

Cretaceous lophocoronids with short proboscis and retractable female genitalia provide the earliest evidence for their feeding and oviposition habits

Weiting Zhang^{a,b,*}, Chungkun Shih^{c,d}, Michael S. Engel^e and Dong Ren^c

^aInstitute of Paleontology, Hebei GEO University, 136 Huaiandonglu, Shijiazhuang, 050031, China; ^bState Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, CAS, Nanjing, 210008, China; ^cCollege of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, Beijing, 100048, China; ^dDepartment of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, 20013-7012, USA; ^eDivision of Entomology, Natural History Museum, and Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, Kansas, 66045, USA

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Abstract

We describe two new species of Lophocoronidae: *Acanthocorona hedida* Zhang, Shih and Engel **sp. n.** and *Acanthocorona venulosa* Zhang, Shih and Engel **sp. n.**, and an undetermined specimen from mid-Cretaceous Kachin amber. Phylogenetic analysis of basal lepidopteran lineages, including three extinct families, was undertaken. The analysis supported monophyly of Glossata although internal relationships remain controversial. *Acanthocorona* and *Lophocorona* form a monophyletic group. It is likely that short and simply structured proboscides of *Acanthocorona* were used to sip water droplets, pollination drops from gymnosperms, nectar from early flowers, or sap from injured leaves. Both retracted and extended ovipositors are preserved in the material reported here, revealing their morphology and indicating that these Cretaceous lophocoronids inserted eggs into the tissues of their host plants.

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Introduction

The Lepidoptera, the moths and butterflies, are one of the most diverse orders of insects, with about 160 000 described species (Kristensen et al., 2007). Since at least the mid-Cretaceous, Lepidoptera have been important pollinators, experiencing significant episodes of diversification alongside the rise of flowering plants. Although many groups remain associated with gymnospermous plants, prior to the mid-Cretaceous Lepidoptera were more extensively linked to gymnosperms as hosts of reproductive organs, with basal moths extending at least into the Early Jurassic and putatively into the latest Triassic (van Eldijk et al., 2018). Today, most moths belong to the diverse

clade Glossata Fabricius, including all of those species with a coilable proboscis, permitting better access to nectar sources. Seven basal clades are recognized within Glossata: Eriocranioidea Rebel (*Dacnonypha* Hinton), Acanthopteroctetoidea Davis (*Coelolepida* Nielsen and Kristensen: *Acanthoctesia* Minet), Lophocoronoidea Common (*Coelolepida*: *Lophocoronina* Common), Neopseustoidea Hering (*Myglossata* Kristensen and Nielsen: *Neopseustina* Davis and Nielsen), Aenigmatineoidea Kristensen and Edwards (*Aenigmaglossata* Engel), Hepialoidea Stephens and Mnesarchaeoidea Eyer (*Exoporia* Common), and Heteroneura Tillyard (*Neolepidoptera* Packard) (Nielsen and Kristensen, 1996; Kristensen et al., 2015).

A phylogenetic framework is fundamental to understand the diversity, morphology, specializations, and ecological roles of Lepidoptera (Regier et al., 2009). Kristensen and Nielsen provided the phylogenetic

*Corresponding author:

E-mail address: zhangweitinghao@163.com

relationships of the order's basal lineages based on morphology (Kristensen, 1984, 1999; Nielsen and Kristensen, 1996), although not all the relationships corroborate with the studies based on molecular data (Regier et al., 2015). Wiegmann et al. (2002) also explored the phylogeny of the earliest-diverging lepidopteran lineages by combining molecular data with published morphological groundplan data, with their results supporting the hypothesis that Micropterigidae Herrich-Schäffer and Agathiphagidae Kristensen are the basal-most lineages of Lepidoptera while also supporting monophyly for Neolepidoptera and Exoporia. Regier et al. (2015) also provided a molecular phylogenetic estimation for the nonditrysian lineages of extant Lepidoptera, and ultimately treated Neotheoridae Kristensen, Anomosetidae Tillyard, Prototheoridae Meyrick, and Palaeosetidae Turner as synonyms of Hepialidae Stephens. Further progress on lepidopteran phylogeny was summarized by Mitter et al. (2017), while most recently Kawahara et al. (2019) used phylogenomics to infer a comprehensive phylogeny for Lepidoptera, reconstructing their evolutionary history using different dating schemes and a set of critically evaluated fossils for calibration.

Mesozoic lepidopterans principally belong to non-glossatan clades, such as Micropterigidae and the extinct families Eolepidopterigidae Rasnitsyn, Mesokristenseniidae Huang, Nel and Minet, and Ascololepidopterigidae Zhang, Shih, Labandeira and Ren (Sohn et al., 2012; Zhang et al., 2013). Mesozoic Glossata are rare (Sohn et al., 2012; Khramov et al., 2020). The affinity of some scales from Triassic-Jurassic sediments in northern Germany is clearly associated with the morphological clade Coelolepida, thus these scales probably represent the earliest Glossatan records (van Eldijk et al., 2018). *Protolepis cuprealata* Kozlov and *Karataunia lapidaria* Kozlov were found from the Upper Jurassic of Kazakhstan (Kozlov, 1989). However, re-examination of *P. cuprealata* revealed that the preservation is insufficient to demonstrate the definitive presence of a proboscis (Grimaldi and Engel, 2005: 564), and these could belong to non-glossatan clades. Further study and more completely preserved specimens are needed. Two adults tentatively placed to Incurvariidae and one glossatan larva were found in Early Cretaceous Lebanese amber (Whalley, 1978; Grimaldi and Engel, 2005: fig. 13.21). From mid-Cretaceous Kachin amber, Grimaldi et al. (2002) reported a definitive glossatan moth, although it was not formally described. Subsequently, *Tanyglossus orectometopus* Poinar (Gracillarioidea Stainton) was described from the same amber deposit (Poinar, 2017), although given the poor description a critical re-evaluation and revision of the fossil is necessary. Recently, eight species placed in Agathiphagidae and Lophocoronidae were also

reported from Kachin amber (Mey et al., 2021). Two undescribed glossatan moths have been reported from Late Cretaceous New Jersey amber, with the head of an adult glossatan moth with a short proboscis presented but not formally described by Grimaldi and Engel (2005: figs. 13.22, 13.28). Skalski (1979) reported a *Lophocorona*-like specimen from Late Cretaceous Siberian amber, but Nielsen and Kristensen (1996) indicated that the fossil can be placed no more precisely than non-heteroneurous Lepidoptera and therein should be considered *incertae sedis*. Mnesarchaeidae in Late Cretaceous Siberian amber (Zherikhin and Sukatsheva, 1973) are also inadequately substantiated (Kristensen, 1999). Nonetheless, glossatan leaf miners are well represented in the Mesozoic (Labandeira et al., 1994). Adding to this scant diversity, we report herein two new glossatan species and one undetermined specimen from mid-Cretaceous Kachin amber, which provide further evidence for exploring the Cretaceous evolution of proboscidian Lepidoptera as well as the piercing ovipositors among such moths.

Materials and methods

Material and terminology

All new fossils described herein were collected in or before 2016 from the Hukawng Valley, Tanai Township, Myitkyina District, Kachin State, northern Myanmar, and are thus in full ethical compliance for the study of Kachin amber (Engel, 2020; Szwedo et al., 2020; Shi et al., 2021). This deposit has yielded many well-preserved insect fossils (e.g., Grimaldi and Ross, 2017; Ross, 2021). A recent radioisotopic date has been established at 98.79 ± 0.62 Ma for Kachin amber (Cruickshank and Ko, 2003; Shi et al., 2012), equivalent to the earliest Cenomanian and within approximately 1 Myr of the boundary between the Early and Late Cretaceous (Walker et al., 2012). The specimens studied in this paper are housed in the Key Lab of Insect Evolution and Environmental Changes, College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, Beijing, China (CNUB).

All specimens were examined and photographed using a Nikon SMZ 18 dissecting microscope with an attached Nikon DS-Ri2 digital camera. The head structures of specimen CNU-LEP-MA-2016016 were captured by Zeiss LSM 780 confocal laser scanning microscope in the College of Life Sciences public laboratory at CNU. The specimens were illustrated using Adobe Photoshop CS6. The wing index is defined as the ratio of wing width/wing length. The family-level classification follows van Nieukerken et al. (2011), while wing venation nomenclature is based on Wootton (1979) and other nomenclature follows Scoble (1992).

Phylogenetic methods

Sampling. A phylogenetic analysis was conducted to confirm the taxonomic positions of our new genera. We sampled a total of 36 terminal species, comprising 34 ingroups (27 extant species and seven fossil species) and two outgroups (Appendix S1). Outgroups were selected based on the most recent phylogenetic analyses of Hexapoda (Misof et al., 2014). As Trichoptera are the sister group of Lepidoptera,

Dolophilodes didactylus Sun and Yang (Philopotamidae Stephens) and *Hydropsyche cabarym* Malicky (Hydropsychidae Curtis) within Trichoptera were selected as outgroups. The sampled ingroups represent the extinct families of Eolepidopterigidae, Mesokristenseniidae, and Ascololepidopterigidae, as well as extant non-glossatan and basal glossatan taxa. The fossil representatives were selected according to the relative completeness of the preserved specimens and the resultant proportion of missing characters in the morphological character matrix (Appendix S1).

Morphological data. The phylogenetic analysis was performed using 65 morphological characters. Some characters were extracted from earlier studies (Nielsen and Kristensen, 1996; Simonsen and Kristensen, 2017), and other characters were chosen and examined by us. These characters were identified and coded as unordered and with equal weights. Inapplicable and unknown characters were respectively coded as “–” and “?”. Descriptions of character states are given in Appendix, and the character matrix (Appendix S1) was edited using Mesquite (Maddison and Maddison, 2018). The character matrix and character list can be obtained in Dryad public repository (<https://doi.org/10.5061/dryad.3j9kd51m1>).

Parsimony analysis. Parsimony analysis was performed using NONA (Goloboff, 1998), implemented within the WinClada interface (Nixon, 2002) and employing a heuristic search method (options set to hold 10 000 trees, 1000 replications, 100 starting tree replications, multiple TBR + TBR search strategy) and TNT Version 1.1 (Goloboff et al., 2008), with a traditional search and 10 000 replications. Bremer’s decay index was calculated using TNT Version 1.1 to assess relative support for individual clades.

Results

Systematic palaeontology

Order Lepidoptera Linnaeus, 1758.
Suborder Glossata Fabricius, 1775.
Infraorder Lophocoronina Common, 1990.
Superfamily Lophocoronoidea Common, 1973.

Family Lophocoronidae Common, 1973.

Type genus. *Lophocorona* Common, 1973.

Genera included. *Lophocorona* Common, 1973; *Acanthocorona* Mey, Léger and Lien, 2021.

Emended diagnosis. Haustellae short; ocellus and chaetosema absent; maxillary palpus with either four or five palpomeres (tetramerous or pentamerous); labial palpus with three palpomeres (trimerous). Spur formula 0-2-4. Forewing and hind wing homoneurous. Forewing length 3–5 mm. Forewing with Rs_4 terminating postapically; three anal veins confluent distally, forming a trident-shape. In male, segment IX ringed with anterior margin nearly straight, valvae with stout apical spines and long spikes. In female, both anterior and posterior apophyses present, ovipositor tip acute and terminal segmental unit of postabdomen with serrated lateral ‘saw’.

Remarks. Lophocoronidae have a single extant genus, *Lophocorona*, with six species (Nielsen and Kristensen, 1996). Mey et al. (2021) established an

extinct genus, *Acanthocorona*, with seven species from mid-Cretaceous Kachin amber. The diagnosis of Lophocoronidae is here emended mainly based on characters of the two newly described extinct species. The absence of an epiphysis is removed from the diagnosis of Lophocoronidae, and the character of the maxillary palpus is revised to include species with either four (tetramerous) or five (pentamerous) palpomeres. The spikes originating from the inner side of the base of the valvae is the synapomorphy of Lophocoronidae (Mey et al., 2021).

Genus *Acanthocorona* Mey, Léger and Lien, 2021.

Type species. *Acanthocorona skalskii* Mey, Léger and Lien, 2021.

