Cretaceous Research 138 (2022) 105270

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Short communication

A new Aenictopecheidae from mid-Cretaceous amber of northern Myanmar (Insecta: Hemiptera)

Jiu-Yang Luo [a, b], Qiang Xie [a, b, *]

[a] State Key Laboratory of Biocontrol, Sun Yat-sen University, 135 Xingangxi Road, Guangzhou, 510275, Guangdong, China
[b] School of Life Sciences, Sun Yat-sen University, 135 Xingangxi Road, Guangzhou, 510275, Guangdong, China

ARTICLE INFO

Article history:
Received 17 November 2021
Received in revised form
16 May 2022
Accepted in revised form 1 June 2022
Available online 9 June 2022

Keywords:
Burmese amber
Lebanese amber
Heteroptera
Aenictopecheidae
New genus and species

ABSTRACT

A new genus and species of unique-headed bug, *Cretocephalus stysi* gen. et sp. nov., is described based on a well-preserved specimen from mid-Cretaceous amber from northern Myanmar. Habitus photographs of the male holotype, photographs and drawings of detailed characters of head, legs, thorax, and photographs under epifluorescence of abdomen and terminalia are provided. The new genus exhibits remarkable differences in the diagnostic characters of all four known aenictopecheid subfamilies. However, it also shares several important characters with Aenictopecheinae, Maoristolinae, and Nymphocorinae. The morphological characters of *Cretocephalus* in pronotum, leg armature, and forewing may provide new insights on the morphological diversity and the higher classification system of this family. Additionally, the fossil genera *Paenicotechys* (Aenictopecheidae) and *Enicocephalinus* (Enicocephalidae) are briefly reviewed and the latter is transferred to Aenictopecheidae.

1. Introduction

Burmese amber, also known as Burmite, is a resin material of Myanmar, mainly from Hukawng Valley of Kachin state. The abundant and highly diverse of Burmese amber inclusions indicate that it probably is one of the most diverse fauna of Mesozoic microbiotas (Grimaldi et al., 2002). Like other groups of insects, Heteroptera display rich diversity in Burmite, and more than 16 families and 50 species have been reported so far (eg. Chen et al., 2019; Du et al., 2019; Tihelka et al., 2020; Heiss & Golub 2021; Ross, 2021).

Enicocephalomorpha, commonly called as unique-headed bugs, is a poorly known group of true bugs. It has long been recognized as one of the basal infraorders within Heteroptera on the basis of morphological and molecular evidence (Schuh 1979; Schuh and Slater 1995; Li et al., 2017; Johnson et al., 2018; Wang et al., 2019). This infraorder comprises two families, Enicocephalidae and Aenictopecheidae. According to recent estimates, about 430 extant species of Enicocephalomorpha have been described, with about 95% of species belonging to Enicocephalidae (Wygodzinsky and Schmidt 1991; Štys 2002; Henry 2017; Schuh and Weirauch 2020). So far, the extant Aenictopecheidae comprise 4 subfamilies, 11 genera, and 22 species worldwide (Štys 1989, 2002; Štys and Baňař 2008, 2013). Fossil Enicocephalomorpha consist of 8 genera and 14 species (Luo et al., 2021), of which only one is an aenictopecheid. Cockerell (1916) described the first fossil enicocephalid species, *Enicocephalus fossilis* Cockerell, 1916 from Burmese amber. Then, Cockerell (1917) described three more fossil enicocephalid species also from Burmese amber. Half a century later, Štys (1969) revised all the species described by Cockerell and established the new genus *Paenicotechys* Štys, 1969 for *Enicocephalus fossilis* and placed it in Aenictopecheidae. Since then, there have beenno more reports of fossil aenictopecheids.

Jeannel (1942), Štys (1969), Grimaldi et al. (1993), Maldonado-Capriles et al. (1996), Azar et al. (1999), and Štys (2010) discussed the possible systematic position of fossil representatives of Enicocephalomorpha, but the relationships between fossil and extant taxa are still unclear. Recent studies have examined in detail the head (Spangenberg et al., 2013) and abdominal (Davranoglou et al., 2017) morphology of extant Enicocephalomorpha, but there is no comprehensive comparative morphological study or a cladistic analysis that includes both extant and fossil species so far. After more than 105 years since the description of the first Burmite aenictopecheid, we describe herein a new genus and species *Cretocephalus stysi* gen. et sp. nov. in Aenictopecheidae, which may improve our understanding of the morphological diversity and evolutionary history of Aenictopecheidae.

* Corresponding author. State Key Laboratory of Biocontrol, Sun Yat-sen University, 135 Xingangxi Road, Guangzhou, 510275, Guangdong, China.
E-mail address: xieq8@mail.sysu.edu.cn (Q. Xie).

https://doi.org/10.1016/j.cretres.2022.105270
0195-6671/

Previously, 14 fossil species belonging to 8 genera have been reported in Enicocephalomorpha, except *Paenicotechys fossilis* (Cockerell, 1916), the other 13 species are all placed in Enicocephalidae. Among these 13 species, *Enicocephalinus acragrimaldii* Azar, Fleck, Nel & Solignac, 1999 was once thought to possess similar characters to Aenictopecheidae (Azar et al., 1999). Indeed, several characters of *Enicocephalinus acragrimaldii* correspond to the following diagnostic features of Aenictopecheidae: posterior lobe of pronotum abbreviated, poorly defined; forewing with distinct short costal fracture; pygophore not subdivided into tergum, laterotergites, and sternum; phallus typically heteropteran; with movable parameres. These characters suggest the need of reconsiderations of its family placement.

2. Materials and methods

The specimen used in this study originated from an amber mine near Noije Bum Village of Tanai Town, Hukawng Valley (Kachin Province) in northern Myanmar (Fig. 1), and obtained by the authors from amber merchant in Tengchong, Yunnan Province, China in July 2015 (see 'Ethical Statement Affidavit' in Supplementary Material). The amber deposits of northern Myanmar have been radiometrically dated at 98.79 ± 0.62 Ma, earliest Cenomanian, based on U–Pb zircon dating of the volcanoclastic matrix (Shi et al., 2012).

The fossil specimen was examined using a Zeiss Discovery V20 stereomicroscope. Measurements (in mm) were taken using Zeiss ZEN 2.5 pro software. Habitus photographs were taken by using a Canon EOS 7D Mark II camera equipped with a tube lens and Mitutoyo M Plan Apo 10X objective lens. Photographs of detailed morphology were taken using a Zeiss Discovery V20 stereomicroscope and Zeiss ZEN 2.5 pro software. The photograph under epifluorescence was taken using Nikon SMZ 25 stereomicroscope. Drawings were made using Zeiss Discovery V20 with a camera lucida. The maps of the amber mine were prepared using SimpleMappr (http://www.simplemappr.net/). The type specimen of *Cretocephalus stysi* gen. et sp. nov. is deposited in the Museum of Biology, Sun Yat-sen University (SYSBM), Guangzhou, China (see 'Museum Catalogue Entry' in Supplementary Material).

The terminology used here mainly follows Wygodzinsky and Schmidt (1991), Grimaldi et al. (1993), Azar et al. (1999), and Štys et al. (2010). Abbreviations used in figures: a – antenna; 1An – first anal vein; 2An – second anal vein; 1An+2An – vein fused with first anal vein and second anal vein; at – antennifer; BC – basal cell; C – costa; cf – costal fracture; cl – clypeus; clf – claval fracture; co – collum; Cu – cubitus; Cu1a – first terminal of cubitus anterior; Cu1b – second terminal of cubitus anterior; Cu-an – crossvein connecting cubitus and the vein fused by first anal vein and second anal vein; DC – discal cell; e – eye; fta – foretarsus; fti – foretibia; ht – hind tibia; ic – inner claw; la – labium; lp – left paramere; ls – lamellar spiniform setae; M – media; m-cu – crossvein connecting media and cubitus; M + Cu – vein fused by media and second cubitus; mf – medial fracture; mlp – middle lobe of pronotum; mp – mandibular plate; mt – middle tibia; o – ocelli; oc – outer claw; p – pronotum; pes – proepisternum; pem – proepimeron; plh – posterior lobe of head; plp – posterior lobe of pronotum; ph – phallus; py – pygophore; R – radius; R1 – first terminal of radius; rp – right paramere; r-m – crossvein connecting radius and media; Rs – radial sector; s – sternite; Sc – subcostal; tp – triangular process; tss – thick spiniform setae of apicitibial armature; tsi – thick spiniform setae on inner margin of fore tibia; wcm – wing coupling mechanisms.

