (Fig. 2D). Procoxa about as long as profemur, carinate anteriorly, profemur slightly flattened, protibia subquadrate, slightly widening apically, about as long as profemur, protarsomeres of similar length, tarsal claws not enlarged, arolium wide. Proleg measurements: profemur length 0.44 mm, protibia length 0.32 mm, protarsus length 0.23 mm, basal protarsomere 0.07 mm, mid protarsomere 0.04 mm, apical protarsomere 0.12 mm, combined length of mid and apical protarsomeres 0.17 mm. Mesocoxa about as long as mesofemur, mesofemur slightly longer than profemur, mesotibia about as long as mesofemur (partly damaged), mesotarsomeres not preserved. Mesoleg measurements: mesofemur length 0.51 mm, mesotibia 0.49 mm. Metacoxa with short, acute meracantha, metatrochanter narrow, ring-like, metafemur flattened, about as long as mesofemur, metatibia elongate, slender, distinctly longer than metafemur, widened apically, with two lateral spines: subgenual one and one lateral placed apically at ½ of metatibia length, with row of 8 apical teeth; basal metatarsomere longer than combined length of mid and apical metatarsomeres, with slightly arcuate row of 6 apical teeth, devoid of subapical setae; mid metarsomere short, about as wide as long, with apical row of 6 teeth, devoid of subapical setae, apical metatarsomere about as long as mid metatarsomere, tarsal claws not enlarged, arolium widely lobate. Metaleg measurements: metafemur length 0.35 mm, metatibia 0.8 mm, metatarsus length 0.43 mm, basal metatarsomere length 0.22 mm, mid metatarsomere 0.09 mm, apical metatarsomere 0.12 mm, combined length of mid and apical metatarsomeres 0.21 mm.

Tegula (Figs 2B, C, 3A) large, flattened, bent medially, not carinated.

Tegmen (Figs 2A, B, E, 4A, 5B) membranous, with venation distinct, about 2.5 times as long as wide at widest point of membrane; corium narrower than membrane, apical half distinctly widened, clavus not exceeding half

of total length of tegmen; costal margin almost straight, anteroapical angle widely rounded, apex rounded, posteroapical angle angulated, tornus concave, posteroclaval margin straight; membrane makes up 52% of forewing length. Costal complex thickened, stem ScP+R+MP+CuA slightly arcuate at base, stem ScP+R+MP leaves basal cell by a very short common stalk, stem ScP+R forks at level of the junction of the claval veins; branch ScP+RA subparallel to costal margin, thickened, terminal ScP ($+RA_1$) recurrent, forks slightly apical of claval apex, two terminals of RA fork apically of the level of *icu* veinlet, RP with single terminal, reaching margin basally of anteroapical angle. Stem MP thickened basally, forks on membrane slightly apical of nodal *mp-cua* veinlet; branch MP_{1+2} forks again on membrane at the level of *ir* veinlet; branch MP_{3+4} single, reaching margin slightly basally of tegmen apex. Stem CuA with very short base, closing basal cell, directed anteriorly (zig-zagging), stem CuA leaving basal cell slightly arcuate, thickened, forks at same level of the fork in ScP+R; branch CuA_1 almost straight, reaching margin at apex of tegmen, branch CuA_2 curved at base posteriorly, then recurved medially and reaches margin before the posteroapical angle. Claval vein CuP straight, claval fold prolonged on membrane, intersecting *icu* veinlet, then curves medially. Clavus open, its apex blunt, claval veins Pcu and A_1 fused apically at half the length of clavus, slightly basal of the forks in the stems of ScP+R and CuA. Nodal veinlet *rp-mp*$_{1+2}$ apical of veinlet *mp-cua*$_1$; veinlet *ir* more apical, apical of *icu* veinlet, apical veinlets *rp-mp*$_1$, *imp* and *mp*$_{3+4}$-*cua*$_1$ on membrane stepwise, arcuate, veinlet *icua* more apical, oblique. Appendix transversely wrinkled, wider at costal margin, narrowing towards posteroapical angle. Costal cell about as wide as cell C1; cell C1 lanceolate, narrowed in apical half; cell C3 subhexagonal, widening posteriorly, shorter than cell C1; cell C5 narrow, lanceolate at base, then distinctly wider, about 1.5× as long as cell C1. Tegmina measurements: length 2.37 mm, width at clavus 0.63 mm; fore wing maximum width 0.9 mm; claval (CuP) length 0.95 mm, claval (A_2) length 0.74 mm; ScP+R stem length 0.42 mm, M stem length 0.84 mm, CuA stem length 0.5 mm; basal cell length 0.13 mm, width 0.04 mm; cell C1 length 0.63 mm, width 0.08 mm; cell C2 length 0.45 mm, width 0.08 mm; cell C3 length 0.48 mm, width 0.12 mm; cell C4 length 0.45 mm, width 0.09 mm; cell C5 length 0.94 mm, width 0.2 mm.