Emended diagnosis. Antennae short, basal flagellomeres broad. Maxillary palpus pentamerous, principal points of flexion at joints 1/2 and 3/4. Epiphysis present. Homoneurous venation. Forewings with accessory and median cells present, Rs_4 running to termen (below apex) in both wings. Valvae of male genitalia with one or more pairs of long, basal spikes.

Remarks. The diagnosis of *Acanthocorona* is emended based on two new species described below. Crossvein r-rs is not always present in *Acanthocorona* species. The rod-like spine on valvae is absent in *Acanthocorona venulosa* Zhang, Shih and Engel sp. n. Therefore, “crossvein r-rs present” and “valvae with a terminal, short, rod-like ‘thorn’” are removed from the emended diagnosis.

Acanthocorona hedida Zhang, Shih and Engel sp. n. (Figs. 1–3)

Material. Holotype: CNU-LEP-MA-2016016, ♀. Paratypes: CNU-LEP-MA-2016002, ♂; CNU-LEP-MA-000735, ♀.

Etymology. The specific epithet is derived from Chinese “hedida”, a Chinese pronunciation of Hebei GEO University, and is treated as euphonious combination of letters. The name honours Hebei GEO University for supporting this research.

Locality and horizon. Hukawng Village, Kachin State, northern Myanmar; Upper Cretaceous (lowermost Cenomanian).

Diagnosis. In forewing, stem of Rs_{1+2} subequal to stem of Rs_{3+4} ; crossvein r-rs absent; crossvein s (rs_2 - rs_3) present. In male, valva trilobate, two finger-like lobes with two long rod-like spines and one broad lobe with several stout apical setae; inner surface of cucullus bearing short stout setae.

Remarks. The combination of a coiled proboscis and homoneurous wings obviously places the new species among the homoneurous Glossata. Five extant lineages are currently recognized within the ‘homoneurous’ grade of Glossata: Eriocranioidea, Acanthopteroctoidea, Lophocoronoidea, Neopseustoidea, and Exoporia (Mnesarchaeoidea and Hepialoidea) (van Nieukerken

et al., 2011). *Acanthocorona hedida* sp. n. can be distinguished from Eriocranioidea and Acanthopteroctoidea by the presence of two pairs of mesotibial spurs (Kristensen, 1999), and from Neopseustoidea by having a proboscis with unique doubled tubes, an antenna longer than the forewing, and the absence of chaetosema (Davis, 1975). *Acanthocorona hedida* sp. n. can be separated from Exoporia by its pentamerous maxillary palpus and female postabdominal segments with apophyses. Hepialoidea have the autapomorphic character of Rs_3 and Rs_4 terminating well posterior to the apex (Kristensen, 1978), thus *A. hedida* sp. n. can be excluded from Hepialoidea by its Rs_3 terminating preapically.

Mey et al. (2021) proposed that the long spikes originating from the inner side of the bases of the valvae is a synapomorphy of *Lophocorona* + *Acanthocorona*. The new specimen with long spikes on valva indicates its affiliation with Lophocoronidae. *Acanthocorona hedida* sp. n. shows further similarity with *Lophocorona*, such as the absence of ocelli, Rs_4 terminating subapically in both wings, and a tibial spur formula of 0-2-4. Nonetheless, *A. hedida* sp. n. differs from *Lophocorona* in the pentamerous maxillary palpus and the presence of an epiphysis. *Acanthocorona hedida* sp. n. can be assigned to *Acanthocorona* by the presence of the epiphysis. Compared to the seven described species by Mey et al. (2021), *A. hedida* sp. n. differs in its forewing lacking crossvein r-rs and the valva of the male genitalia trilobate.

Poinar (2017) described the genus, *Tanyglossus* Poinar (Gracillarioidea) from Kachin amber, and *A. hedida* sp. n. is easily distinguished by its larger body size (4 mm vs. less than 1 mm in body length), shorter proboscis (vs. proboscis longer than body length), and Rs_4 terminating subapically (vs. Rs_4 terminating preapically). *Acanthocorona hedida* sp. n. is differentiated from *Protolepis* by its antenna less than one-half forewing length (vs. antenna long, at least 7/8 as long as the forewing), and the presence of an epiphysis (vs. absent), and from *Karataunia* by the absence of ocelli (vs. present) and stem of M vein present (vs. the loss of stem of M vein result in the discal cell very large).

Description. Body length 3.2–4 mm. Forewing length 3.1–4 mm; hind wing length 2.4–3.6 mm. Body and wings covered with scales of various sizes and shapes; scales of frons and vertex erect.

Antenna short, 0.45× forewing length; scape and pedicel slightly broader than basal flagellomeres; flagellum with 23–25 flagellomeres; flagellomeres barrel-shaped except terminal flagellomere triangular. Ocelli and chaetosema absent. Maxillary palpus slender, pentamerous, palpomere II slightly longer than palpomere I, palpomere III subequal to palpomere IV and ca. 2.6× length of palpomere II, palpomere V crassate, tapering apically. Labial palpus slightly shorter than

maxillary palpus, trimerous, palpomere I shortest, palpomere III longest, nearly 1.7× length of palpomere II, terminal palpomere with long bristles. Mandible nonfunctional. Galeae short (Figs. 1e, 3c), ca. 0.28–0.33 mm, their lengths almost as long as length of labial palpus, external galeal wall furnished with several sensilla styloconica arranged linearly.

Tibial spur formula 0-2-4; epiphysis arising from inner surface of protibia; all tibiae with irregularly arranged spines; tarsus pentamerous; all tarsomeres with terminal spinules; pretarsus possessing simple claws, arolium present.

Margins of both fore- and hind wings bearing elongate fringe scales, almost reaching 0.4 mm. Forewing moderately broad, forewing index (ratio of wing width/wing length) 0.33; humeral vein absent; Sc forking from 1/3 of stem length; Sc_1 slightly beyond 2/5 wing length from its base; Sc_2 extending to midpoint of wing along costal margin; R unforked; Rs 4-branched; Rs_3 terminating preapically, Rs_4 terminating subapically; crossveins s (rs_2 - rs_3) and rs-m present; crossvein s connecting Rs_2 and Rs_3 , originating near Rs_{1+2} furcation and terminating near Rs_{3+4} furcation; M forking to M_{1+2} and M_3 , M_{1+2} further forking to veins M_1 and M_2 ; crossvein m (m_2 - m_3) slanted obliquely; crossvein m-cua present; CuA bifurcating; CuP simple; crossvein cua-cup present near base of forewing; crossvein cup-a present; three anal veins confluent distally, 1A and 3A bending to 2A, 2A straight and reaching posterior margin (Figs. 1c, 1d, 3d). Hind wing with two frenular bristles (wing coupling apparatus) arising near base of costa; both Sc and R unforked; Rs_4 terminating subapical; crossvein rs_4 -m present on CNU-LEP-MA-2016016 [not observable on CNU-LEP-MA-2016002].

Female: Caudal margin of sternum VII of female truncate, with long setae. Abdomen with retractable oviscapt (Fig. 1f, 2a). Both anterior and posterior apophyses present.

Male: Abdominal segment IX forming a broad, strongly sclerotized ring, not differentiated into tegumen and vinculum, anterior margin nearly straight ventrally; apical part of valva trilobate, finger-like lower lobes with two long apical spines, one broad upper lobe with several stout apical spines (Figs. 3e, 3f); inner surface of valva bearing small spines; two extremely long spikes at base of each valva.

Remarks. These specimens were found in close vicinity of each other, and there are many shared similarities in morphology between them, thus we consider them to be conspecific.

***Acanthocorona venulosa* Zhang, Shih and Engel sp. n.** (Fig. 4)

Material. Holotype: CNU-LEP-MA-000653, ♂.

Etymology. The specific epithet is derived from the Latin *venula* (“small vein”) and the suffix *-osus* (suffix

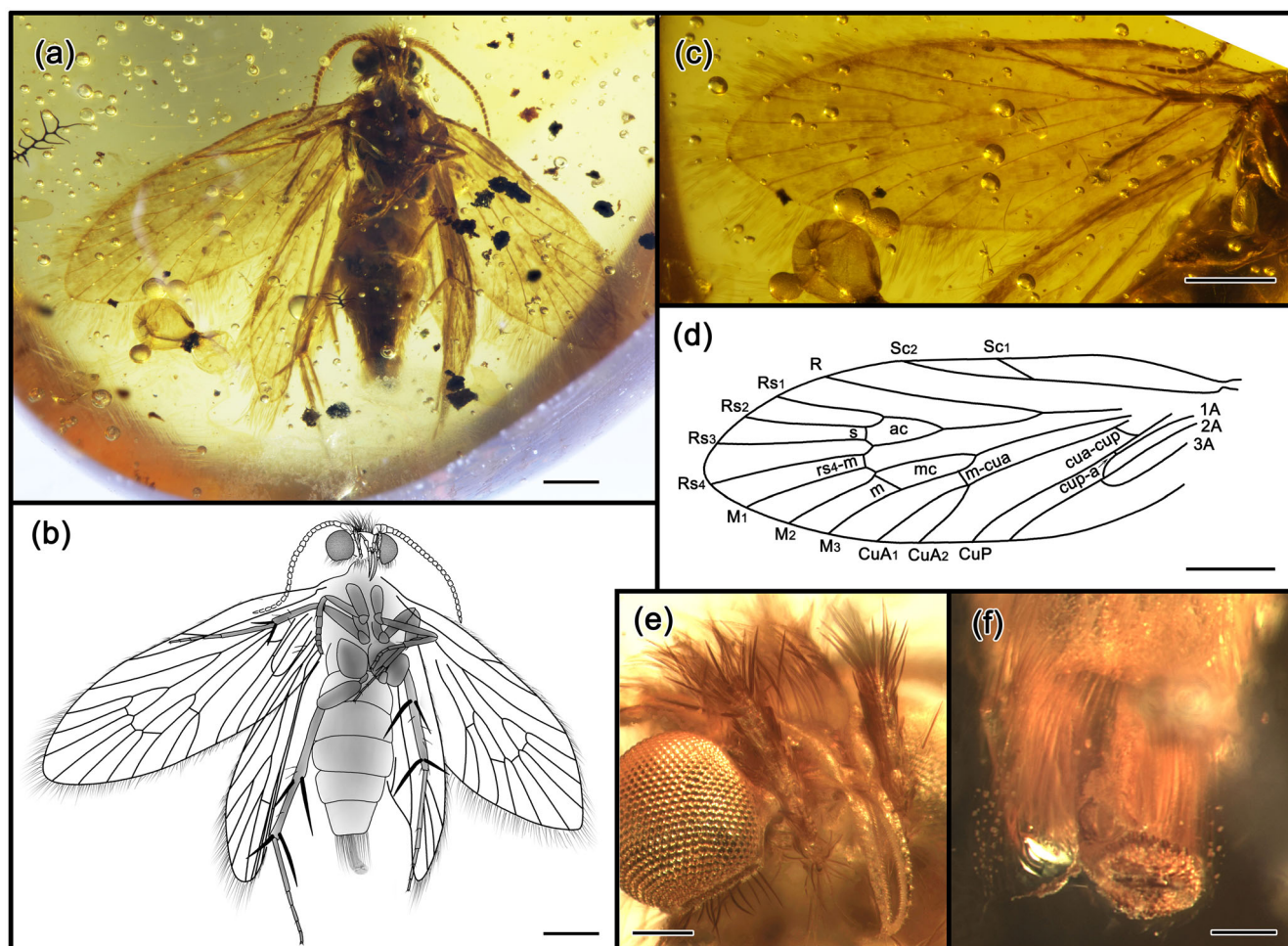


Fig. 1. *Acanthocorona hedida* Zhang, Shih and Engel **sp. n.**, holotype, ♀, CNU-LEP-MA-2016016. (a) photo, ventral view; (b) line-drawing, ventral view; (c) photo, forewing; (d) line drawing, forewing; (e) photo, head; (f) photo, retracted ovipositor. Scale bars for (a) – (d) = 0.5 mm; scale bars for (e), (f) = 0.1 mm.

forming adjectives from nouns, denoting, “full of”), and referring to the more complete crossvenation due to the presence of r-rs.