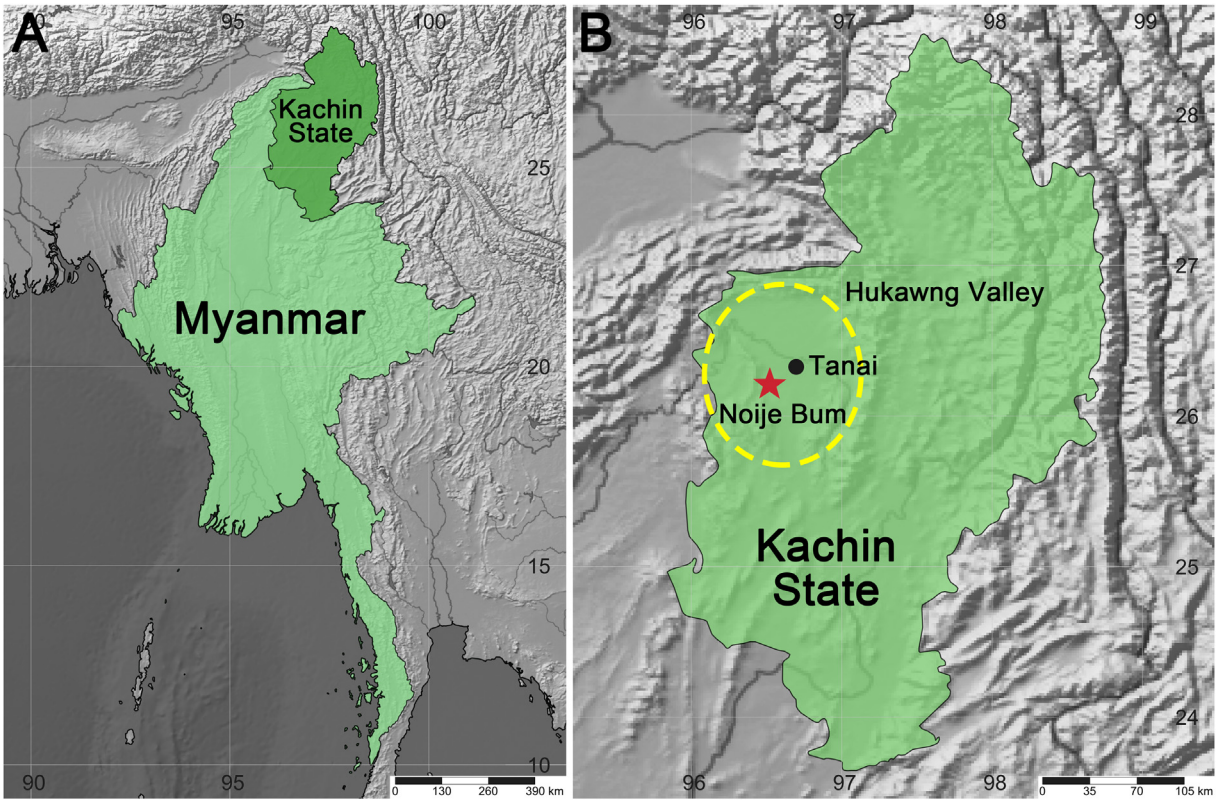

Fig. 1. Map of the amber locality near Tanai Village in Hukawng Valley, Kachin State of Myanmar. The red star represents the locality of amber mine. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Fig. 2. *Cretocephalus stysi* gen. et sp. nov., male holotype, SYS-XLAB-MMR-HET-21056, habitus. A. Dorsal view. B. Ventral view. Scale bars = 0.5 mm.

3. Systematic paleontology

Order Hemiptera Linnaeus, 1758
Suborder Heteroptera Latreille, 1810
Infraorder Enicocephalomorpha Stichel, 1955
Family Aenictopecheidae Usinger, 1932

Genus ***Cretocephalus*** gen. nov.
(Figs. 2–5)
ZooBank LSID: urn:lsid:zoobank.org:act:03798FC9-B2B9-404D-949F-6BAE182F130A

Etymology. Generic name is combination of Latin root, creta (chalk) and latinized Greek word cephalus (head); alludes to "unique headed bug from Cretaceous period", masculine.
Type species: *Cretocephalus stysi* sp. nov. by present designation.
Diagnosis. *Cretocephalus* gen. nov. could be placed in Aenictopecheidae based on the forewing with distinct short costal fracture; well-developed movable parameres; and pronotum seemingly consisting of 2 lobes. The new genus can be distinguished from other aenictopecheids by the following combination of characters: (1) pronotum seemingly consisting of 2 lobes; (2) tarsal formula 1-2-2; basal cell of forewing slender; (3) ventral surface of foretibia with 2 thick spiniform setae; (4) foretibia with 7 spiniform setae and the innermost 2 blade-shaped lamellar; (5) ventral surfaces of middle and hind tibia with spiniform setae; (6) dorsum of distal portion of foretibia with a triangular process (Table 1).
Description. **Body and coloration.** Small sized (2.61 mm), elongate, and relatively flattened, appendages slender (Figs. 2A–B). Body yellowish brown to brown, head, prothorax and genitalia darker. **Integument and vestiture.** Body with moderate density of fine, short, semi-erect setae; antenna and legs with dense semi-erect to erect setae; basal area of veins with short sparse setae, and outer edge of forewing with relatively dense short setae; dorsal margin of middle and hind tibiae, and paramere with prominent long setae (Figs. 2A–B, 3A).

