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Short communication

The latest record of Hexagenitidae (Insecta: Ephemeroptera) with elongated abdominal sternum IX from mid-Cretaceous Myanmar amber

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ABSTRACT

A new species, *Hexameropsis elongatus* sp. nov., in the extinct family Hexagenitidae of Ephemeroptera, is described and figured based on two well-preserved male mayflies from the mid-Cretaceous Myanmar (Burmese) amber. The new species has the following diagnostic characters: fewer cross-veins and intercalary veins, R_{3b} in contact with R_2, the first curved loop-like triad wider than the other two triads in forewing, MA of hind wing branched at the quarter length near wing margin and abdominal sternum IX well-developed, more than three times as long as abdominal tergum X and tapered from the base of gonostyli to the apical. The well-developed abdominal sternum IX of *H. elongatus* sp. nov. is a unique feature in Ephemeroptera because abdominal sternum IX is usually covered by abdominal tergum X in almost all extant or fossil mayflies documented up to date. The new finding, the first record in Myanmar amber and the latest Hexagenitidae hitherto, provides important morphological characters to enhance our understanding of the evolution of Hexagenitidae. To clarify and compare the morphological characters of various genera and species of Hexagenitidae imagoes, a Key based on venational characters is provided.

1. Introduction

Ephemeroptera, known as mayflies, are currently considered as or the sister group of the Odonatoptera under Hydropalaeoptera (Kukalová-Peck et al., 2009). This is a rather small insect order comprising 42 families with over 3124 extant species (Zhang, 2013) distributed throughout the world. Dated back to 2007, only 218 species in 40 families of fossil mayflies have been described, including 20 extinct families and 83 species (Huang et al., 2007a). To date, there are about 270 fossil mayfly species recorded in 41 families. The first fossil species in Prosopistomatidae, comprising only extant species before, has been described in Myanmar amber recently (Lin et al., 2018). Some fossil taxa have been documented from poorly preserved fossils with isolated wings or incomplete bodies. Recently, well-preserved mayfly specimens in amber with complete bodies and wings provide morphological characters and evidence for a better understanding of the evolutionary development of mayflies in the Mesozoic.

Hexagenitidae Lameere, 1917, a small extinct family, are distinctive based on the following characters: forewing CuA bifurcates to CuA_1 and CuA_2, iCu bifurcates to form several triads following one another and all branches of these triads extend to basitornal margin of wing (Kluge, 2004). Up to date, 14 known genera with 24 species have been reported from the Lower Jurassic to the Lower Cretaceous. Besides, 6 genera with 9 species are recorded in winged stage: *Hexagenites* Scudder, 1880 in Germany (Carpenter, 1932; Demoulin, 1953, 1955; 1967, 1970; Tshernova, 1961), *Ephemeropsis* Eichwald, 1864 in Transbaikalia and Mongolia (both nymph and imago) (Cockerell, 1924; Tshernova, 1961), *Hexameropsis* Tshernova & Sinitshenkova, 1974 in Ukraine and Algeria (Tshernova and Sinitshenkova, 1974), *Mongologenites* Sinitshenkova, 1986 in Mongolia (both nymph and imago) (Sinitshenkova, 1986), *Cratogenitoides* Martins-Neto, 1996 in Brazil (Martins-Neto, 1996), *Epicharmeropsis* Huang, Ren & Shih, 2007 in China (Huang et al., 2007b). Most of them were described based on wings only, except for three genera possessing body details:

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Ephemeropsis with seven-segmented gonostyli (Demoulin, 1955); *Epicharmeropsis* with almost complete body and wings of male and female (Huang et al., 2007b); *Mongologenites* with details of legs. Other 8 genera 15 species are discovered as nymphs only in Mongolia (Sinitshenkova, 1986), China (Lin and Huang, 2001; Zhang and Kluge, 2007; Huang et al., 2011) and Brazil (Martins-Neto, 1996; Staniczek, 2007).

For the Jehol Biota, three key representatives in the early studies are the conchostracan *Eosestheria middendorfii*, mayfly larva and imago *Ephemeropsis trisetalis,* and fish *Lycoptera jobolensis* (Zhang et al., 2003). Based on the study of Huang et al. (2007b), the *Ephemeropsis*-like imago specimens reported before from China, which was classified as *Ephemeropsis trisetalis*, should be placed into *Epicharmeropsis* Huang, Ren & Shih, 2007.