Locality and horizon. Hukawng Village, Kachin State, northern Myanmar; Upper Cretaceous, lowermost Cenomanian.

Diagnosis. Stem of Rs_{1+2} shorter than stem of Rs_{3+4} ; crossvein r-rs and s (rs_2 - rs_3) present. Male genitalia with valva undivided, spade- or scoop-shaped, distal margin and subapical inner surface of valva with peg-like spines, but without terminal rod-like ‘thorn’.

Remarks. *Acanthocorona venulosa* **sp. n.** can be placed to Lophocoronidae owing to the short haustellae, absence of ocelli and chaetosema, tibial spur formula 0-2-4, Rs_4 terminating subapically in both wings, the forewing with three anal veins confluent distally, and the spikes originating from the inner side of the base of the valva. *Acanthocorona venulosa* **sp. n.** belongs to *Acanthocorona* owing to the presence of an epiphysis, but differs from other species in that the

male genitalia are spade-shaped and without a terminal rod-like ‘thorn’.

Description. Body length 3.3 mm. Forewing length 3.4 mm; hind wing length about 3.1 mm. Head with tufts of elongate piliform scales on frons and vertex.

Antenna short, nearly one-half forewing length; flagellum with 34 flagellomeres, flagellomeres barrel-shaped except terminal flagellomere triangular. Ocelli and chaetosema absent. Galeae short, 0.32 mm.

Tibial spur formula 0-2-4, spurs of metatibia greatly elongate; protibia with epiphysis (Fig. 4c); all the tibia with spines; tarsus pentamerous; all tarsomeres with terminal spinules; pretarsus with simple claws, arolium present.

Margins of both fore- and hind wings with fringe, about 0.2 mm long. Forewing index 0.31; humeral vein absent; Sc forked; Sc_1 beyond 1/3 wing length from its base; Sc_2 extending to midpoint of wing along costal margin; R unforked; crossvein r-rs present; Rs 4-branched; Rs_3 terminating preapically, Rs_4

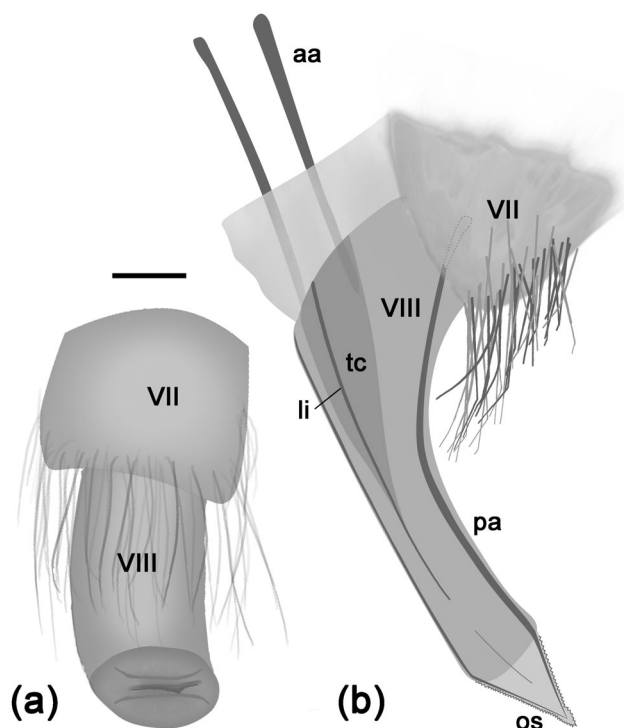


Fig. 2. The female terminalia of mid-Cretaceous lophocoronids. (a) *Acanthocorona hedida* Zhang, Shih and Engel *sp. n.*, CNU-LEP-MA-2016016, retracted ovipositor; (b) Species *Incertae sedis*, CNU-LEP-MA-2016035, extended ovipositor. Abbreviations: VII, 7th sternite; VIII, 8th sternite; aa, anterior apophysis; li, longitudinal inflection; os, oviscapt saw; pa, posterior apophysis; tc, thickened cuticle. Scale bar = 0.1 mm.

terminating subapically; crossveins *s* (rs_2 – rs_3) and rs_4 –*m* present; *M* forking to M_{1+2} and M_3 , M_{1+2} further forking to veins M_1 and M_2 ; crossveins *m* (m_2 – m_3) and *m*–*cua* present; *CuA* bifurcating; *CuP* simple; crossvein *cua*–*cup* present near base of forewing; crossvein *cup*–*a* present; three anal veins confluent distally, 1A and 3A bending to 2A, 2A straight (Fig. 4d). Hind wing with three frenular bristles arising near base of costa; both *Sc* and *R* unforked; Rs_4 terminating postapically; *M* 3-branched; crossvein *s* present; *CuA* bifurcating.

Male (Figs. 4e, 4f): Part of tergum X forming a mid-dorsal uncus, uncus with sides curved, apex truncate; a pair of valvae large, flattened and tapering abruptly to a rounded apex; distal margin and subapical inner surface of valva with peg-like spines; two pairs of long spikes present on basal part of valva. Phallus gracile.

Acanthocorona sp. (Figs. 2, 5)

Material. CNU-LEP-MA-2016035, ♀.

Locality and horizon. Hukawng Village, Kachin State, northern Myanmar; Upper Cretaceous, lowermost Cenomanian.

Description. Body length 3.5 mm. Forewing length 3.4 mm; hind wing length about 3.1 mm. Head with tufts of elongate piliform scales on frons and vertex.

Antenna less than one-half forewing length; flagellum with 27 flagellomeres, flagellomeres barrel-shaped except terminal flagellomere triangular. Ocellus and chaetosema absent. Maxillary palpus slender. Labial palpus with bristles, trimerous, palpomere III longest. Proboscides short.

Tibial spur formula 0-2-4, spurs of metatibia greatly elongate; protibia with epiphysis; all tibiae with spines; tarsus pentamerous; all tarsomeres with terminal spinules; pretarsus with simple claws, arolium present.

Margins of both fore- and hind wings with fringe, about 0.4 mm long. Forewing index 0.35; *Sc* forked; Sc_1 beyond 1/3 wing length from its base; Sc_2 extending to midpoint of wing along costal margin; *R* unforked; crossvein *r*–*rs* present; Rs 4-branched; Rs_3 terminating preapically, Rs_4 terminating subapically; crossveins *s* (rs_2 – rs_3) and rs_4 –*m* present. *M* 3-branched; crossveins *m* (m_2 – m_3) and *m*–*cua* present, *CuA* bifurcating (Fig. 5d). Hind wing with four frenular bristles arising near base of costa; both *Sc* and *R* unforked; Rs_4 terminating postapically; *M* 3-branched; crossveins *m* and *m*–*cua* present; *CuA* bifurcating, *CuP* simple (Fig. 5d).

Female (Figs. 2b, 5c): Caudal margin of sternum VII of female truncate, with comb of spines. A prominent longitudinal inflection in dorsal midline of cone; thickened cuticle along longitudinal inflection. Both anterior and posterior apophyses present. Abdomen with retractable oviscapt, ovipositor tip acute, terminal segment of female postabdomen with finely serrated lateral ‘saw’.

Remarks. CNU-LEP-MA-2016035 shows venational similarities with *Acanthocorona*. This specimen is different from *A. hedida* *sp. n.* in the presence of crossvein *r*–*rs*. Since the primary difference among *Acanthocorona* are essentially in the male genitalia, it is difficult to determine the taxonomic position based on an isolated female. Thus, we prefer to leave it unassigned at this time. Nonetheless, this specimen is perhaps conspecific with *A. venulosa* *sp. n.* or NIGP 173719 (NIGP) and # 7098 (TF) described by Mey et al. (2021).

Phylogeny of basal lineages of Lepidoptera

The parsimony analyses using WinClada and TNT, respectively, yielded almost identical results (Figs. 6, 7). The parsimony analysis yielded two equally parsimonious trees with the following descriptive statistics: tree length = 191 steps, consistency index (CI) = 0.42, retention index (RI) = 0.76. Our results for living basal lineages of Lepidoptera (Fig. 8) are basically identical to prior estimates (Kristensen, 1984, 1999).

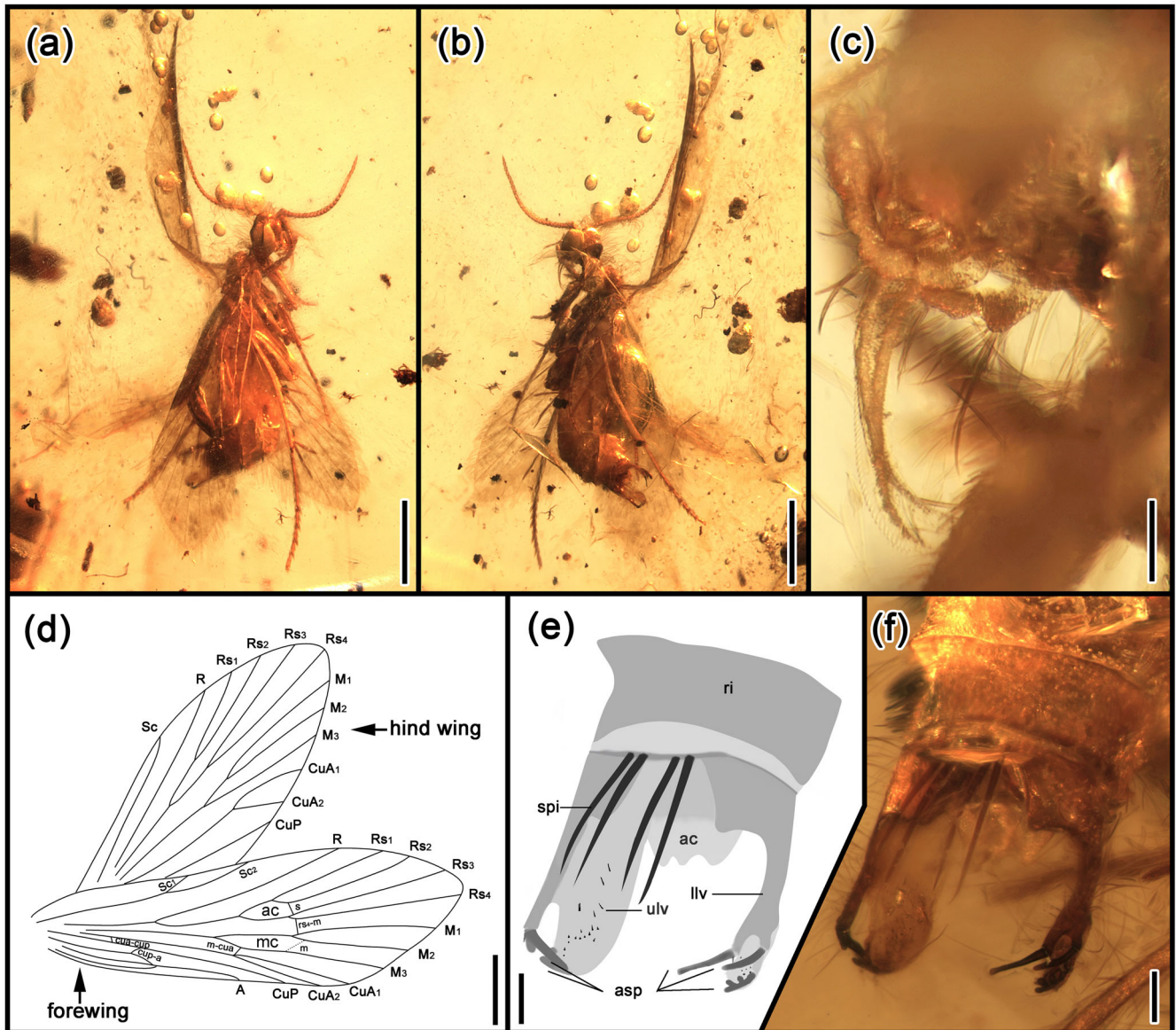


Fig. 3. *Acanthocorona hedida* Zhang, Shih and Engel sp. n., paratype, ♂, CNU-LEP-MA-2016002. (a) photo, dorsal view; (b) photo, ventral view; (c) photo, mouthparts; (d) line drawing, forewing and hind wing; (e) line drawing, male genitalia; (f) photo, male genitalia, ventral view. Abbreviations: ac, anal cone; asp, apical spines; llv, lower lobe of valva; ri, segment IX ring; spi, spike; ulv, upper lobe of valva. Scale bars for (a), (b) = 1 mm; scale bars for (c), (e), (f) = 0.1 mm; scale bar for (d) = 0.5 mm.