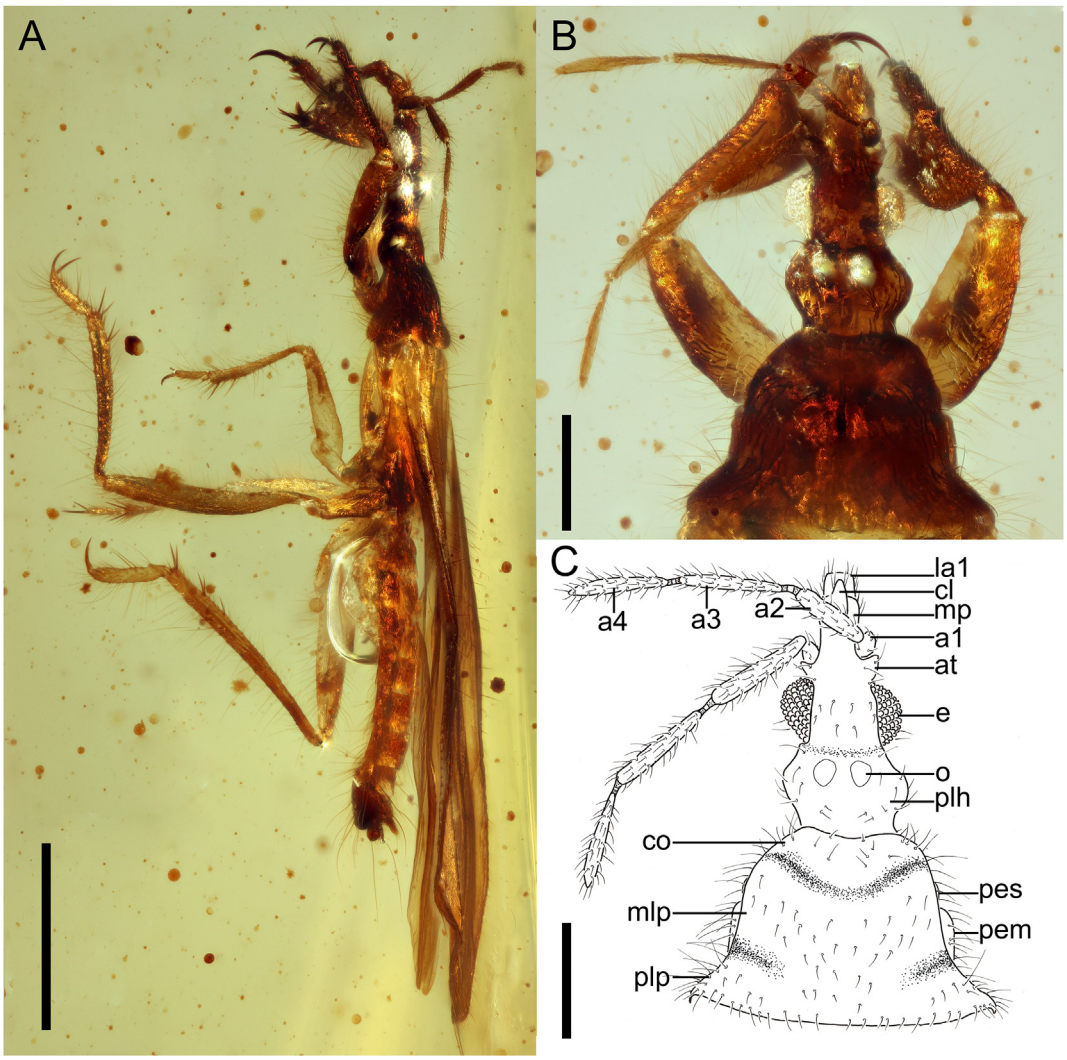

Fig. 3. *Cretocephalus stysi* gen. et sp. nov., holotype (male), SYS-XLAB-MMR-HET-21056, habitus and morphological details of head and pronotum. A. Lateral view. B. Head and pronotum, dorsal view. C. Head and pronotum, dorsal view. Scale bars = 0.5 mm (A), 0.2 mm (B–C). Abbreviations: a1–4 = antennal segment 1–4; at = antennifer; cl = clypeus; co = collum; e = eye; la1–4 = labium segment 1–4; mlp = middle lobe of pronotum; mp = mandibular plate; o = ocellus; pes = proepisternum; pem = proepimeron; plh = posterior lobe of head; plp = posterior lobe of pronotum.

Structures. **Head.** Long and flat, the length of head longer than pronotum. Postocular constriction distinct and shallow, only present on dorsum. Antennae clavate and four-segmented, shorter than head and pronotum together, segment I shortest and widest, segments II–IV subequal in length (Fig. 4A). Eyes medium sized, strongly developed ventrally. Antennifer short, prominent. Posterior lobe of head globular and wide, with the length half of the width (Fig. 3B–C). Neck present. Ocelli present, normally developed. Labium short, third segment longest (Figs. 3A, 4A).

Thorax and appendages. Pronotum bell shaped, flat and wide, wider than long (Fig. 3B–C). Collum present, relatively flat, delimited by a shallow postcollar furrow. Middle area of the postcollar furrow shallower than sides. Middle of lateral margin of pronotum slightly concave. Middle lobe slightly convex delimited from posterior lobe by shallow impression on lateral margins, middle region with impression indistinct, boundaries of posterior lobe indistinguishable (Fig. 3C). Posterior lobe narrow and slightly globular, posterior margin slightly convex. Mesoscutellum triangular, rounded apically. Propleuron small, with minute proepisternum and apically rounded proepimeron. Both proepisternum and proepimeron visible in dorsal view (Fig. 3B–C). Fore acetabula, distinctly open behind (Fig. 2B). Forelegs distinctly stout, tibia shorter than femur. Forecoxae broad, trochanter short, femur robust, with ventral furrow. Foretibia significantly thickened towards apex, distal ventral portion with conspicuous process with apicitibial armature. Dorsum of distal portion of foretibia with a triangular process (Fig. 4C, E–F). Bristle comb of foretibia present. Apicitibial armature consisting of 7 thick spiniform setae, including two blade-shaped lamellar spiniform setae (Fig. 4C, E–F), arranged in a) ventral row of two blade-shaped lamellar spiniform setae; b) medial row of three robust, long spiniform setae; and c) two thinner and shorter setae placed above setae of the medial row. Ventral surface of foretibia with two thick spiniform setae. Tarsus one-segmented, tarsal armature consisting of four spiniform setae, distal inner one semicircular (Fig. 4C, E–F), similar to the enicocephalid genus *Enicocephalus* Westwood, 1837. Inner foreclaw slightly shorter than the outer one. Mesoscutellum large, and apically rounded. Mesosternum developed, convex. Middle coxae distinctly separated. Middle femur and tibia slender, middle tibia with two spiniform setae on apex (Fig. 4D, G). Middle tarsus two segmented, with two unequal claws, inner claw longer than the outer one. Metasternum small, and hind coxae subcontiguous. Hind femur

Table 1
Diagnostic characters of all subfamilies and fossil genera of Aenictopecheidae.

Characters		† *Cretocephalus*	† *Enicocephalinus*	† *Paenicotechys*	Aenictopecheinae	Maoristolinae	Murphyanellinae	Nymphocorinae
1	Compound eye	normal	normal	normal	normal	normal	normal	reduced to a single ommatidium
2	Tarsal formula	1-2-2	1-1-1	1-2-2	1-2-2	2-22	1-1-1	1-1-1
3	Shape of pronotum	seemingly 2 lobes	indistinctly 3 lobes	unilobate	seemingly 2 lobes	seemingly 2 lobes	distinct 3 lobes	seemingly 2 lobes
4	Rs of forewing	nonbranching	nonbranching	nonbranching	nonbranching	branching	nonbranching	absent
5	Costal fracture on forewing	present	present	present	present	present	absent	absent
6	Number of thick spiniform setae on apex of foretibia	7	7	3	6	8	3 or 5	4 or 6
7	Number of spiniform setae on foretarsus	4	2	unknown	2 or 4	4	0	4
8	A notch dividing apical armature on foretibia into two clusters	absent	absent	absent	present	absent	absent	absent
9	Thick spiniform setae on ventral surface of foretibia	two thick spiniform setae on ventral surface of foretibia	absent	absent	absent	absent	absent	one or two thick spiniform setae on ventral surface of foretibia
10	Composition of apical armature on foretibia	with two blade-shaped lamellar spiniform setae	with two blade-shaped lamellar spiniform setae	all setae	with two rounded or bilobate, peglike spiniform setae	all setae	all setae	all setae
11	Thick spiniform setae on ventral face of middle and hind femora	absent	absent	absent	absent	absent	absent	present
12	Phallus	unknown	probably non-inflatable	unknown	non-inflatable	inflatable	inflatable or beaklike	inflatable
13	Paremeres	movable	movable	probably movable	movable	movable	movable, probably immobile in *Timahocoris*	movable