Here we report a new species based on two nearly-complete male mayflies from the mid-Cretaceous amber of northern Myanmar. The new mayflies are the first Hexagenitid in Myanmar amber and the latest record of Hexagenitidae hitherto, providing more important morphological characters of this family.

2. Material and methods

The amber type specimens studied in this paper were collected from the mine on Noije Bum hill, approximately 15 km southwest of the Village of Tanai Village (26°21′33.41″N, 96°43′11.88″E) in the Hukawng Valley of northern Myanmar (Fig. 1) (Cruickshank and Ko, 2003; Shi et al., 2012; Dong et al., 2015; Zhang et al., 2017). The age of Myanmar amber is documented as 98.79 ± 0.62 Ma (Shi et al., 2012). It displays clear traces of redeposition which shows that Myanmar amber was formed earlier than its enclosing rocks as it could be of mid-Cretaceous age (Cenomanian) (Ross, 2015). Numerous new records and new taxa of insects have been described from the Myanmar amber nowadays, for example, detailed mouthpart structure of *Oligopsychopsis penniformis* in Neuroptera (Chang et al., 2018), new record of ichneumonid wasps (Li et al., 2016) and aphids (Liu et al., 2018; Poinar, 2018). Some special new taxa from Myanmar amber also provided important characters to elucidate evolution of insects, such as earliest euplantula structure of Timematids revealing the diversity of euplantulae in Polyneoptera during the Mesozoic which might have increased friction and helped these mid-Cretaceous stick insects to climb more firmly on various surfaces (Chen et al., 2018a) and *Elasmophasma stictum* with multiple expansions of the terga showing early development of body expansions used to improve crypsis for stick or leaf insects (Chen et al., 2018b).

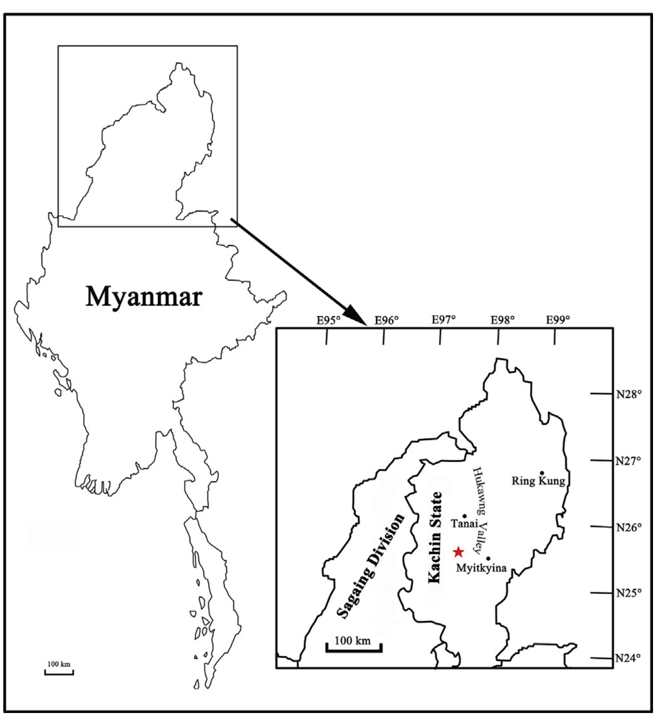

Fig. 1. Map of the amber locality near Tanai in Hukawng Valley (after Dong et al., 2015).

Both of the two male mayflies are preserved in yellow amber. The holotype specimen No. CNU-EPH-MA2018001 with better preservation is in an oval amber of about 21.2 mm in greatest length, 17.1 mm in greatest width and 3.8 mm in greatest thickness. The mayfly is positioned near the upper surface, while a bit far away from the lower surface (dorsal view). The paratype specimen No. CNU-EPH-MA2018002 is in a rectangle amber, about 40.0 mm in greatest length, 25.3 mm in greatest width, and 4.2 mm in greatest thickness. The mayfly is oblique in amber due to its right foreleg (in dorsal view) near upper surface while left middle leg (in dorsal view) near lower surface. Both type specimens are deposited in the Key Lab of Insect Evolution & Environmental Changes, Capital Normal University, Beijing, China (CNUB; Dong Ren, Curator). The present work has been registered in ZooBank LSID under urn:lsid:zoobank.org:pub:9EBFAC37-87B4-475E-858D-E53E1F409B9C.