However, the positions of the extinct families, *i.e.*, Eolepidopterigidae, Mesokristenseniidae, and Ascololepidopterigidae, have seldom been discussed previously. The phylogenetic position of Ascololepidopterigidae is different in the topologies yielded by WinClada and TNT respectively. It is not strongly supported whether Ascololepidopterigidae cluster with Mesokristenseniidae + Eolepidopterigidae + Micropterigidae (Fig. 6) or diverged prior to all the other Lepidoptera (Fig. 7). Because those subtle details can be difficult to observe or appear ambiguously, the phylogenetic position of the rare Jurassic family Ascololepidopterigidae requires further study

and confirmation. To date, 16 fossil species of Eolepidopterigidae have been reported worldwide ranging from the Middle Jurassic to the Early Cretaceous. As shown in the diagram by Rasnitsyn and Quicke (2002: fig. 297), Eolepidopterigidae were hypothesized to be the sister group to Micropterigidae. Our topology, as shown in Figs. 6, 7, supports this hypothesis. Mesokristenseniidae cluster with Eolepidopterigidae + Micropterigidae, but due to the limited identifiable characters of Eolepidopterigidae and Mesokristenseniidae, there is no unambiguous synapomorphy supporting these clades. Agathiphagidae are the sister group of a clade comprising all remaining lineages of

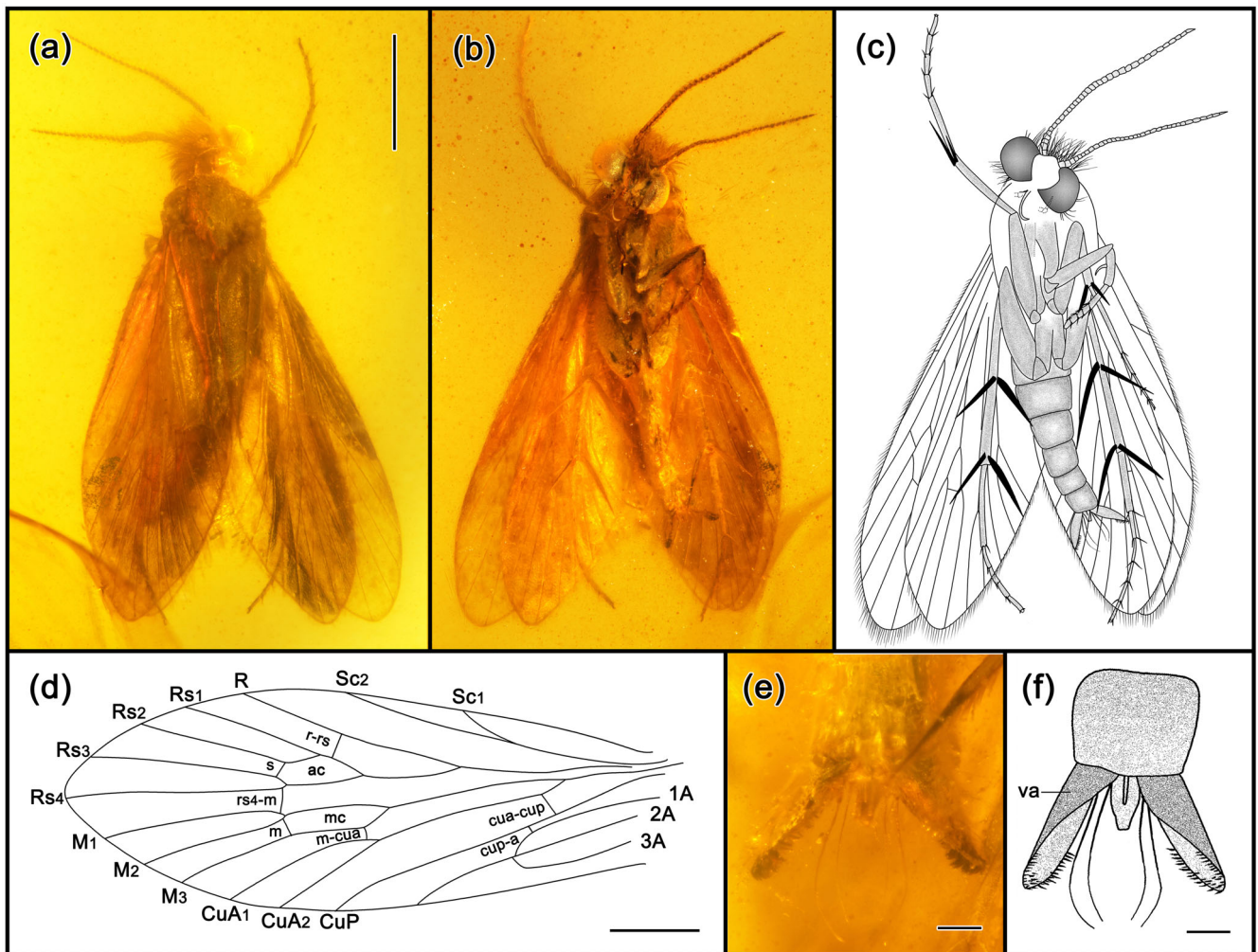


Fig. 4. *Acanthocorona venulosa* Zhang, Shih and Engel sp. n., holotype, ♂, CNU-LEP-MA-000653. (a) photo, dorsal view; (b) photo, ventral view; (c) line drawing, ventral view; (d) line drawing, forewing; (e) photo, male genitalia, ventral view; (f) line drawing, male genitalia. Abbreviations: va, valva. Scale bars for (a), (b), (c) = 1 mm; scale bar for (d) = 0.5 mm; scale bars for (e), (f) = 0.1 mm.

Lepidoptera (*i.e.*, clade Angiospermivora of Regier et al., 2015), while Heterobathmiidae diverge next as the sister group of Glossata.

The monophyly of Glossata is not surprisingly supported here, with the Bremer's decay index of 5 for this clade (Fig. 7), but the inner relationships among glossatan lineages remain controversial. Based on molecular data, Kristensen et al. (2015) contradicted the myoglossatan monophyly, in favour of the clade Acanthopteroctetidae + Aenigmatineidae + Neopseustidae monophyly, and regarded Aenigmatineidae as the sister group of Neopseustidae. The morphology-based phylogenetic hypothesis presented here contradicts coelolepidan monophyly, but supports the lineages of Myoglossata and Neolepidoptera as monophyletic (Fig. 7). Actually, the monophyly of Coelolepida has also been questioned in prior studies (Mutanen et al. 2010; Regier et al. 2015; Mitter et al. 2017). Aenigmatineidae + Lophocoronidae +

Myoglossata are considered here to be a clade, although the relationships among them are unclear. Two synapomorphies confirm the monophyly of Myoglossata, consisting of Neopseustida + Exoporia + Heteroneura: sharply upturned anterior part of the first abdominal tergum and female with two genital openings (Fig. 6).

Our two new species, the species considered as *incertae sedis*, and *Lophocorona* formed a monophyletic group in the analysis, with a Bremer's decay index of 2 for this clade (Fig. 7). Long spikes originating from the base of the valvae and trident-shaped anal veins were recovered as a synapomorphy for this grouping (Fig. 6), which was also noticed by Common (1973). Forewing Sc forked and the postapical Rs_4 shared by our specimens and *Lophocorona* were considered to be homoplasious. The wing venation of our specimens shows considerable similarity to that of *Lophocorona*, but our specimens differ from *Lophocorona* in the

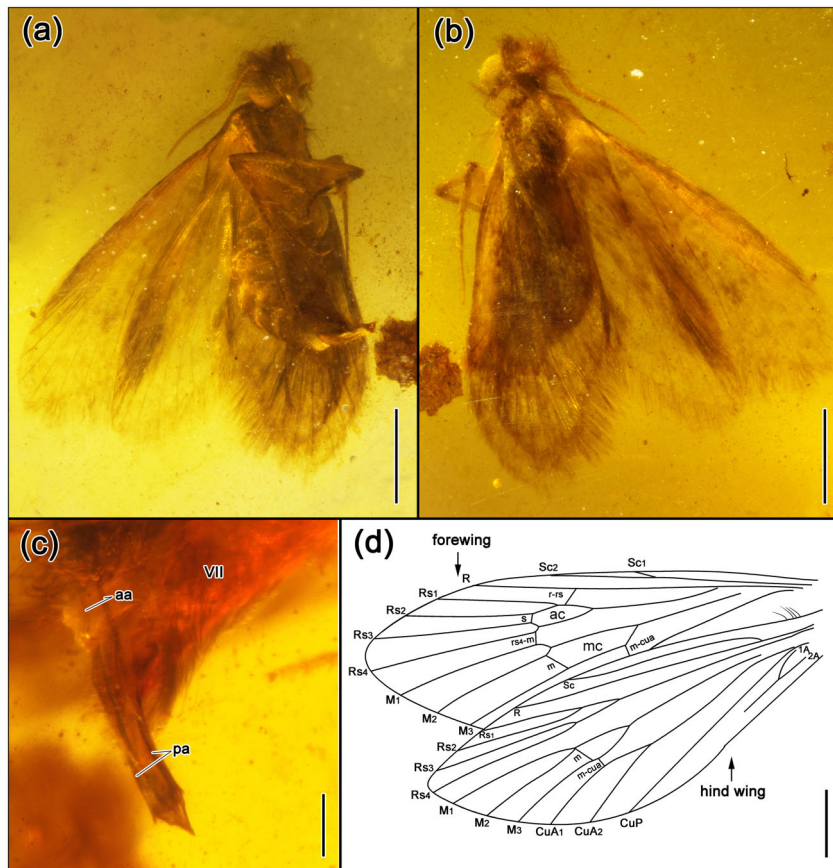


Fig. 5. *Acanthocorona* sp., ♀. CNU-LEP-MA-2016035. (a) photo, ventral view; (b) photo, dorsal view; (c) photo, extended ovipositor; (d) line drawing, forewing and hind wing. Abbreviations: aa, anterior apophysis; pa, posterior apophysis. Scale bars for (a), (b) = 1 mm; scale bar for (c) = 0.2 mm; scale bar for (d) = 0.5 mm.

presence of a protibial epiphysis. Kristensen (1999: 55) regarded the absence of an epiphysis as an autapomorphy of *Lophocorona*. However, it is not uncommon in Lepidoptera for a family to include species with or without epiphyses, such as Micropterigidae, Eriocraniidae, Hepialidae, etc. (Kristensen, 1999). Thus, the presence or absence of an epiphysis is here recognized as variable within Lophocoronidae and merely an intergeneric difference. Species of *Acanthocorona* have pentamerous maxillary palpi, which differs from those of *Lophocorona*. Pentamerous maxillary palpi may be a plesiomorphic condition, with tetramerous maxillary palpi apomorphic for this clade.