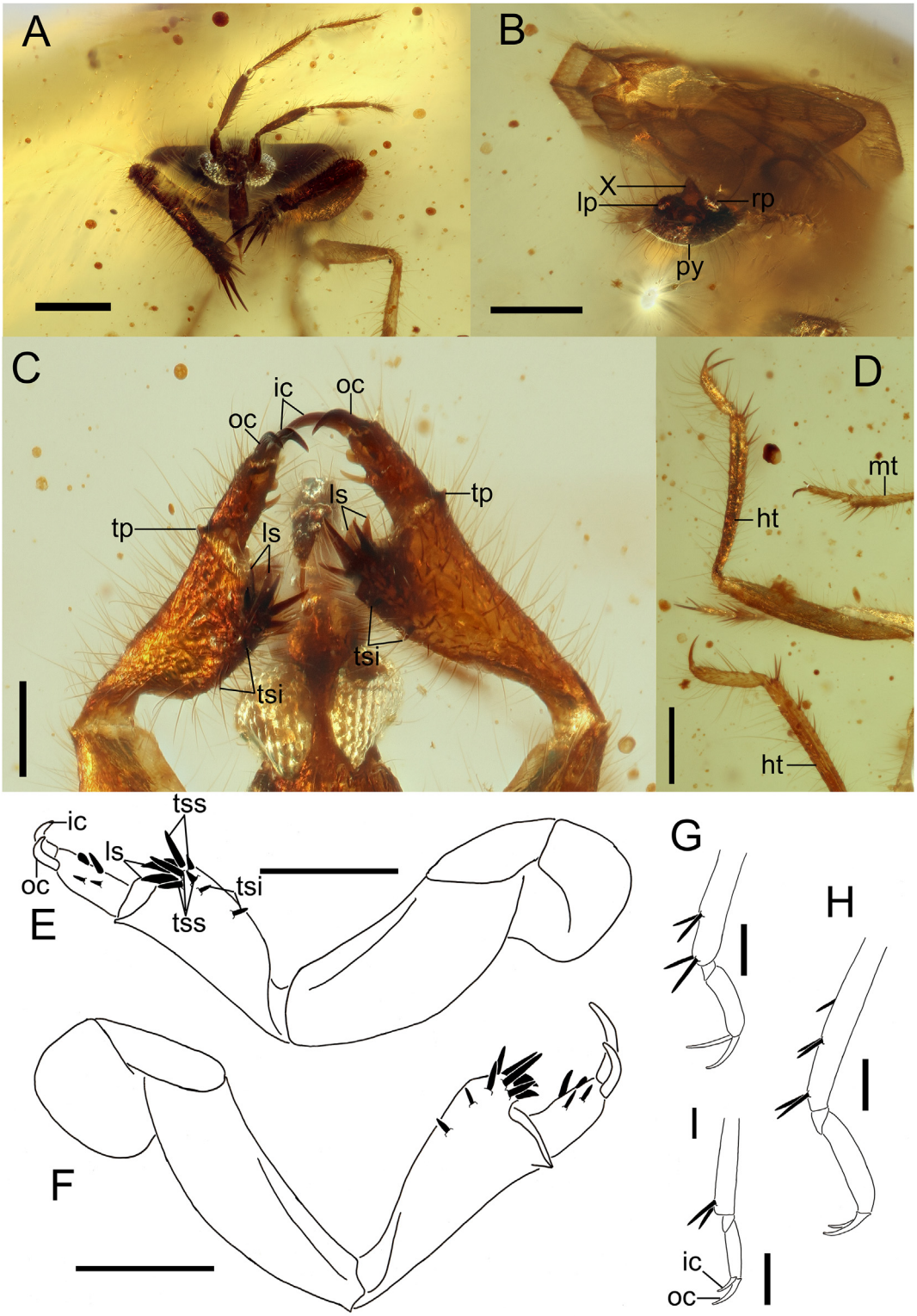

Fig. 4. *Cretocephalus stysi* gen.et sp. nov., holotype (male), SYS-XLAB-MMR-HET-21056, morphological details of head, terminalia and legs. A. Head, prothorax and forelegs, frontal view. B. Terminalia, caudal view. C., ventral view. D. Middle and hind legs. E. right foreleg. F. left foreleg. G. left hind leg. H. right hind leg. I. right middle leg. Scale bars = 0.2 mm (A–B, D–F), 0.1 mm (C, G–I). Abbreviations: ht = hind tibia; ic = inner claw; lp = left paramere; ls = lamellar spiniform setae; mt = middle tibia; oc = outer claw; py = pygophore; rp = right paramere; tp = triangular process; tsi = thick spiniform setae on inner margin of foretibia; tss = thick spiniform setae of apicitibial armature; x = segment X.