The amber specimens were examined under a Leica M205C dissecting microscope. Photographs were taken using a Nikon SMZ 25 microscope with a Nikon DS-Ri 2 digital camera system, while details of the specimens were photographed by a Nikon ECLIPSE Ni microscope with a Nikon DS-Ri 2 digital camera system. Line drawings were prepared using Adobe Illustrator CC and Adobe Photoshop CC graphics software.

In the text, higher rank group names use the Kluge classification and descriptive terminology excluding wing venations generally follows Kluge (2004). Wing venation follows the nomenclature of Tillyard (1932).

3. Systematic palaeontology

Order Ephemeroptera Latreille, 1810
Suborder Euplectoptera Tillyard, 1932
Infraorder Anteritorna Kluge, 1993
Family Hexagenitidae Lameere, 1917

Genus ***Hexameropsis*** Tshernova & Sinitshenkova, 1974
Type species: *Hexameropsis selini* Tshernova & Sinitshenkova, 1974

Emended diagnosis. Moderate size, forewing lengths ranging from 7.8 to 20 mm. The wing venation profuse, inner margin of forewing a bit shorter than outer margin; longitudinal veins of forewing almost straight in apical half, except MA and CuA slightly curved (angle less than 10°); MP branched in one fourth of wing near base; several intercalary veins situated between iMP and MP_2; twinning of the veins apparent in some places as R_2 and R_{4+5}, MA_1 and MA_2, MP_1 and MP_2; three curved loop-like triads in cubital field. Hind wing well-developed, less than half the length of the forewing. Legs well-developed, long and sturdy, tarsi 5-segmented, fore tarsi elongated to a great degree, claws of each leg both acute and hooked; abdomen slender and long, abdominal sternum IX elongated in great degree and tapered to acute at the base of gonostyli; gonostyli four-segmented in male; two multi-segmented cerci fulfilled with setae, without paracercus.
Remarks. The species can be assigned to Hexagenitidae easily for CuA branched into CuA_1 and CuA_2 and a series of regularly looped curved veins rising from CuA_1 to the posterior wing margin (Kluge, 2004). *Hexameropsis* Tshernova & Sinitshenkova, 1974 was established by

two poorly-preserved forewings and a hind wing (Tshernova and Sinitshenkova, 1974). To date, only the type species *Hexameropsis selini* Tshernova & Sinitshenkova, 1974 was attributed to the genus. The new and almost complete amber specimens, the smallest in Hexagenitidae hitherto, can provide more important morphological characters, including even the penis. *Hexameropsis* can be easily distinguished from *Ephemeropsis* Eichwald, 1864 (forewing length 35–43 mm) from the Upper Jurassic and *Epicharmeropsis* Huang, Ren & Shih, 2007 (forewing length 34–38.5 mm) from the Lower Cretaceous by their moderate size (forewing length 7.8–20 mm) and hind wing less than half as long as forewing. In addition, *Hexameropsis* has two unique features: one is three curved loop-like triads in cubital field (vs. other genera have four to six loop-like triads) and the other is abdominal sternum IX elongated in great degree and tapered toward the apical, posterolateral projections normal (vs. abdominal sternum IX with normal length is covered by abdominal tergum X for all other genera, posterolateral projections of the ninth segment are very long and sharp in *Epicharmeropsis*, other genera without preserved abdomen). The gonostyli of *Hexameropsis* are four-segmented, but *Hexagenites* Demoulin, 1955 are seven-segmented.