Discussion

Mouthparts and feeding habit

Chewing mouthparts occur in the representatives of the basal lepidopteran lineages, such as Micropterigidae, Agathiphagidae, and Heterobathmiidae, and are universally reconstructed as plesiomorphic for

Lepidoptera (Figs. 8a–c). The proboscis represents an autapomorphy of Glossata (Figs. 6, 7, 8d–j). The transformation of generalized galeae into a coilable proboscis was one of the most significant events in the early evolution of the Lepidoptera (Krenn and Kristensen, 2000; Mitter et al., 2017), yet the fossil evidence of early coilable proboscides is sparse. Although the five earliest potential glossatan fossil records (the fossil scales from northern Germany, *Protolepis cuprealata*, *Karataunia lapidaria*, an undescribed eriocraniid, and an undescribed nepticulid leaf mine) were found in Triassic–Jurassic deposits (Skalski, 1979; Kozlov, 1989; Kozlov et al., 2002; van Eldijk et al., 2018), for none of them is the mouthparts described in detail or they are not preserved at all. The mouthpart structures reported herein provide more evidence of early proboscides. Kawahara et al.'s (2019) phylogenomic analysis of Lepidoptera considered that the appearance of the tube-like proboscis took place in the mid-Triassic (ca. 241 Ma), an age significantly older than the earliest fossil Glossata and even older than any definitive Lepidoptera (fossil records are summarized in Fig. 8). Either their divergence estimates are

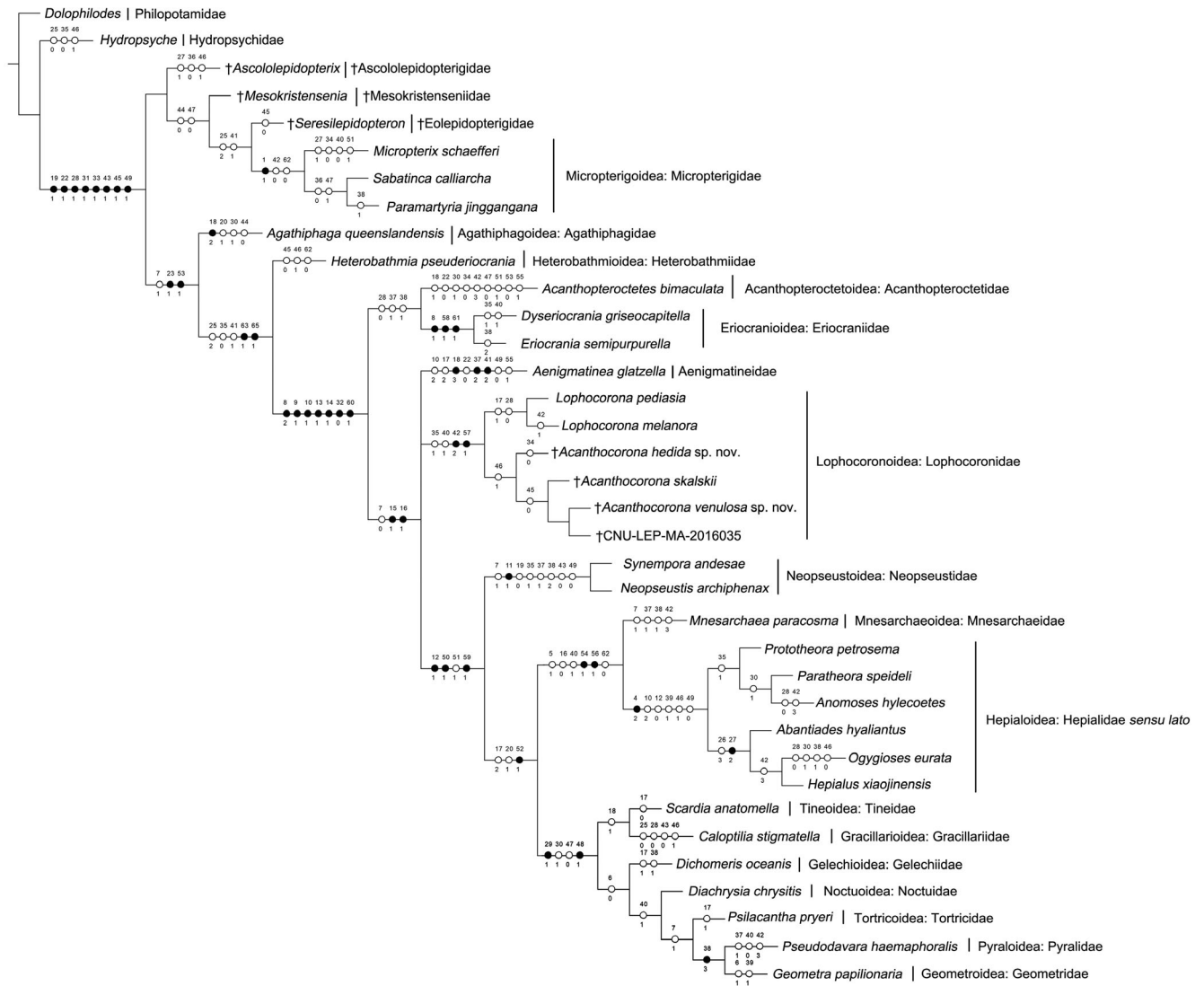


Fig. 6. The strict consensus tree yielded by WinClada with characters and character states mapped. (●) nonhomoplasious; (○) homoplasious; (†) fossils.

considerably off, or there remains a significant diversity of early lepidopterans to be discovered from Triassic and Jurassic deposits.

The great majority of adult Glossata, except Neopseustidae, possess galeae that are linked both by dorsal and ventral legulae on the dorsal and ventral surfaces of the median food canal (Krenn, 2010). The outer surface of each glossatan galea usually bears microtrichia, sensilla basiconica, sensilla trichodea (sensilla chaetica), and sensilla styloconica (Krenn, 2010). Papillae are present on the external galeal wall of our specimens (Fig. 9). Similar papillae are also visible on the specimen found in Late Cretaceous (Turonian) New Jersey amber (Grimaldi and Engel, 2005: 564, fig. 13.22). These papillae are obvious and arranged linearly on the external surface of

the proboscis. According to the size of each papilla and the arrangement of these papillae, we consider these papillae may be sensilla styloconica (Bauder et al., 2013: fig. 2).

Faucheux (2008, 2013) noted that during lepidopteran evolution, the first uniporous sensilla styloconica of the galeae appeared with the Neopseustidae. In our phylogeny, Lophocoronidae diverged prior to Neopseustidae, and form a monophyletic group with Aenigmatineidae and Myoglossata (Fig. 8) (i.e., Coleoptera are polyphyletic in this analysis). The finding of sensilla styloconica on mid-Cretaceous lophocoronids indicates sensilla styloconica have a more ancient origin, and had already appeared on an extinct basal group (although if the tree presented in Mitter et al., 2017, is accurate, then the clade including neopseustids

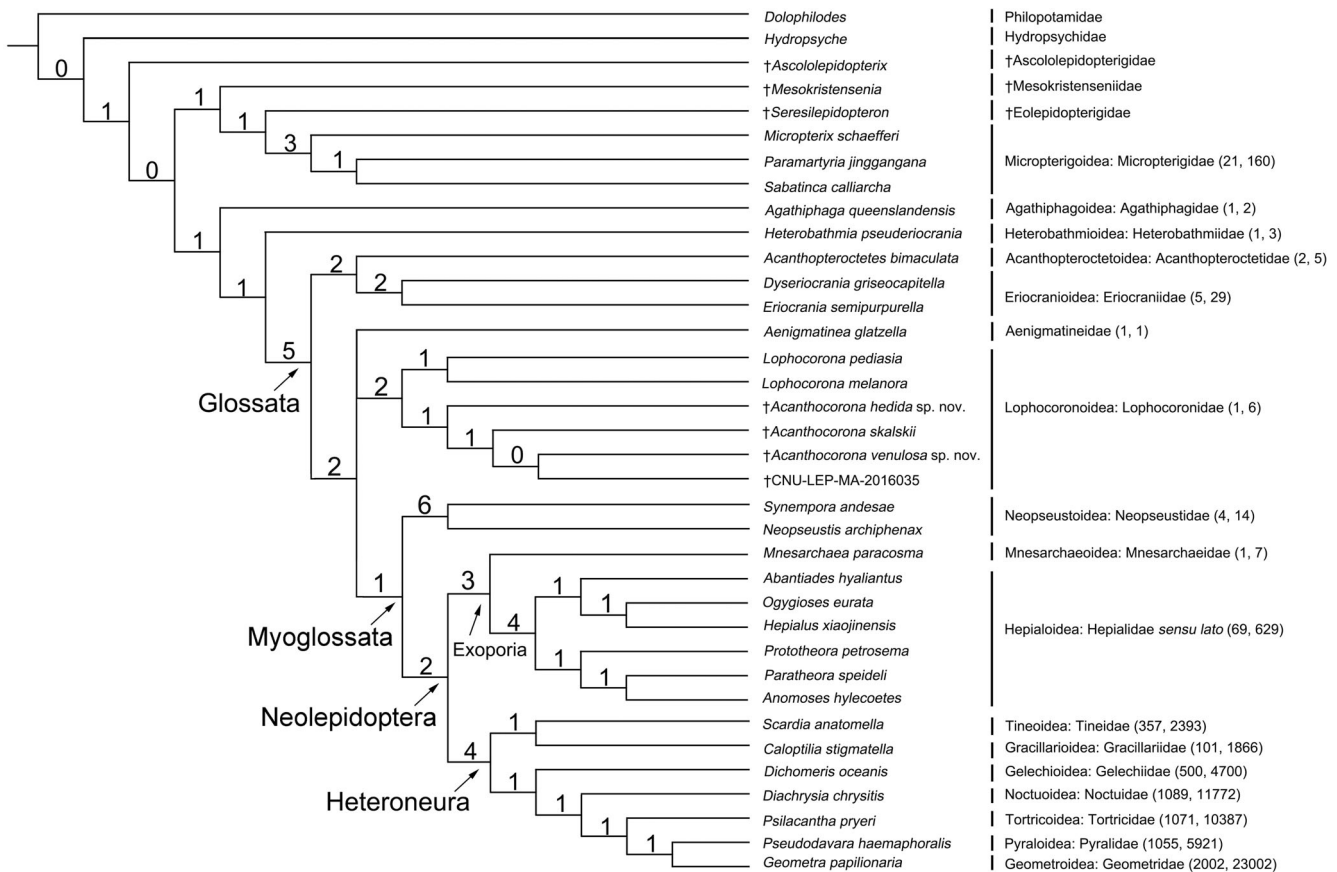


Fig. 7. Phylogeny of basal Lepidoptera recovered from the parsimony analysis, with Bremer support values yielded by TNT mapped at nodes. (†) fossils. The numbers in brackets represent the number of extant genera and species (van Nieukerken et al., 2011).

diverged prior to Lophocoronidae, emphasizing the need for continued phylogenetic exploration to resolve these nodes with greater confidence).

The food sources of Lepidoptera are diverse, such as nectar, pollen, fruit, and even tears blood (Krenn, 2010). Adult Glossata take up only liquid food and achieve this by the feeding tube of the proboscis (Krenn, 2010). The morphology of the proboscis and its sensilla are closely associated with adult feeding habits (Krenn, 2010; Chen et al., 2018). Like the condition in more primitive moths, the galeae of *Acanthocorona* are reduced in length (0.28 to 0.33 mm), about 10% of the body length. The proboscis length of *Acanthocorona* is obviously shorter than those modern species of other families with long proboscides that are generally associated with long-corolla flowers (Krenn, 2010). In our specimens, the galeae of each species always ‘split’ apart (Fig. 9). It is supposed that the cohesion of the galeae is perhaps weak in *Acanthocorona*. Sensilla styloconica occur more on the distal 2/3 of the proboscis, which represents a relatively long tip-region. The split proboscis and longer proboscis tip-regions would appear to be

advantageous for handling openly accessible food sources instead of inserting into the corolla for nectar feeding, as interpreted by Krenn (2010). Sensilla styloconica may be developed as a specialization for sucking free liquids. Although sensilla styloconica were previously regarded as restricted to nectar-feeding taxa, it is not surprising that they would also be found in some non-nectar feeding species (Krenn, 2010; Ma et al., 2019). It should be noted that early angiosperm flowers found in Kachin amber are typically small, and have a flat, trilobed nectar gland from which project three short, arched styles (Chambers et al. 2010; Poinar and Chambers, 2017), which could accommodate small pollinators with a proboscis, such as small scorpionflies and moths (Lin et al., 2019). Efficient nectar extraction requires a proboscis that roughly matches the length of the corolla tube (Torres and Galetto, 2002). The angiosperms have cup-shaped flowers with nectaries exposed externally, so they can be used by insects with short proboscides. Thus, we cannot exclude the possibility that the short proboscis of *Acanthocorona* might be suitable for nectar feeding from such small flowers with cup-shaped corollae.