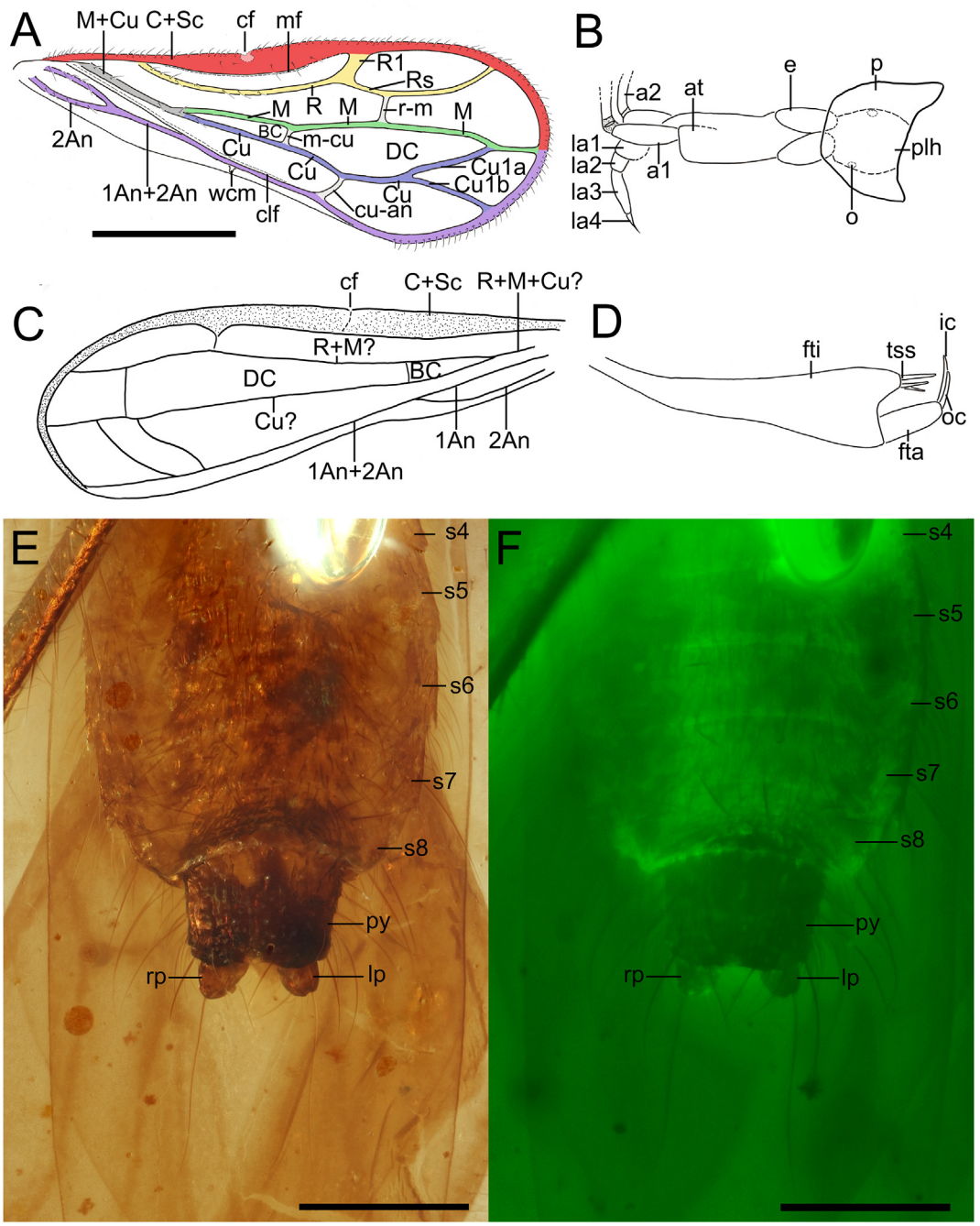

Fig. 5. *Cretocephalus stysi* gen. et sp. nov., holotype (male) SYS-XLAB-MMR-HET-21056 (A, E, F) and *Paenicotechys fossilis* (Cockerell, 1916), holotype (B–D), morphological details. A. Right forewing, dorsal view. B. Head and pronotum, latero-dorsal view, based on (Štys, 1969: Fig. 1). C. Forewing, dorsal view, based on (Štys, 1969: Fig. 3). D. Foreleg, based on (Štys, 1969: Fig. 2). E. distal part of abdomen and genitalia. F. distal part of abdomen and genitalia under epifluorescence. Scaler bars = 0.5 mm (A), 0.2 mm (E–F). Abbreviations: a1–2 = antennal segment 1–2; at = antennifer; e = eye; cf = costal fracture; clf = claval fracture; fta = foretarsus; fti = foretibia; ic = inner claw; la1–4 = labium segment 1–4; lp = left paramere; o = ocellus; oc = outer claw; p = pronotum; plh = posterior lobe of head; py = pygophore; rp = right paramere; s4–8 = abdominal sternite 4–8; tss = thick spiniform setae of apicitibial armature; wcm = wing coupling mechanisms.

and tibia slender, apices of left hind tibia with two spiniform setae on apex, two on ventral margin near apex, right hind tibia with one additional spiniform seta on ventral margin (Fig. 4D, G–H). Forewings macropterous, narrowly oval, apex rounded, exceeding abdominal apex. Forewing with a distinct short costal fracture, on 2/5 from the base of whole wing. Venation as in members of Aenictopecheinae, with a triangular basal cell and a closed discal cell, the former over 1/2 as long as the latter. 1An and 2An well separated before half of clavus. Wing coupling mechanism of forewing near center of inner margin (Fig. 5A).

Pregenital abdomen. Abdomen narrowly oval, flattened, moderately sclerotized (Figs. 3A, 5E–F); segment II to VIII can be differentiated, posterior margin of tergites II to VIII with membrane area exposed, membrane area of sternites II to VIII not exposed (Figs. 3A, 5E–F). Pleural membrane and spiracles of each segment not visible in ventral view.

Male genitalia. Male pygophore enlarged, strongly sclerotized, not invaginated into eighth segment. Lateral margin of pygophore nearly straight, posterior margin concave. Proctiger sclerotized exceeding apex of pygophore (Fig. 3A). Parameres sclerotized, symmetrical, rounded apically, with a conspicuously long setae on each one (Fig. 5E–F).
Female unknown.

Cretocephalus stysi gen. et sp. nov.
ZooBank LSID: urn:lsid:zoobank.org:pub:4D8AE178-E2EC-46B7-B049-7ECD73EC698A

Etymology. The specific epithet is patronymic, dedicated to the memory of Prof. Pavel Štys (1933–2018), an eminent specialist in morphology, taxonomy, systematics and biology of Heteroptera, especially in Enicocephalomorpha and Dipsocoromorpha (Kment et al., 2019).
Type material. Holotype: male, SYS-XLAB-MMR-HET-21056 (SYSBM), from Burmese amber.
Locality and horizon. Hukawng Valley, Kachin State, northern Myanmar; mid-Cretaceous (Albian–Cenomanian).
Diagnosis. As in generic diagnosis.
Description.
Macropterous male.
Body and coloration. Small sized (2.61 mm), elongate, and relatively flattened. Body yellowish brown to brown, head, prothorax and genitalia darker. The eyes and ocelli translucent (Fig. 1A–B).
Structures. Head. Dorsal and ventral surface covered with short, relatively sparse semi-erect pilosity. Anterior part of head long, ratio of distance from anterior margin of eye to apex of antennifer/eye length ~0.73:1. Eyes big, dorsal ocular index (minimum width of vertex/maximum width of eye) 2.20. Ocelli present, close together. Posterior lobe wide and rounded, ratio of maximum width to median length ~1.91:1. Antennae four segmented, with semi-erect setae on all segments and the length sub-equal to segment diameter. Scape shortest and widest antennal segment, pedicel and flagellomeres fusiform, ratio of antennal segments I:II:III:IV = 1:2.8:3.2:3. Labium four segmented, densely covered with short, semi-erect setae, segment I widest, segment III longest (Figs. 3A, 4A). The ratio of labial segments I:II:III:IV = 1.3:1:3:1.5.
Thorax and appendages. Pronotum covered with short, sparse semi-erect setae, and long setae on lateral margin. Structures as in generic description. Forecoxae, trochanter, and femur with moderately dense short erect setae, tibia and tarsus densely covered with short erect setae. Femur thickened, distal portion strikingly wide, ratio of length to maximum width 2.8:1. Tibia distally robust and wide, apicitibial armature consisting of 7 thick spiniform setae, the innermost two broader than the others. Tarsus clavate, ratio of length to maximum width 2.5:1. Length of the inner claw equal to that of tarsus. Both middle and hind legs covered with short, sparse semi-erect setae from coxa to femur. Middle femur longer than tibia. Ventral side of apex of middle tibia bearing two spiniform setae. Middle tarsus slender, with two unequal claws, the inner claw longer than the outer one (Fig. 4D, I), tarsal segment II about a third of the length of segment I. Hind femur shorter than hind tibia, covered with dense, short, erect setae. Hind tibia with very long setae on dorsal margin. Ventral side of apex of hind tibia bearing four spiniform setae, and two or three on ventral margin near apex. Hind tarsus slender, claws equally developed, tarsal segment II about 4 times the length of segment I. Venation of forewings complete, as shown in (Fig. 5A), basal cell present, slender, discal cell closed, the length of the latter shorter than two times of the former. 1An and 2An joined before middle of clavus. Setae on veins of forewing could be observed on basal part of C + Sc, R, M + Cu, 1An and 2An (Fig. 5A).
Pregenital abdomen. Abdomen with short, moderately dense semi-erect setae. The ratio of maximum length of abdomen/maximum width of abdomen ~2.10:1.
Male genitalia. Pygophore enlarged and strongly sclerotized, with conspicuously long setae. Lateral margin of pygophore nearly straight, posterior margin concave. Proctiger sclerotized, protruding from pygophore (Fig. 3A: x). Parameres movable, with conspicuously long setae (Fig. 5E–F: lp, rp).
Female unknown.
Measurements (in mm). (holotype): Total body length 2.61; length of head (without neck) 0.41, length of posterior lobe 0.11, width of posterior lobe 0.21; distance of eye to apex of antennifer 0.08; diatone (maximum width across eyes) 0.21, dorsal synthlipsis (minimum interocular distance) 0.11, ventral synthlipsis 0.02; length of eye 0.11; interocellar distance 0.02, distance of ocellus to lateral margin of posterior lobe of head 0.05; total length of labium 0.27, lengths of segment I 0.05, II 0.04, III 0.12, IV 0.06; total length of antenna 0.60, lengths of segment I 0.06, II 0.17, III 0.19, IV 0.18; maximum length of pronotum 0.33, median length of collum 0.10, maximum width of collum 0.24, maximum width of middle lobe 0.39, maximum length of middle lobe and posterior lobe 0.23, maximum width of posterior lobe 0.51; length of scutellum 0.23, width of scutellum 0.37; length of forefemur 0.42, maximum width of forefemur 0.15, length of foretibia 0.30, maximum width of foretibia 0.11, length of foretarsus 0.10, maximum width of foretarsus 0.04, length of inner foreclaw 0.10, length of outer foreclaw 0.09; length of middle femur 0.34, length of middle tibia 0.27, length of middle tarsus 0.11; length of hind femur 0.56, length of hind tibia 0.63, length of hind tarsus 0.20; length of scutellum 0.39/0.41, width of scutellum 0.47/0.45; length of forewing 1.85; maximum length of abdomen 0.88, maximum width of abdomen 0.42.