Hexameropsis elongatus Lin, Shih, & Ren, sp. nov.
(Figs. 2–5)

Etymology. The specific name is from a Latin word “elongatus”, meaning “elongate”, referring to the elongated abdominal sternum IX. The gender is masculine.
Material. Holotype: Male imago. No. CNU-EPH-MA2018001. An almost complete specimen (Figs. 2–4). Paratype: Male subimago? No. CNU-EPH-MA2018002. A normally preserved specimen without head, prothorax and forelegs (Fig. 5).
Diagnosis. Moderate size. Male imago. The new amber specimens distinctly differs from *Hexameropsis selini* by the following characters: 1) fewer cross-veins and intercalary veins (vs. normal cross-veins and intercalary veins in *H. selini*); 2) R_{3b} in contact with R_2 (vs. due to poor preservation, R_{3b} approaching to R_{4+5}?); 3) the first curved loop-like triad wider than the other two triads (vs. the third curved loop-like triad wider than the other two triads); 4) MA of hind wing branched at the quarter length near wing margin (vs. MA of hind wing branched at almost the middle of wing?); 5) abdominal sternum IX well-developed, more than three times as long as abdominal tergum X and tapered from to acute at the base of gonostyli (vs. unknown)
Description. Holotype No. CNU-EPH-MA2018001; Male imago as identified by its wing margin without setae and wing membrane transparent without granular tubercles (Edmunds and McCafferty, 1988).