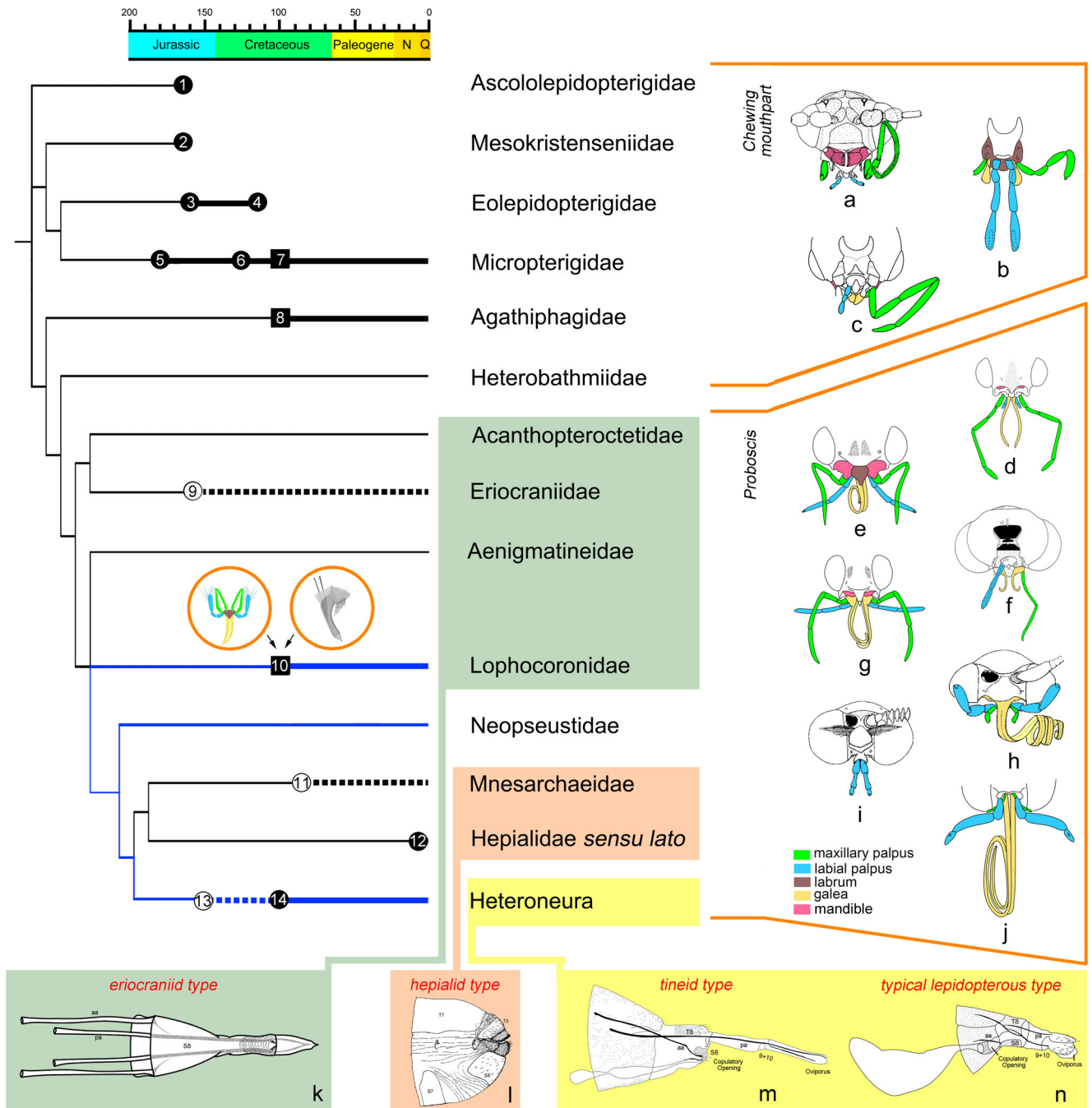


Fig. 8. Phylogeny of basal Lepidoptera. White circles indicate questionable fossil identifications; black circles indicate the fossil identifications based on reasonable evidence; black squares indicate the fossil records from the mid-Cretaceous amber of Myanmar. The numbers within the circles and squares represent the fossil records, see Appendix S2 for details. The taxa with sensilla styloconica on the proboscis are denoted by blue lines. The types of female terminalia are labelled in red [the female terminalia of Neopseustidae do not fit completely into these four types (Mutuura, 1972)]. (a) Micropterigidae, redrawn from Dugdale (1988); (b) Agathiphagidae, redrawn from Dumbleton (1952); (c) Heterobathmiidae, redrawn from Kristensen and Nielsen (1979); (d) Acanthopteroctetidae, redrawn from Davis (1978); (e) Eriocraniidae, redrawn from Davis (1978); (f) Lophocoronidae, redrawn from Nielsen and Kristensen (1996); (g) Neopseustidae, redrawn from Davis (1975); (h) Mnesarchaeidae, redrawn from Dugdale (1988); (i) Hepialidae, redrawn from Dugdale (1988); (j) Pyralidae, redrawn from Grimaldi and Engel (2005); (k) Eriocraniidae, redrawn from Davis (1978); (l) Hepialidae, redrawn from Dugdale (1994); (m) Tineidae, redrawn from Mutuura (1972); (n) Heliodinidae, redrawn from Mutuura (1972).

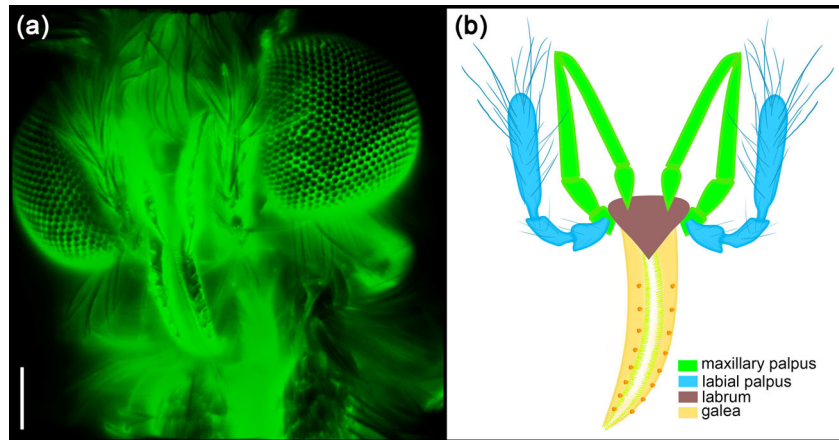


Fig. 9. Mouthparts of *Acanthocorona hedida* Zhang, Shih and Engel **sp. n.**, holotype, ♀, CNU-LEP-MA-2016016. (a) under confocal laser scanning microscopy; (b) reconstruction of mouthparts structure. Scale bar for (a) = 0.1 mm.

According to the above, the short and simple proboscis of *Acanthocorona* may have been used to drink water droplets, pollination drops from gymnosperms, nectar from early angiosperm flowers, or sap from injured leaves, as in many of the basalmost extant lineages of Lepidoptera (van Eldijk et al., 2018).

Ovipositor

Since few extant female lophocoronid specimens have been observed, let alone studied (Nielsen and Kristensen, 1996), the female postabdomen and oviposition are poorly understood. Fortunately, female lophocoronids found in Kachin amber provide more information about the female genitalia. Ovipositors of mid-Cretaceous lophocoronids are long, corresponding to well-developed internal apophyses (Figs. 2, 5c). The anterior apophyses arise from abdominal segment VIII, and the apex of the distally fused posterior apophyses forms a sawing organ (Figs. 2b, 5c). Lepidopteran apophyses serve as sites for the attachment of retractor muscles, which gives the ovipositor considerable flexibility and allow it to be retracted during rest and extended for oviposition (Scoble, 1992). Both retracted and extended states are present in our specimens, e.g., specimen CNU-LEP-MA-2016016 has a retracted ovipositor (Figs. 1f, 2a), while the abdomen and genitalia of CNU-LEP-MA-2016035 are curved with the ovipositor extended (Figs. 2b, 5c). The female terminalia of Lepidoptera can be classified into four categories: hepialid-type, typical lepidopterous-type, eriocraniid-type, and tineid-type (Fig. 8k–n, Mutuura, 1972). The mid-Cretaceous female lophocoronids with retractable female genitalia, well-developed internal apophyses, and a piercing apex are fundamentally the same as an eriocraniid-type ovipositor. The presence of an eriocraniid-type ovipositor also occurs in Eriocraniidae, Acanthopteroctetidae, and

Aenigmatineidae (Kristensen et al., 2015), although these families do not form a monophyletic group (Fig. 8). Kristensen (2003: 115) proposed a parsimonious explanation that eriocraniid-type ovipositor represents the glossatan groundplan. Kozlov et al. (2002: 266, fig. 300) provided a picture of an undescribed potential eriocraniid from the Late Jurassic of Karatau in Kazakhstan, but no information on terminalia was provided, if they were preserved at all. Accordingly, the eriocraniid-type ovipositor reported herein represents the earliest record of this terminal arrangement, and indicates this form of lepidopteran ovipositor is at least as old as the mid-Cretaceous.

Ovipositor shape is closely related to the mode and site of oviposition (Scoble, 1992). Lepidopteran eggs may be laid by injecting them into plant tissue, by inserting them into cracks and crevices, or by sticking them onto the surface of the substrate (Scoble, 1992). In the mid-Cretaceous female lophocoronids, the tip of the ovipositor is acute and the posteriorly united part of the posterior apophyses forms a knife with serrated lateral ‘saw’ for cutting host plants. The present-living basal Lepidoptera with this type of ovipositor, such as Eriocraniidae and Acanthopteroctetidae, are known to be leaf-mining moths (Eiseman, 2016). Thus, it is logical to suggest that the eggs of mid-Cretaceous lophocoronids were inserted into the tissue of food plants, and their larvae were likely internal feeders. This may also be true for modern Lophocoronidae.

Conclusion

Two new species of fossil Lophocoronidae – *Acanthocorona hedida* Zhang, Shih and Engel **sp. n.** and *Acanthocorona venulosa* Zhang, Shih and Engel **sp. n.** – are described and figured from mid-Cretaceous Kachin amber. A phylogenetic analysis of basal lepidopteran

lineages reveals: (1) *Acanthocorona* with the new species and *Lophocorona* form a monophyletic group; (2) Aenigmatineidae + Lophocoronidae + Myoglossata are considered here to be a clade; and (3) the clades of Myoglossata and Neolepidoptera are robustly supported. It is likely that short and simply structured proboscides of *Acanthocorona* were used to sip from openly accessible food sources, such as water droplets, pollination drops from gymnosperms, nectar from early flowers, or sap from injured leaves. Well-preserved retracted and extended ovipositors reported here indicate that these Cretaceous lophocoronids inserted eggs into the tissues of their host plants.

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Conflict of Interest

None declared.