4. Discussion

The new taxon could be ascribed to Enicocephalomorpha based on the following morphological characteristics: head subdivided into anterior and posterior lobe by a conspicuous constriction; forewings completely membranous, medial fracture situated in front of R; foreleg raptorial, apicitibial, and pretarsal armature bearing spiniform setae. The new taxon could also be ascribed to Aenictopecheidae based on the middle and hind lobe of pronotum undivided; forewing with short costal fracture; pygophore enlarged and not subdivided into tergum, laterotergites, and sternum; and male with movable parameres.

Aenictopecheidae currently contain four subfamilies—Aenictopecheinae, Maoristolinae, Murphyanellinae and Nymphocorinae (Štys 1989, 2002; Schuh and Weirauch 2020). The new taxon shares several subfamily-level diagnostic characters from each of the known subfamilies of Aenictopecheidae, but there are also differences in some important ones (see in Table 1). The form of forewing venation in *Cretocephalus* is highly similar to Aenictopecheinae: costal fracture present, nonbranching Rs, presence of basal cell and closed discal cell. But differ from Aenictopecheinae in foretibial apical armature undivided by a notch into two clusters, and without 2 rounded or bilobate, peg-like spiniform. *Cretocephalus* is similar to Nymphocorinae in ventral surface of foretibia with thick spiniform setae. But it differs from Nymphocorinae in eye normally developed, tarsal formula 1-2-2, and lack of thick

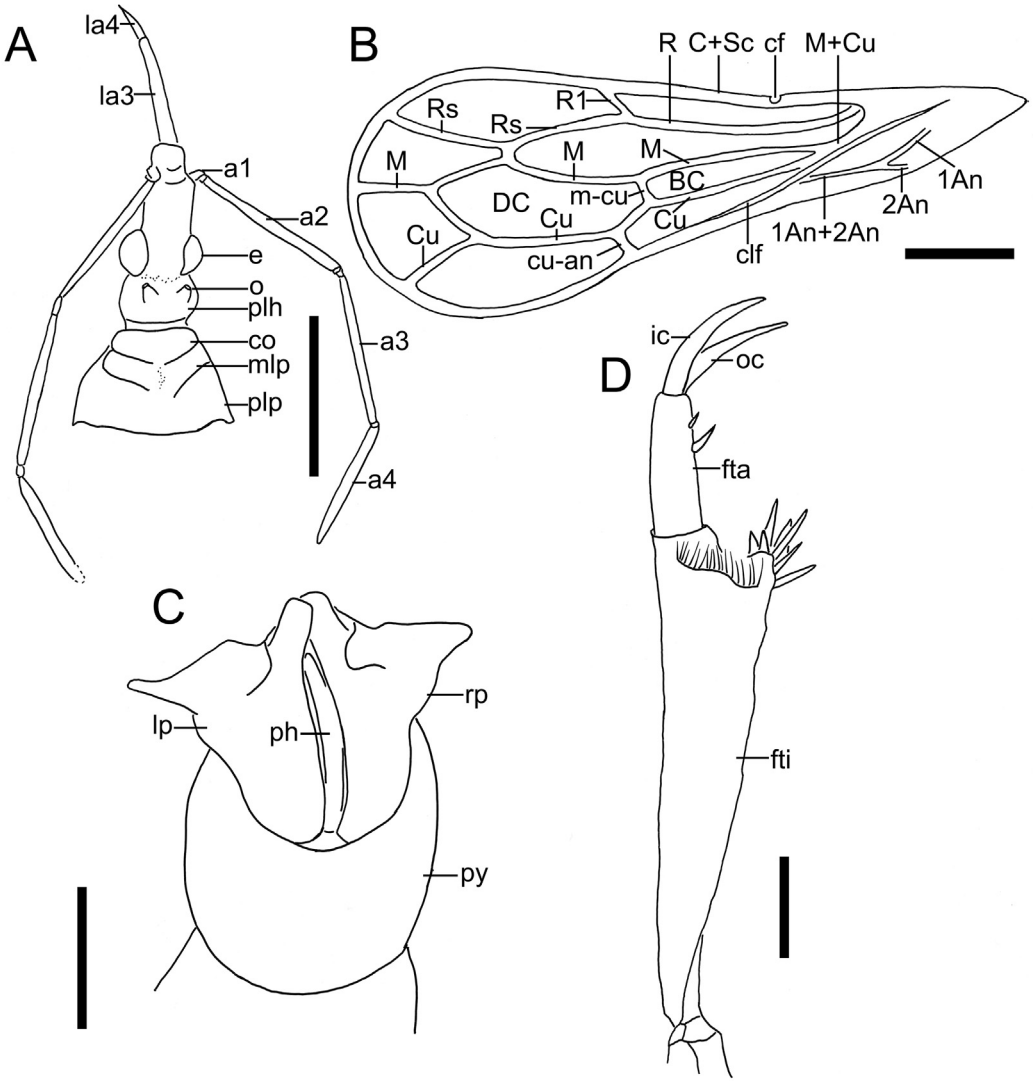

Fig. 6. *Enicocephalinus acragrimaldii* Azar, Fleck, Nel & Solignac, 1999, holotype (male), morphological details. A. Head and pronotum, dorsal view. B. Forewing, dorsal view. C. Genitalia, ventral view. D. Foreleg, inner view. All based on Azar et al. 1999: Figs. 1 (for A), 3 (for B), 9 (for C), 6 (for D). Scaler bars = 0.5 mm (A), 0.3 mm (B), 0.1 mm (C–D). Abbreviations: a1–2 = antennal segment 1–2; e = eye; cf = costal fracture; clf = claval fracture; fta = foretarsus; fti = fore tibia; ic = inner claw; la1–4 = labium segment 1–4; lp = left paramere; mlp = middle lobe of pronotum; o = ocellus; oc = outer claw; ph = phallus; plh = posterior lobe of head; plp = posterior lobe of pronotum; y = pygophore; rp = right paramere.

spiniform setae on the ventral surface of middle and hind femora. Finally, *Cretocephalus* differ from Maoristolinae and Murphyanellinae in characters of tarsi, pronotum and forewing (Table 1). Therefore, it is not possible to place this new taxon in any present subfamily of Aenictopecheidae without a detailed phylogenetic analysis.

Azar et al. (1999) described *Enicocephalinus acragrimaldii* Azar, Fleck, Nel & Solignac, 1999, from Lebanese amber, and placed it in Enicocephalidae, as closely related to Enicocephalinae + Alienatinae. According to our present results, *Cretocephalus* is similar to *Enicocephalinus* in 1) having 7 spiniform setae on foretibia, the inner two blade-shaped spiniform setae; 2) Rs of forewing nonbranching; 3) ventral margin of middle and hind tibia with paired spiniform setae. More importantly, these two genera share the important diagnostic characters of Aenictopecheidae: posterior lobe of pronotum abbreviated, poorly defined; forewing with distinct short costal fracture; pygophore not subdivided into tergum, laterotergites, and sternum; phallus neither formed from structures including paired elements homologous to the genital plates of Auchenorrhyncha, nor transformed to racquet-shaped distally perforated "guide" associated with the ventral margin of posterior foramen of pygophore; male genitalia with movable paramere (Fig. 6A–D) (Table 1). The original author of *Enicocephalinus* believed that *Enicocephalinus* has a clustering of the foretibial spiniform setae disposed in one group as in Enicocephalinae and one-segmented tarsi as in Alienatinae of Enicocephalidae. However, all subfamilies of Aenictopecheidae have foretibial spiniform setae in one group except for Aenictopecheinae, and one-segmented tarsi also appears in Murphyanellinae and Nymphocorinae of Aenictopecheidae. Considering these circumstances, although has some similar characters to the family Enicocephalidae, *Enicocephalinus* should undoubtedly be placed in the family Aenictopecheidae. So we here transfer genus *Enicocephalinus* from Enicocephalidae to Aenictopecheidae. Similar with *Cretocephalus*, *Enicocephalinus* also lacks the same diagnostic characters as each subfamily of Aenictopecheidae. Therefore, we do not place *Enicocephalinus* in any present subfamilies of Aenictopecheidae.