Hind wing (Figs 2F, 4B) membranous, smoky, with visible venation. Costal margin thickened and distinctly arcuate at base, concave at level of wing coupling lobe, then arcuate to angulated rounded anteroapical angle, widely arcuate to CuP incision, arcuate to anal lobe, anal lobe distinct, wide, with angulate posterior angle and arcuate posterior margin. Short common stalk ScP+R+MP forks at base; costal cell distinct, basal cell absent; stem ScP+R forks at level of coupling lobe, ScP+RA reaches margin well basal of anteroapical angle, RP reaches margin basally of anteroapical angle; stem MP forks at level of CuP incision, slightly basal of *rp-mp*$_{1+2}$ veinlet, branches MP_{1+2} and MP_{3+4} reach margin slightly below anteroapical angle; stem CuA slightly arcuate at base, forks slightly apical of ScP+R fork, well basal of MP fork; branch CuA_1 forks again, apical of MP fork, shallow incision where the slight sigmoid CuP reaches margin; Pcu strongly curved at base, distinctly arcuate with arc shifted towards CuP in apical section; A_1 straight at base, forks about ½ way along anal fold, A_{1a} reaches cubital margin at double the distance between terminal points CuP-Pcu; vein A_2 arcuate, with arc directed posteriorly, thickened, widely obsolete in apical section not reaching margin. Veinlet *mp*$_{3+4}$-*cua*$_1$ weak (light). Medial fold not intersecting level of veinlet *mp*$_{3+4}$-*cua*$_1$; cubitoposterior fold indistinct, parallel to CuP, not forked. Hind wing length 2.1 mm (Figs 1F and 3B).

Abdomen longer than wide, flattened; abdominal sternites not divided, not chevron-shaped; measurements: dorsal length 1.1 mm, ventral length 1.43 mm, width 0.83 mm. Terminalia damaged, likely male.

Age and occurrence. Cenomanian, early Upper Cretaceous; Kachin amber, Hukawng Valley, northern Burma/Myanmar.

DISCUSSION

Amphignomini Emeljanov, 1991 was originally defined by characters regarded as apomorphic for this tribe, namely: genae with subantennal carinae, broad postclypeus indistinctly separated from lora; mesonotum without lateral carinae; two lateral spines on mesotibia, metatarsi without subapical setae below apical row of teeth, both pairs of wings with nodal fracture; hind wings lacking 'arculus' (very basal section of CuA) and basal cell; uninterrupted line of veins running across wing in nodal region composed of sections of longitudinal veins and transverse veinlets; and a medial fold not intersecting transverse veinlet (Emeljanov, 1991, 1992). The head capsule with subantennal carina, or the enlargement of that part of the gena below the antennal fovea, is also present in some other planthoppers, for example in some Derbidae (presumed sister-group of Achilidae: Urban & Cryan, 2007), Delphacidae and Flatidae. In respect of Derbidae, the subantennal section of the head capsule in some taxa is often strongly modified to form prominent lobate structures (Emeljanov, 1995). The fusion of postclypeus with lora is rather exceptional, however it is also observed in a few other planthoppers, e.g., in some Flatidae: *Antillormenis* Fennah, 1942 and *Flatoidinus* Melichar, 1923. Mesonotum lacking lateral carinae is a feature rarely found in the Achilidae and only a few genera have such a feature, e.g., some *Rhotala* Walker, 1857 (Myconinae: Rhotalini), *Parelidiptera* Fennah, 1950 and *Flatchilus* Fennah, 1950 (Achilinae: Achilini) have obsolete mesonotal carinae, vestigial to absent. Indistinct or absent mesonotal carinae also occur exceptionally in other planthoppers, e.g., in some *Mnemosyne* Stål, 1866 (Cixiidae: Mnemosynini). Sclerotization of stigmata is a neglected subject. Stigmal areas in *Amphignoma* bear rounded, concave sclerotizations, while in *Amphignokachinia* Brysz & Szwedo, gen. n. the whole stigmal areas are sclerotized. In some other Achilidae they are partially modified by the presence of a few additional veins, concavities, incisions and breaks in costal margin, but these are rare.