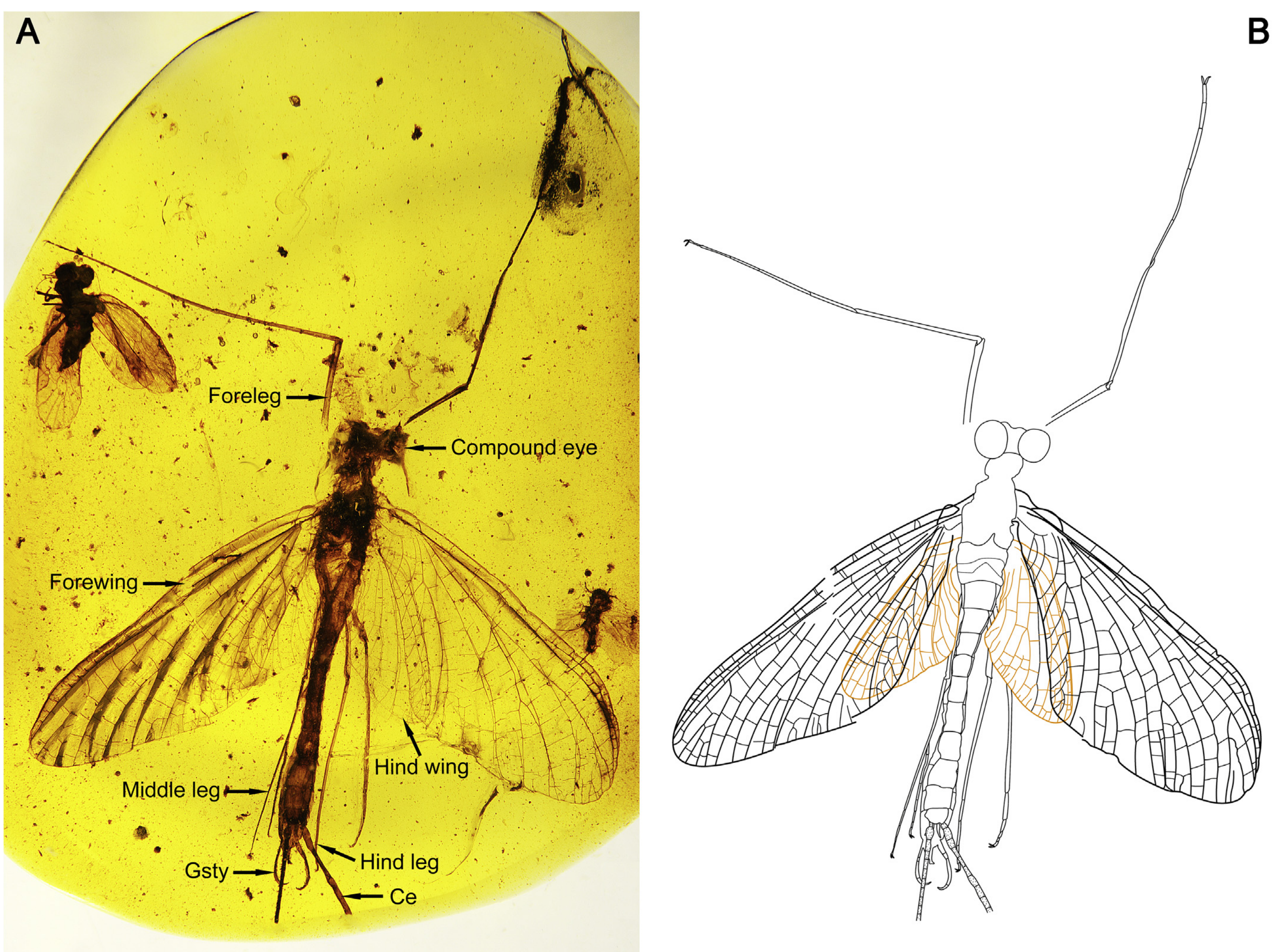

Fig. 2. *Hexameropsis elongatus* sp. nov. Holotype No. CNU-EPH-MA2018001. A, Photograph of habitus in dorsal view. B, Line drawing in dorsal view. Ce: Cerci; Gsty: Gonostylus. (Scale bars = 1 mm).

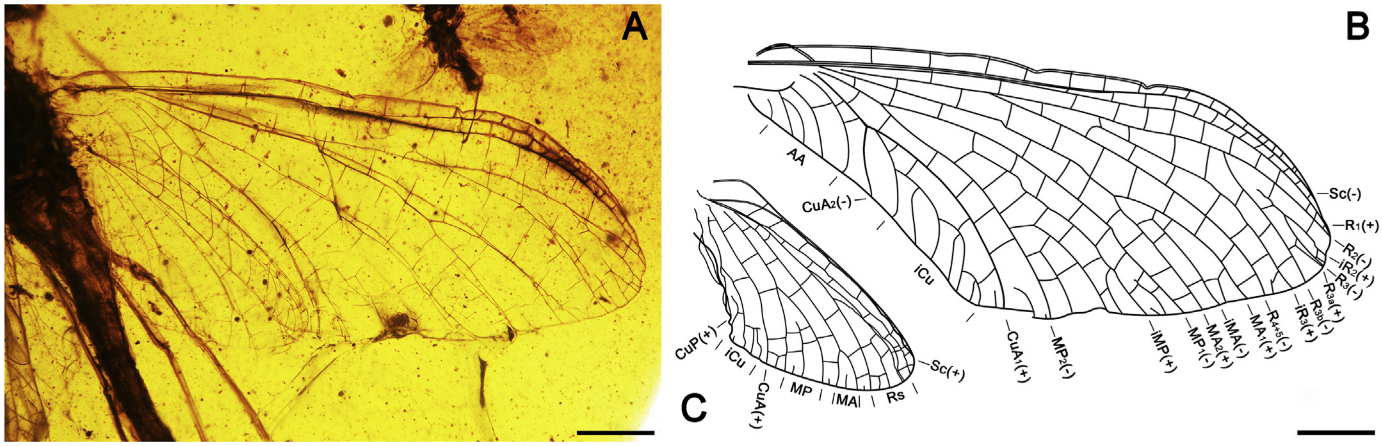

Fig. 3. *Hexameropsis elongatus* sp. nov. Holotype No. CNU-EPH-MA2018001. A, Photograph of forewing and hind wing. B, Forewing reconstruction. C, Hind wing reconstruction. (Scale bars = 1 mm).