In addition, based on (Cockerell 1916; Štys, 1969) *Paenicotechys fossilis* (Cockerell, 1916) has an excised posterior margin of the pronotum, dorsally contiguous eyes, a globular posterior lobe of the head, the anteocular portion of the head greatly elongated, and unilobate pronotum (Fig. 5B–D), these characters are different from all subfamilies of Aenictopecheidae, so it cannot be placed in any present subfamily provisionally. Considering the large amount of Enicocephalomorpha in the true bug inclusions of Burmese amber, more and more of "the missing pieces of puzzle" linking extant and fossil species will show up, and they can help us to understand phylogenetic relationships of unique-headed bugs more accurately. In order to facilitate future work, we do not establish new higher taxa for these remarkable species. And we adjusted the present higher classification of Aenictopecheidae including extinct and extant groups.

The extant diversity of Aenictopecheidae is much lower than its sibling Enicocephalidae, with only 22 species distributed mainly in the pan-tropical regions including Southeast Asia (*Aenictopechys* Breddin, 1905, *Murphyanella* Wygodzinsky & Štys, 1982, and *Timahocoris* Wygodzinsky & Štys, 1982), Central and South America (*Tornocrusus* Kritsky, 1977), East Africa and Madagascar (*Lomagostus* Villiers, 1958, and *Ulugurocoris* Štys & Baňař, 2013), Australia and New Zealand (*Australostolus* Štys, 1980, *Maoristolus* Woodward, 1956, and *Nymphocoris* Woodward, 1956) (Wygodzinsky and Schmidt 1991; Štys 2008; Štys and Baňař 2013). But two genera occur in temperate regions: the Holarctic genus *Boreostolus* Wygodzinsky & Štys, 1970 in eastern Russia and western North America, and *Gamostolus* Bergroth, 1927 in southern South America. Although aenictopecheids have been recorded from all zoogeographical realms in the world, the pattern is very scattered and the distribution ranges of most species are quite limited. The low diversity and limited distribution of Aenictopecheidae might result from the difficulty of collecting, the real diversity of this group could be underestimated. The known fossil species of Aenictopecheidae distributed in tropical regions of southern Eurasia and northeastern Africa in the Cretaceous.

The present higher classification of Aenictopecheidae is listed below, the distributions of the established extant genera are based on Štys (2008) and Štys and Baňař (2013).

Aenictopecheidae Usinger, 1932

Diagnosis. Aenictopecheidae could be distinguished from Enicocephalidae by: (1). Posterior lobe of pronotum abbreviated, pronotum seemingly consisting of 2 lobes only (except Murphyanellinae); (2) with short costal fracture on forewing (except Murphyanellinae); (3) male with movable parameres; (4) with typically heteropteran phallus, inflatable or not; and (5) ovipositor usually fully developed (Štys 1989, 1995; Wygodzinsky and Schmidt 1991).

Aenictopecheinae Usinger, 1932

Aenictopecheini Usinger, 1932

Aenictopechys Breddin, 1905 (Oriental: Indonesia)

Lomagostus Villiers, 1958 (Afrotropical: Madagascar)

Ulugurocoris Štys & Baňař, 2013 (Afrotropical: Tanzania)

Gamostolini Štys, 1989

Australostolus Štys, 1980 (Australian: Australia)

Boreostolus Wygodzinsky & Štys, 1970 (Holarctic: Canada, Russia, USA)

Gamostolus Bergroth, 1927 (Neotropical: southern Argentina and Chile)

Tornocrusus Kritsky, 1977 (Neotropical: Brazil, Columbia, Costa Rica, Ecuador, Guadeloupe, Peru, Venezuela)

Maoristolinae Štys, 1989

Maoristolus Woodward, 1956 (Australian: New Zealand)

Murphyanellinae Štys, 1989

Murphyanella Wygodzinsky & Štys, 1982 (Oriental: Singapore)

Timahocoris Wygodzinsky & Štys, 1982 (Oriental: Singapore)

Nymphocorinae Štys, 1989

Nymphocoris Woodward, 1956 (Australian: Australia and New Zealand)

incertae sedis:

† *Cretocephalus* gen. nov. (Burmese amber fossil, mid-Cretaceous)

† *Enicocephalinus* Azar, Fleck, Nel & Solignac, 1999 (Lebanese amber fossil, early Cretaceous)

† *Paenicotechys* Štys, 1969 (Burmese amber fossil, mid-Cretaceous)

5. Conclusions

Cretocephalus stysi gen. et sp. nov. from mid-Cretaceous Burmese amber is described, and assigned to Aenictopecheidae, and all fossil species that may belong to this family are briefly reviewed. Based on the morphological characters, we transfer *Enicocephalinus* to the family Aenictopecheidae. The fossil genera *Cretocephalus* gen. nov., *Enicocephalinus* and *Paenicotechys* possess prominent differences with all known subfamilies of aenictopecheids but also share important characteristics with some subfamilies, therefore, we don't place these genera in any present subfamilies of Aenictopecheidae.

Acknowledgements

We are grateful to Dr. Eduardo Koutsoukos (Editor-in-Chief of Cretaceous Research) and the two anonymous reviewers for reviewing the manuscript and providing valuable comments and constructive suggestions. This project was supported by the National Science Foundation Projects of China (grant number: 31222051), the Fundamental Research Funds for the Central Universities, Sun Yat-sen University (grant number: 22qntd2624).

References

Azar, D., Fleck, G., Nel, A., Solignac, M., 1999. A new enicocephalid bug, *Enicocephalinus acragrimaldii* gen. nov., sp. nov., from the Lower Cretaceous amber of Lebanon (Insecta, Heteroptera, Enicocephalidae). Estudios del Museo de Ciencias Naturales de Alava 14, 217–230.

Chen, J., Wang, B., Zheng, Y., Zhang, H.C., 2019. A well-preserved minute litter bug in mid-Cretaceous Kachin amber from northern Myanmar (Heteroptera, Dipsocoromorpha). Cretaceous Research 96, 6–13. https://doi.org/10.1016/j.cretres.2018.12.003.

Cockerell, T.D.A., 1916. Insects in Burmese amber. American Journal of Science 4 (42), 135–138.

Cockerell, T.D.A., 1917. Arthropods in Burmese amber. American Journal of Science 4 (44), 360–368.

Davranoglou, L., Baňař, P., Schlepütz, C.M., Mortimer, B., Taylor, G.K., 2017. The pregenital abdomen of Enicocephalomorpha and morphological evidence for different modes of communication at the dawn of heteropteran evolution. Arthropod Structure & Development 46, 843–868. https://doi.org/10.1016/j.asd.2017.08.006.

Du, S.L., Hu, Z.K., Yao, Y.Z., Ren, D., 2019. New genus and species of the Yuripopovinidae (Pentatomomorpha: Coreoidea) from mid-Cretaceous Burmese amber. Cretaceous Research 94, 141–146. https://doi.org/10.1016/j.cretres.2018.10.022.

Grimaldi, D.A., Engel, M.S., Nascimbene, P.C., 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. American Museum novitates (3361), 1–72.

Grimaldi, D.A., Michalski, C., Schmidt, K., 1993. Amber fossil Enicocephalidae (Heteroptera) from the Lower Cretaceous of Lebanon and Oligo-Miocene of the Dominican Republic: with biogeographic analysis of *Enicocephalus*. American Museum Novitates 3071, 1–28.