Sigmoid CuA_2 is a feature shared by Amphignomini and Plectoderini, but the latter is not a monophyletic unit and requires careful revision. Metatibia with two lateral spines is a condition similar to that found in some Plectoderini and extinct Ptychoptilini (incertae sedis group, whose affiliation to Achilidae is questionable; paper in preparation). All other achilid tribes have either none, or three or more, lateral metatibial spines (Fennah, 1950; Emeljanov, 1991, 1992). The hind wing with thickened vein A_2 not reaching wing margin and curving arcuately medially is an autapomorphic character of the Amphignomini.

Considering that the only known fossil representative of the Amphignomini (*Amphignokachinia* Brysz & Szwedo, gen. n.) comes from the Cenomanian, Late Cretaceous amber of the Kachin State of northern Myanmar, and the only extant representative (*Amphignoma* Emeljanov, 1991) from north Vietnam, it could be postulated that Amphignomini is a relic group. With the record of this group spanning 100 million years the questions of its evolutionary origin and traits arise. Emeljanov (1992) placed Amphignomini as one of early branches of his Achilidae relationship tree, and finding a fossil in resin about 100 Ma old confirms the antiquity of the group and its possible current status as a group likely in the last stages of extinction.

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REFERENCES

Anufriev G.A. & Emeljanov A.F. 1988: Suborder Cicadinea (Auchenorrhyncha). In Ler P.A. (ed.): *Keys to the Insects of the Far East of the USSR. Vol. 2.* Nauka, Leningrad, pp. 12–495 [in Russian].

Asche M. 2015: The West Palaearctic Achilidae (Hemiptera, Fulgoromorpha: Fulgoroidea) – a review with description of five new species from the Mediterranean. — *Nova Supplementa Entomol.* **25**: 1–135.

Bourgoin T., Wang R.R., Asche M., Hoch H., Soulier-Perkins A., Stroiński A., Yap S. & Szwedo J. 2015: From micropterism to hyperpterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns of planthoppers (Hemiptera: Fulgoromorpha). — *Zoomorphology* **134**: 63–77.

Cruickshank R.D. & Ko K. 2003: Geology of an amber locality in the Hukawng Valley, Northern Myanmar. — *J. Asian Earth Sci.* **21**: 441–455.

Emeljanov A.F. 1991: To the problem of the limits and subdivisions of the family Achilidae (Homoptera, Cicadina). — *Entomol. Obozr.* **70**: 373–393 [in Russian].

Emeljanov A.F. 1992: Description of tribes of the subfamily Achilinae (Homoptera, Achilidae) and reconsideration of their composition. — *Entomol. Obozr.* **71**: 574–594 [in Russian].

Emeljanov A.F. 1995: On the problem of a system and a phylogeny of the family Derbidae. — *Entomol. Obozr.* **73**[1994]: 783–811 [in Russian].

Evans J.W. 1946: A natural classification of leaf-hoppers (Jassoidea, Hemiptera). Part 1. External morphology and systematic position. — *Trans. R. Entomol. Soc. Lond.* **96**: 47–60.

Fennah R.G. 1942: Notes on some West Indian Flatidae. — *Proc. Entomol. Soc. Wash.* **44**: 155–167.

Fennah R.G. 1950: A generic revision of the Achilidae (Homoptera: Fulgoroidea) with descriptions of new species. — *Bull. Br. Mus. Nat. Hist. (Entomol.)* **1**: 1–170.

Haug C., Reumer J.W., Haug J.T., Arillo A., Audo D., Azar D. & Reich M. 2020: Comment on the letter of the Society of Vertebrate Paleontology (SVP) dated April 21, 2020 regarding "Fossils from conflict zones and reproducibility of fossil-based scientific data": the importance of private collections. — *Paläontol. Z.* **94**: 413–429.

Helm O. 1892: On a new, fossil, amber-like resin occurring in Burma. — *Rec. Geol. Surv. India* **25**: 180–181.

Helm O. 1893: Further note on Burmite, a new amber-like fossil resin from Upper Burma. — *Rec. Geol. Surv. India* **26**: 61–64.

ICZN 1999: *International Code of Zoological Nomenclature. Fourth Edition.* International Trust for Zoological Nomenclature, c/o Natural History Museum, London, xxix+306 pp.