References

- Bauder, J.A.-S., Handschuh, S., Metscher, B.D. and Krenn, H.W., 2013. Functional morphology of the feeding apparatus and evolution of proboscis length in metalmark butterflies (Lepidoptera: Riodinidae). *Biol. J. Linn. Soc.* 110, 291–304.
- Common, I.F.B., 1973. A new family of Daconypha (Lepidoptera) based on three new species from Southern Australia, with notes on the Agathiphagidae. *J. Aust. Ent. Soc.* 12, 11–23.
- Cruikshank, R.D. and Ko, K., 2003. Geology of an amber locality in the Hukawng valley, northern Myanmar. *J. Asian Earth Sci.* 21, 441–455.
- Chambers, K.L., Poinar, G., Jr. and Buckley, R., 2010. *Tropidogyne*, a new genus of Early Cretaceous eudicots (Angiospermae) from Burmese amber. *Novon* 20, 23–29.
- Chen, Q.X., Li, W.L., Chen, Y.W., Chen, J. and Song, Y.Q., 2018. Morphological comparison of proboscides and associated sensilla of *Helicoverpa armigera* and *Mythimna separata* (Lepidoptera: Noctuidae). *Arthropod Struct. Dev.* 49, 119–127.
- Davis, D.R., 1975. Systematics and Zoogeography of the Family Neopseustidae with a proposal of a new superfamily (Lepidoptera: Neopseustoidea). Smithsonian Institution Press, Washington D.C.
- Davis, D.R., 1978. A revision of the North American moths of the superfamily Eriocranioidea with the proposal of a new family, Acanthopteroctetidae (Lepidoptera). Washington D.C., Smithsonian Institution Press.
- Dugdale, J.S., 1988. Lepidoptera - annotated catalogue, and keys to family-group taxa. *Faun. New Zeal.* 14, 1–264.
- Dugdale, J.S., 1994. Hepialidae (Insecta: Lepidoptera). *Faun. New Zeal.* 30, 1–194.
- Dumbleton, L.J., 1952. A new genus of seed-infesting micropterygid moths. *Pac. Sci.* 6, 17–29.
- Eiseman, C.S., 2016. Notes on the larval hosts and habits of some north American Eriocraniidae and Acanthopteroctetidae. *J. Lepid. Soc.* 70, 79–81.
- Engel, M.S., 2020. Myanmar: palaeontologists must stop buying conflict amber. *Nature* 584, 525.
- Faucheux, M.J., 2008. Mouthparts and associated sensilla of a South American moth, *Synempora andesae* (Lepidoptera: Neopseustidae). *Rev. Soc. Entomol. Arge.* 67, 21–33.
- Faucheux, M.J., 2013. Sensillum types on the proboscis of the Lepidoptera: a review. *Ann. Soc. Entomol. Fr. (N.S.)* 49, 73–90.
- Goloboff, P.A., 1998. NONA, Version 2.0. Program and Documentation. American Museum of Natural History, New York.
- Goloboff, P.A., Farris, J.S. and Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24, 774–786.
- Grimaldi, D.A. and Engel, M.S., 2005. Evolution of the Insects. Cambridge University Press, New York.
- Grimaldi, D.A., Engel, M.S. and Nascimbene, P.C., 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *Am. Mus. Novit.* 3361, 1–71.
- Grimaldi, D.A. and Ross, A.J., 2017. Extraordinary Lagerstätten in amber, with particular reference to the Cretaceous of Burma. In: Fraser, N.C. and Sues, H.-D. (Eds.), *Terrestrial Conservation Lagerstätten: Windows into the Evolution of Life on Land*. Dunedin Academic Press, Edinburgh, pp. 287–342.
- Kawahara, A.Y., Plotkin, D., Espeland, M., Meusemann, K., Toussaint, E.F.A., Donath, A., Gimnich, F., Frandsen, P.B., Zwick, A.Z., dos Reis, M., Barber, J.R., Peters, R.S., Liu, S., Zhou, X., Mayer, C., Podsiadlowski, L., Storer, C., Yack, J.E., Misof, B., Breinholt, J.W., 2019. Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths. *Proc. Natl. Acad. Sci. U. S. A.*, 116, 22657–22663.
- Khranov, A.V., Bashkuev, A.S. and Lukashovich, E.D., 2020. The fossil record of long-proboscid nectarivorous insects. *Entomol. Rev.* 100, 881–968.
- Kozlov, M.V., 1989. New Upper Jurassic and Lower Cretaceous Lepidoptera (Papilionida). *Paleontol. J.* 23, 34–39.
- Kozlov, M.V., Ivanov, V.D. and Rasnitsyn, A.P., 2002. Order Lepidoptera Linné, 1758. The butterflies and moths (= Papilionida). In: Rasnitsyn, A.P. and Quicke, D.L.J. (Eds.), *History of Insects*. Kluwer Academic Publishers, Dordrecht, Boston and London, pp. 220–227.
- Krenn, H.W., 2010. Feeding mechanisms of adult Lepidoptera: structure, function, and evolution of the mouthparts. *Annu. Rev. Entomol.* 55, 307–327.
- Krenn, H.W. and Kristensen, N.P., 2000. Early evolution of the proboscis of Lepidoptera (Insecta): external morphology of the galea in basal glossatan moth lineages, with remarks on the origin of the pilifers. *Zool. Anz.* 239, 179–196.
- Kristensen, N.P., 1978. A new familia of Hepialoidea from South America, with remarks on the phylogeny of the suborder Exoporia (Lepidoptera). *Ent. Germ.* 4, 272–294.
- Kristensen, N.P., 1984. Studies on the morphology and systematics of primitive Lepidoptera (Insecta). *Steenstrupia* 10, 141–191.
- Kristensen, N.P., 1999. Lepidoptera, Moths and Butterflies Volume 1: Evolution, Systematics and Biogeography. Walter de Gruyter, Berlin, New York.
- Kristensen, N.P., 2003. Lepidoptera, Moths and Butterflies Volume 2: Morphology, Physiology and Development. Walter de Gruyter, Berlin, New York.

- Kristensen, N.P. and Nielsen, E.S., 1979. A new subfamily of micropterigid moths from South America. A contribution to the morphology and phylogeny of the Micropterigidae, with a generic catalogue of the family (Lepidoptera: Zeugloptera). *Steenstrupia* 5, 69–147.
- Kristensen, N.P., Scoble, M.J. and Karsholt, O.K., 2007. Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. *Zootaxa* 1668, 699–747.
- Kristensen, N.P., Hilton, D.J., Kallies, A., Milla, L., Rota, J., Wahlberg, N., Wilcox, S.A., Glatz, R.V., Young, D.A., Cocking, G., Edwards, T., Gibbs, G.W. and Halsey, M., 2015. A new extant family of primitive moths from Kangaroo Island, Australia, and its significance for understanding early Lepidoptera evolution. *Syst. Entomol.* 40, 5–16.
- Labandeira, C.C., Dilcher, D.L., Davis, D.R. and Wagner, D.L., 1994. Ninety-seven million years of angiosperm-insect association: Paleobiological insights into the meaning of coevolution. *Proc. Natl. Acad. Sci. U. S. A.* 91, 12278–12282.
- Lin, X.D., Labandeira, C.C., Shih, C.K., Hotton, C.L. and Ren, D., 2019. Life habits and evolutionary biology of new two-winged long-proboscid scorpionflies from mid-Cretaceous Myanmar amber. *Nat. Commun.* 10, 1235.
- Ma, L., Hu, K., Li, P., Liu, J. and Yuan, X., 2019. Ultrastructure of the proboscis sensilla of ten species of butterflies (Insecta: Lepidoptera). *PLoS ONE* 14, e0214658.
- Maddison, W. P. and Maddison D.R., 2018. Mesquite: a modular system for evolutionary analysis. Version 3.51. <http://www.mesquiteproject.org>
- Mey, W., Léger, T. and Lien, V.V., 2021. New taxa of extant and fossil primitive moths in South-East Asia and their biogeographic significance (Lepidoptera, Micropterigidae, Agathiphagidae, Lophocoronidae). *Nota Lepidopterologica* 44, 29–56.
- Misof, B., Liu, S. and Meusemann, K., 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science* 346, 763–767.
- Mitter, C., Davis, D.R. and Cummings, M.P., 2017. Phylogeny and evolution of Lepidoptera. *Annu. Rev. Entomol.* 62, 265–283.
- Mutuura, A., 1972. Morphology of the female terminalia in Lepidoptera, and its taxonomic significance. *Can. Entomol.* 104, 1055–1071.
- Mutanen, M., Wahlberg, N. and Kaila, L., 2010. Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. *Proc. R. Soc. B* 277, 2839–2848.
- Nielsen, E.S. and Kristensen, N.P., 1996. The Australian moth family Lophocoronidae and the basal phylogeny of the Lepidoptera – Glossata. *Invertebr. Syst.* 10, 1199–1302.
- Nixon, K.C., 2002. WinClada, Version 1.00.08. Program and Documentation, Cornell University, Ithaca, New York.
- Poinar, G., Jr., 2017. A new genus of moths (Lepidoptera: Gracillarioidea: Douglasiidae) in Myanmar amber. *Hist. Biol.* 31, 898–902.
- Poinar, G., Jr. and Chambers, K.L., 2017. *Tropidogyne pentaptera* sp. n., a new mid-Cretaceous fossil angiosperm flower in Burmese amber. *Palaeodiversity* 10, 135–140.
- Rasnitsyn, A.P. and Quicke, D.L.J., 2002. *History of Insects*. Kluwer Academic Publishers, London, Dordrecht, Boston.
- Regier, J.C., Mitter, C., Kristensen, N.P., Davis, D.R., Van Nieukerken, E.J., Rota, J., Simonsen, T.J., Mitter, K.T., Kawahara, A.Y., Yen, S.-H., Cummings, M.P. and Zwick, A., 2015. A molecular phylogeny for the oldest (nonditrysian) lineages of extant lepidoptera, with implications for classification, comparative morphology and life-history evolution. *Syst. Entomol.* 40, 671–704.
- Regier, J.C., Zwick, A., Cummings, M.P., Kawahara, A.Y., Cho, S., Weller, S., Roe, A., Baixeras, J., Brown, J.W., Parr, C., Davis, D., Epstein, M., Hallwachs, W., Hausmann, A., Janzen, D.H., Kitching, I.J., Solis, M.A., Yen, S.-H., Bazinet, A.L. and Mitter, C., 2009. Toward reconstructing the evolution of advanced moths and butterflies (Lepidoptera: Ditrysia): an initial molecular study. *BMC Evol. Biol.* 9, 280.
- Ross, A.J., 2021. Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2020. *Palaeoentomology* 4, 57–76.
- Scoble, M.J., 1992. *The Lepidoptera: Form, Function and Diversity*. New York, Natural History Museum Publications, Oxford University Press.
- Shi, G.H., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q. and Li, X., 2012. Age constraint on Burmese amber based on U-PB dating of zircons. *Cretaceous Res.* 37, 155–163.
- Shi, C., Cai, H.-H., Jiang, R.-X., Wang, S., Engel, M.S., Yuan, J., Bai, M., Yang, D., Long, C.-L., Zhao, Z.-T., Zhang, D.-X., Zhang, X.-C., Peng, H., Wang, Y.-D. and Spicer, R.A., 2021. Balance scientific and ethical concerns to achieve a nuanced perspective on 'blood amber'. *Nat. Ecol. Evol.* 5, 705–706.
- Simonsen, T.J., 2001. The wing vestiture of the non-ditrysian Lepidoptera (Insecta). *Comparative morphology and phylogenetic implications. Acta Zool.* 82, 275–298.
- Simonsen, T.J. and Kristensen, N.P., 2017. Revision of the endemic Brazilian 'neotheorid' hepialids, with morphological evidence for the phylogenetic relationships of the basal lineages of Hepialidae (Lepidoptera: Hepialoidea). *Arthropod Syst. Phylo.* 75, 281–301.
- Skalski, A.W., 1979. Records of the oldest Lepidoptera. *Nota Lepidopterologi.* 2, 61–66.
- Sohn, J.C., Labandeira, C.C., Davis, D. and Mitter, C., 2012. An annotated catalog of fossil and subfossil Lepidoptera (Insecta: Holometabola) of the world. *Zootaxa* 3286, 1–132.
- Szwedo, J., Wang, B.O., Soszyska-Maj, A., Azar, D. and Ross, A.J., 2020. International palaeoentomological society statement. *Palaeoentomology* 3, 221–222.
- Torres, C. and Galetto, L., 2002. Are nectar sugar composition and corolla tube length related to the diversity of insects that visit Asteraceae flowers? *Plant Biol.* 4, 360–366.
- van Eldijk, T.J.B., Wappler, T., Strother, P.K., van der Weijst, C.M.H., Rajaei, H., Visscher, H. and van de Schootbrugge, B., 2018. A Triassic-Jurassic window into the evolution of Lepidoptera. *Sci. Adv.* 4, e1701568.
- van Nieukerken, E.J., Kaila, L., Kitching, I.J., Kristensen, N.P., Lees, D.C., Minet, J., Mitter, C., Mutanen, M., Regier, J.C., Simonsen, T.J., Wahlberg, N., Yen, S.-H., Zahiri, R., Adamski, D., Baixeras, J., Bartsch, D., Bengtsson, B.A., Brown, J.W., Bucheli, S.R., Davis, D.R., de Prins, J., de Prins, W., Epstein, M.E., Gentili-Poole, P., Gielis, C., Hättenschwiler, P., Hausmann, A., Holloway, J.D., Kallies, A., Karsholt, O., Kawahara, A.Y., Koster, S., Kozlov, M., Lafontaine, J.D., Lamas, G., Landry, J., Lee, S., Nuss, M., Park, K.-T., Penz, C., Rota, J., Schintlmeister, A., Schmidt, B.C., Sohn, J.-C., Solis, M.A., Tarmann, G.M., Warren, A.D., Weller, S., Yakovlev, R.V., Zolotuhin, V.V. and Zwick, A., 2011. Order Lepidoptera Linnaeus, 1758. In: Zhang, Z.-Q. (Ed.), *Animal Biodiversity: An Outline of Higher-level Classification and Survey of Taxonomic Richness. Zootaxa* 3148, 212–221.
- Walker, J.D., Geissman, J.W., Bowring, S.A. and Babcock, L.E., 2012. The geological society of America geologic time scale. *Geol. Soc. Am. Bull.* 125, 259–272.
- Whalley, P.E., 1978. New taxa of fossil and recent Micropterigidae with a discussion of the evolution and a comment on the evolution of the Lepidoptera (Insecta). *Ann. Transv. Mus.* 31, 72–86.
- Wiegmann, B.M., Regier, J.C. and Mitter, C., 2002. Combined molecular and morphological evidence on the phylogeny of the earliest lepidopteran lineages. *Zool. Scr.* 31, 67–81.
- Wootton, R.J., 1979. Function, homology and terminology in insect wings. *Syst. Entomol.* 4, 81–93.
- Zhang, W.T., Shih, C.K., Labandeira, C.C., Sohn, J.C., Davis, D.R., Santiago-Blay, J.A., Flint, O. and Ren, D., 2013. New fossil Lepidoptera (Insecta: Amphiesmenoptera) from the Middle Jurassic Jiulongshan Formation, northeastern China. *PLoS One* 8, e79500.
- Zherikhin, V.V. and Sukatsheva, L.D., 1973. On Cretaceous "ambers" (retinites) with insects of North Siberia. In: Narchuk,