Heiss, E., Golub, V.B., 2021. A new genus and species of Tingidae from Cretaceous Burmese amber (Hemiptera, Heteroptera). Palaeoentomology 4 (2), 137–140. https://doi.org/10.11646/palaeoentomology.4.2.2.
Henry, T.J., 2017. Biodiversity of Heteroptera. In: Foottit, R.G., Adler, P.H. (Eds.), Insect Biodiversity: Science and Society, second ed., vol. I. John Wiley & Sons, pp. 279–335.
Jeannel, R., 1942. Les Hénicocephalides. Monographie d'un groupe d'Hémiptères hématophages. Annales de la Sociét Entomologique de France 110, 273–368.
Johnson, K.P., Dietrich, C.H., Friedrich, F., Beutel, R.G., Wipfler, B., Peters, R.S., Allen, J.M., Petersen, M., Donath, A., Walden, K.K.O., Kozlov, A.M., Podsiadlowski, L., Mayer, C., Meusemann, K., Vasilikopoulos, A., Waterhouse, R.M., Cameron, S.L., Weirauch, C., Swanson, D.R., Percy, D.M., Hardy, N.B., Terry, I., Liu, S., Zhou, X., Misof, B., Robertson, H.M., Yoshizawa, K., 2018. Phylogenomics and the evolution of hemipteroid insects. Proceedings of the National Academy of Sciences 115 (50), 12775–12780.
Kment, P., Baňař, P., Bílý, S., Pluot-Sigwalt, D., Polhemus, D.A., Schuh, R.T., 2019. In memoriam of Professor Pavel Štys (1933-2018): biography, memories, bibliography and list of described taxa. Acta Entomologica Musei Nationalis Pragae 59 (2), 351–379. https://doi.org/10.2478/aemnp-2019-0028.
Latreille, P.A., 1810. Considérations generales sur l'ordre naturel des animaux composant les classes des crustaces, des arachnides, et des insectcs. avec tableau methodique de leurs genres, disposes en families. Schnell, Paris.
Li, H., Leavengood Jr., J.M., Chapman, E.G., Burkhardt, D., Song, F., Jiang, P., Zhou, X., Cai, W., 2017. Mitochondrial phylogenomics of Hemiptera reveals adaptive innovations driving the diversification of true bugs. Proceedings of the Royal Society B: Biological Sciences 284 (1862), 1–10.
Linnaeus, C., 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. In: Editio decima, reformata. Sal vii, Holmiae.
Luo, J.Y., Baňař, P., Xie, Q., 2021. Allocephalocorinae, a new subfamily of Enicocephalidae, based on *Allocephalocoris zhengi* gen. et sp. nov., in mid-Cretaceous amber from northern Myanmar (Insecta: Hemiptera). Cretaceous Research 118, 104628. https://doi.org/10.1016/j.cretres.2020.104628.
Maldonado-Capriles, J., Santiago-Blay, J.A., Poinar Jr., G.O., 1996. *Paralienates hyalinus* n. gen. and n. sp. (Enicocephalidae: Heteroptera): fossil gnat bug from Dominican amber (lower Oligocene-upper Eocene). Journal of Agriculture of the University of Puerto Rico 80 (1–2), 47–54.
Ross, A.J., 2021. Burmese (Myanmar) amber taxa, p. 27 on-line supplement v.2021.1. http://www.nms.ac.uk/explore/stories/natural-world/burmese-amber/.
Schuh, R.T., 1979. Evolutionary trends in Heteroptera. Part II. Mouthpart-structures and feeding strategies, by R. H. Cobben. Systematic Zoology 28, 653–656.
Schuh, R.T., Slater, J.A., 1995. True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornell University Press, Ithaca, NY, p. 5.
Schuh, R.T., Weirauch, C., 2020. True bugs of the world (Hemiptera: Heteroptera): classification and natural history, second ed. Siri Scientific Press, Manchester.
Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research 37, 155–163.
Spangenberg, R., Friedemann, K., Weirauch, C., Beutel, R.G., 2013. The head morphology of the potentially basal heteropteran lineages Enicocephalomorpha and Dipsocoromorpha (Insecta: Hemiptera: Heteroptera). Arthropod Systematics & Phylogeny 71 (2), 103–136. http://www.whose-tadpole.de/SNSD/AS&P/ASP_71_2/04_ASP_71_2_Spangenberg_103-136.pdf.
Stichel, W., 1955–1956. Illustrierte Bestimmungstabellen der Wanzen. II. Europa. (Hemiptera-Heteroptera Europae), vol. 1. Selbstverlag, Berlin-Hermsdorf, p. 168.
Štys, P., 1969. Revision of fossil and pseudofossil Enicocephalidae (Heteroptera). Acta Entomologica Bohemoslovaca 66, 352–363.
Štys, P., 1989. Phylogenetic systematics of the most primitive true bugs (Heteroptera: Enicocephalomorpha, Dipsocoromorpha). Práce Slovenskej entomologickej spoločnosti SAV 8, 69–85.
Štys, P., 1995. Aenictopecheidae. In: Schuh, R.T., Slater, J.A. (Eds.), True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornell University Press, Ithaca, NY, pp. 68–70.
Štys, P., 2002. Key to the genus-group taxa of the extant Enicocephalomorpha of the World, their list, and taxonomic changes (Heteroptera). Acta Universitatis Carolinae-Biologica 45 (4), 339–368.
Štys, P., 2008. Zoogeography of Enicocephalomorpha (Heteroptera). Bulletin of Insectology 61 (1), 137–138.
Štys, P., 2010. A fossil head of an enicocephalomorphan (Hemiptera: Heteroptera) from England revisited: Identity of the first fossil species of Enicocephalidae from Europe. European Journal of Entomology 107 (3), 455–460.
Štys, P., Baňař, P., 2008. A new species of *Tornocrusus* (Hemiptera: Heteroptera: Aenictopecheidae) from Ecuador, and morphological notes. Proceedings of the Entomological Society of Washington 110 (4), 1220–1232.
Štys, P., Baňař, P., 2013. Eastern Arc Mountains in Tanzania: Hic sunt Aenictopecheidae. A first genus and species of Afrotropical Aenictopecheidae (Hemiptera: Heteroptera: Enicocephalomorpha). European Journal of Entomology 110 (4), 677–688.
Štys, P., Baňař, P., Drescher, J., 2010. A new *Oncylocotis* Stål (Hemiptera: Heteroptera: Enicocephalidae) from Sabah: a predacious species associated with the yellow crazy ant, *Anoplolepis gracilipes* (Smith) (Hymenoptera: Formicidae). Zootaxa 2651, 27–42.
Tihelka, E., Engel, M.S., Huang, D.Y., Cai, C.Y., 2020. Mimicry in Cretaceous Bugs. iScience 23 (7), 101280. https://doi.org/10.1016/j.isci.2020.101280.
Usinger, R.L., 1932. Miscellaneous srudies in the Henicocephalidae (Hemiptera). Pan-Pacific Entomologist 8, 145–156.
Wang, Y.H., Wu, H.Y., Rédei, D., Xie, Q., Chen, Y., Chen, P.P., Dong, Z.E., Dang, K., Damgaard, J., Štys, P., Wu, Y.Z., Luo, J.Y., Sun, X.Y., Hartung, V., Kuechler, S.M., Liu, Y., Liu, H.X., Bu, W.J., 2019. When did the ancestor of true bugs become stinky? Disentangling the phylogenomics of Hemiptera-Heteroptera. Cladistics 35 (1), 42–66.
Wygodzinsky, P.W., Schmidt, K., 1991. Revision of the New World Enicocephalomorpha (Heteroptera). Bulletin of the AMNH 200, 1–265.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2022.105270.