Jiang T., Szwedo J. & Wang B. 2018: A giant fossil Mimarachnidae planthopper from the mid-Cretaceous Burmese amber (Hemiptera, Fulgoromorpha). — *Cretaceous Res.* **89**: 183–190.

Jiang T., Szwedo J. & Wang B. 2019: A unique camouflaged mimarachnid planthopper from mid-Cretaceous Burmese amber. — *Sci. Rep.* **9**: 13112, 11 pp.

Kania I., Wang B. & Szwedo J. 2015: *Dicranoptycha* Osten Sacken, 1860 (Diptera, Limoniidae) from the earliest Cenomanian Burmese amber. — *Cretaceous Res.* **52**: 522–530.

Laufer B. 1906: Historical jottings on amber in Asia. — *Mem. Am. Anthropol. Assoc.* **1**: 211–244.

Linnaeus C. 1758: *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. Laurentii Salvii, Holmiae, [4]+824 pp.

Melichar L. 1923: Homoptera; fam. Acanaloniidae, Flatidae et Ricaniidae. In Wytsman P. (ed.): *Genera Insectorum. Vol. 182.* L. Desmet-Verteneuil, Bruxelles, 185 pp.

Nel A., Prokop J., Nel P., Grandcolas P., Huang D.-Y., Roques P., Guilbert E., Dostál O. & Szwedo J. 2012: Traits and evolution of wing venation pattern in paraneopteran insects. — *J. Morphol.* **273**: 480–506.

Ridd M.F., Crow M.J. & Morley C.K. 2019: The role of strike-slip faulting in the history of the Hukawng Block and the Jade Mines Uplift, Myanmar. — *Proc. Geol. Assoc.* **130**: 126–141.

Ross A.J. 2022: Burmese (Myanmar) amber checklist and bibliography 2021. — *Palaeoentomology* **5**: 27–45.

Ross A.J., Mellish C., York P. & Crighton B. 2010: Chapter 12. Burmese amber. In Penney D. (ed.): *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, pp. 208–235.

Scotese C.R. 2013: Map Folio 23, Early Cretaceous (late Albian, 101.8 Ma). PALEOMAP PaleoAtlas for ArcGIS, volume 2, Cretaceous Paleogeographic, Paleoclimatic and Plate Tectonic Reconstructions, PALEOMAP Project. DOI: 10.13140/2.1.2863.1368

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 Res.* **37**: 155–163.

So J.F. 2013: Scented trails: Amber as aromatic in Medieval China. — *J. Roy. Asiatic Soc.* **23**: 85–101.

Stål C. 1866: Hemiptera Homoptera Latr. In: *Hemiptera Africana. Vol. 4*. Holmiæ, Ex Officina Norstedtiana, pp. 1–276, 1 pl.

Szwedo J. & Nel A. 2015: The Cretaceous insects: A promising state of the art. — *Cretaceous Res.* **52**: 628–630.

Szwedo J., Wang B., Soszyńska-Maj A., Azar D. & Ross A.J. 2020: International palaeoentomological society statement. — *Palaeoentomology* **3**: 221–222.

Thu K. & Zaw K. 2017: Gem deposits of Myanmar. In Barber A.J., Zaw K. & Crow M.J. (eds): *Myanmar: Geology, Resources and Tectonics. Vol. 48*. Geological Society, London, pp. 497–529.

Urban J.M. & Cryan J.R. 2007: Evolution of the planthoppers (Insecta: Hemiptera: Fulgoroidea). — *Mol. Phylogenet. Evol.* **42**: 556–572.

Walker F. 1857: Catalogue of the Homopterous insects collected at Sarawak, Borneo, by Mr. A.R. Wallace, with descriptions of new species. — *J. Proc. Linn. Soc. Lond.* **1**: 141–175.

Westerweel J., Roperch P., Licht A., Dupont-Nivet G., Win Z., Poblete F. & Aung D.W. 2019: Burma Terrane part of the Trans-Tethyan arc during collision with India according to palaeomagnetic data. — *Nature Geosci.* **12**: 863–868.

Yu T., Kelly R., Mu L., Ross A., Kennedy J., Broly P. & Dilcher D. 2019: An ammonite trapped in Burmese amber. — *Proc. Natn. Acad. Sci.* **116**: 11345–11350.

Zherikhin V.V. & Ross A.J. 2000: A review of the history, geology and age of Burmese amber (Burmite). — *Bull. Nat. Hist. Mus. (Geol.)* **56**: 3–10.

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