E.P. (Ed.), Problems in insect palaeontology, XXIV annual lectures in memory of N.A. Kholodkovskogo, 1–2 April 1971. Nauka Press, Leningrad, pp. 3–48 [In Russian].

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Character matrix, comprising 36 taxa and 65 characters.

Appendix S2 The list of fossil specimens cited in Fig. 8 with the literature sources of the described fossil species.

Appendix S3 The 3D reconstruction of head for *Acanthocorona hedida* Zhang, Shih and Engel **sp. n.** (holotype, ♀, CNU-LEP-MA-2016016).

APPENDIX

Morphological character descriptions and character argumentation

1. Antennal scape and pedicel: normal (0); enlarged (1).
2. Antennal sensilla auricillica: absent (0); present (1). [Sensilla auricillica are absent in Lophocoronidae, Neopseustidae and Mnesarchaeidae (Nielsen and Kristensen, 1996).]
3. Antennal ascoids: absent (0); present (1).
4. Intercalary sclerite: absent (0); small, microtrichiated, restricted to the membrane between scape and pedicellus (1); elongate, basal end sunken into a pocket below terminal edge of scape (2). [The presence of intercalary sclerite is considered a lepidopteran groundplan autapomorphy (Kristensen, 2003), and elongated intercalary sclerite is an autapomorphy of hepialoid (Simonsen and Kristensen, 2017).]
5. Dorsal cranial condyles at antennal base: absent (0); present (1). [Dorsal cranial condyle independently evolved at least in the Lophocoronidae and the Exoporia (Nielsen and Kristensen, 1996; Kristensen, 2003: 42).]
6. Ocellus: present (0); absent (1). [Nielsen and Kristensen, 1996]
7. Chaetosema (known also as Jordan's or Eltringham's organ): absent (0); present (1). [The postmentum in Lophocoronidae lacks the chaetosema found in Agathiphagidae, Eriocraniidae and Mnesarchaeidae (Compton, 1973).]
8. Epistomal sulcus (frontoclypeal sulcus): well-developed, with pronounced cuticular thickening (0); a zone of close-set grooves, cuticle of individual grooves without pronounced thickening (1); absent, clypeus not in any way demarcated from frons (2). [Nielsen and Kristensen, 1996]
9. Galeae linking mechanism: absent (0); galeae are linked to each other by dorsal and ventral legulae to form the food canal (1).
10. Proboscis: absent (0); developed (1); fully reduced, non-coilable (2). [The proboscis is reduced and probably non-functional in all Hepialoidea (Krenn and Kristensen, 2000).]
11. Proboscis: without double-tube structure (0); proboscis with a unique double-tube structure, the inner wall of each galea being strongly concave and forming by itself a functionally closed tube (1).
12. Intrinsic proboscis musculature: absent (0); present (1). [Nielsen and Kristensen, 1996]
13. Mandible: functional (0); non-functional (1).
14. Lacinia: lobe-like (0); vestigial or absent (1).
15. Labrum: generalized (0); without frontal retractors (1). [Within the Glossata, labrum with extrinsic (frontal) retractor muscles is retained in Eriocraniidae and Acanthopteroctetidae (Nielsen and Kristensen, 1996).]
16. Postlabial area: with arched, setose/scaly sclerotisation (0); membranous and naked (1). [Nielsen and Kristensen, 1996]
17. Maxillary palpus: pentamerous (0); tetramerous (1); at most trimerous (2).
18. Labial palpus: trimerous (0); dimerous (1); tetramerous (2); absent (3).
19. vom Rath's organ: absent (0); terminal labial palpomere with vom Rath's organ located in a depression (1).
20. Maxillary palpus and labial palpus: maxillary palpus longer than labial palpus (0); maxillary palpus shorter than labial palpus (1).
21. Paraglossae: present (0); absent (1).
22. Posteromedial arms on the cervical sclerites: absent (0); present (1). [*Aenigmatinea* and acanthopteroctetids share the absence of posteromedial arms on the cervical sclerites, otherwise ascribed to the lepidopteran ground pattern and occurring throughout the homoneurans (Kristensen et al., 2015).]
23. Metathoracic furcal stem: without anteromedial process (0); with anteromedial process (1). [Anteromedial process is absent in Microptergidae and Trichoptera, but present in Aglossata and the glossatan groundplan (Kristensen and Nielsen, 1979; Kristensen, 1984)]
24. Precoxal bridge: absent (0); between the prothoracic pleuron and sternum (1). [Aenigmatineidae and neopseustids share a strong

- precoxal bridge that have been paralleled in the Heteroneura (Nielsen and Kristensen, 1996; Kristensen et al., 2015).]
25. Foretibia: with two spurs (0); with one spur (1); without spur (2).
 26. Mesotibia: with four spurs (0); with two spurs (1); with one spur (2); without spur (3).
 27. Metatibia: with four spurs (0); with two spurs (1); without spur (2).
 28. Epiphysis: absent (0); present (1).
 29. Wing venation on fore- and hind wings: homoneurous (0); heteroneurous (1).
 30. Microtrichia on forewing: present (0); absent (1).
 31. Scales on wings: absent (0); present (1).
 32. Herring-bone on scale: absent (0); present (1). [Herring-bone patterning is present only in the three most primitive extant families of Lepidoptera, i. e. Micropterigidae, Agathiphagidae, and Heterobathmiidae (Simonsen, 2001)]
 33. Nygmata on wings: located at the base of the $Rs_3 + Rs_4$ vein (0); absent (1).
 34. Humeral vein: absent (0); present (1).
 35. Sc on forewing: unforked (0); forked (1). [The forewing Sc is forked in several primitive Lepidoptera, and this condition is believed to be plesiomorphous in both Lepidoptera and Trichoptera (Kristensen and Nielsen, 1979).]
 36. R on forewing: forked (0); unforked (1).
 37. Rs on forewing: 4-branched (0); less than 4-branched (1).
 38. Rs on forewing: Rs dichotomously branched (0); Rs pectinately branched (1); Rs_1 and Rs_2 totally coalescent (2); Rs_2 and Rs_3 partly or totally coalescent (3).
 39. Rs_3 on forewing: terminating preapical/apical (0); terminating postapical (1).
 40. Rs_4 on forewing: terminating preapical/apical (0); terminating postapical (1).
 41. M vein on forewing: 4-branched (0); 3-branched (1); 1-branched (2).
 42. Anal veins: two anal veins form a single Y-shaped (0); three anal veins form a double Y-shaped, 3A coalesces with 2A and the combined vein then coalesces with 1A (1); three anal veins form a trident-shaped, 1A and 2A coalesce first and the combined vein then joined by 3A (2); only one anal vein present (3).
 43. M vein: M_1 and M_2 are stalked beyond crossvein r-m (0); free section of M_1 meeting crossvein r-m and markedly angulate at this junction (1).
 44. Crossvein sc-r on forewing: present (0); absent (1). [The presence of a crossvein sc-r is to be plesiomorphous in Amphiesmenoptera, since it is normally present in Trichoptera and Aglossata, and a parallel loss of this crossvein occurred in the Glossata (Kristensen and Nielsen, 1979). The absence of crossvein sc-r is a synapomorphy of the Heterobathmiina and Glossata (Kristensen, 1984).]
 45. Crossvein r-rs on forewing: present (0); absent (1).
 46. Crossvein m on forewing: absent (0); present (1).
 47. Crossvein m-cu on forewing: absent (0); present (1).
 48. Jugate on forewing: present (0); absent (1).
 49. Costal margin of hind wing: without frenular bristles (0); with frenular bristle (1).
 50. First abdominal tergum: normal (0) first abdominal tergum with sharply upturned anterior part (1). [The sharply upturned anterior part of the first abdominal tergum previously considered the diagnostic specialization of Myoglossata (Nielsen and Kristensen, 1996), is lacking in acanthopteroctetids and *Aenigmatinea* (Kristensen et al., 2015).]
 51. Abdominal glands on 5th sternite: present (0); absent (1). [Nielsen and Kristensen, 1996]
 52. Spermathecal duct: simple, without distinct spiral coiling (0); at least on part of its course distinctly spiralled (1). [Nielsen and Kristensen, 1996]
 53. Spermathecal duct: simple (0); the division of the spermatheca duct into two sections (1). [The two-compartment duct structure has been considered to be an important groundplan autapomorphy of a clade comprising all non-micropterigid Lepidoptera (Kristensen, 2003).]
 54. Transverse muscles in male postgenital segments: not developed (0); very strong development (1). [Very strong development of transverse muscles in male postgenital segments is well known from Hepialoidea (Nielsen and Kristensen, 1996)]
 55. Transtilla in male genitalia: absent (0); present (1). [*Aenigmatinea* and acanthopteroctetids share in their male genitalia the remarkably similarly shaped ‘transtilla’, otherwise unrecorded in the homoneurous grade (Kristensen et al., 2015).]
 56. Sclerotized tubular intromittent organ on male genitalia: present (0); male genitalia without sclerotized tubular intromittent organ (1). [The absence of sclerotized tubular intromittent organ is a probable synapomorphy of Mnesarchaeoidea and Hepialoidea (Kristensen, 1978)]
 57. Valva: without long spikes (0); long spikes originating from the inner side of the base of the valva (1).
 58. Valva: large and protruding (0); greatly shortened (1). [Valvae greatly shortened is a probable autapomorphy of Eriocraniidae (Kristensen, 1999: 51)]

59. Female genital apparatus: single genital orifice (0); separate copulatory orifice and ovipore (1).
60. Oviscapt: without piercing apex (0); with piercing apex (1).
61. Female with complex ‘vaginal sclerite’ in posterior part of genital chamber encircling egg passage: absent (0); present (1). [The presence of complex ‘vaginal sclerite’ is a probable autapomorphies of Eriocraniidae (Kristensen, 1999: 51)]
62. Apodemes (=apophyses): absent (0); present (1).
63. Larval head capsule: without adfrontal and hypostomal ridges (0); with prominent adfrontal and hypostomal ridges (1). [Head capsule with prominent adfrontal and hypostomal ridges are probable synapomorphies with *Glosata* (Kristensen, 1999).]
64. Larval prolegs: absent (0); present on III-VI and X, with crotchets and extrinsic muscles (1). [Nielsen and Kristensen, 1996]
65. The pupal mandibles: without apical teeth (0); bear apical teeth (1).