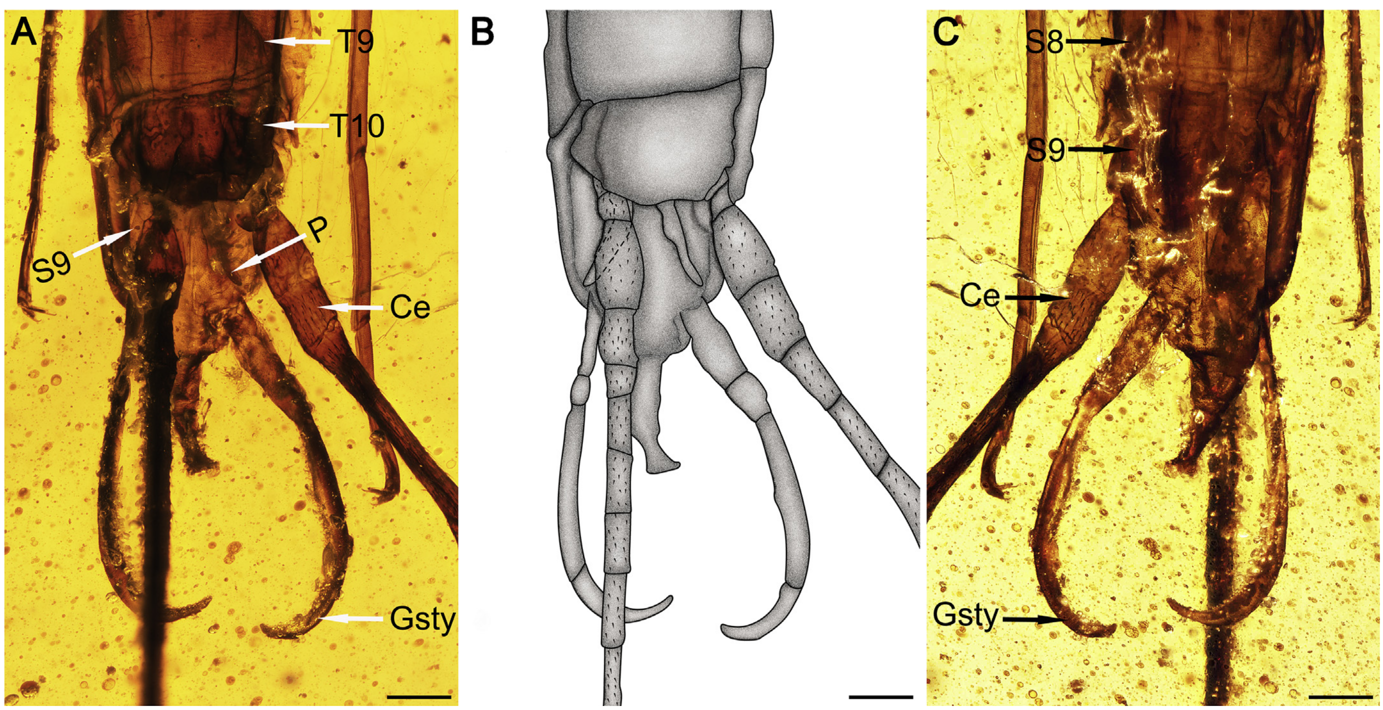

Fig. 4. *Hexameropsis elongatus* sp. nov. Holotype No. CNU-EPH-MA2018001. A, Photograph of genitalia in dorsal view. B, Line drawing of genitalia in dorsal view. C, Photograph of genitalia in ventral view. Ce: Cerci; Gsty: Gonostylus; P: Penis; S8-S9: Abdominal sternum VIII-IX; T9-T10: Abdominal tergum IX-X. (Scale bars = 0.2 mm).

Moderate size. Compound eyes big and contiguous(?). Because of the poor preservation, antennae lost. Prothorax small, pterothorax well-developed, mesothorax extremely large, metathorax a bit smaller than mesothorax (Fig. 4A, B).

Forewings (Fig. 3A, B) triangular, long and narrow; costal brace obvious; cross-veins developed. Rs system branched two times, R_2 together with R_{4+5} forming a triad at a quarter near the base, R_{3b} contacting with R_2 forming a triad at a quarter approaching to the wing margin; MA branched at one third of the wing close to wing margin; MP branched almost at the same place as MA; iMP long situated at the middle of the wing; CuA bifurcating to CuA_1 and CuA_2, from the bifurcation a vein "iCu" arising and forming 3 triads: every triad in contact with anterior triad to form next triad; between every triad an intercalary vein in contact with posterior vein of triad; all branches of these triads extending to basitornal margin of wing. Costal process of hind wings (Fig. 3C) obvious; basitornal margin slightly turned-over and overlapped; Sc and R_1 field large; R_2 in contact with R_{4+5}; MP forming a triad at the middle of wing; an intercalary veins situated in the cubital field; CuP situated behind tornus; several anal veins situated posterior of CuP.

Legs well-developed and relatively sturdy and long (Fig. 2A, B). Though preserved poorly, femur remnant still long, tibia of three legs almost at same length. Tarsi 5-segmented, fore tarsi elongated to a great degree, 1st and 2nd tarsi of middle and hind tarsi longer than normal; claws of each leg both acute and hooked.

Abdomen long and slender; abdomen tapered from first abdominal segment to sixth segment then broadened till ninth

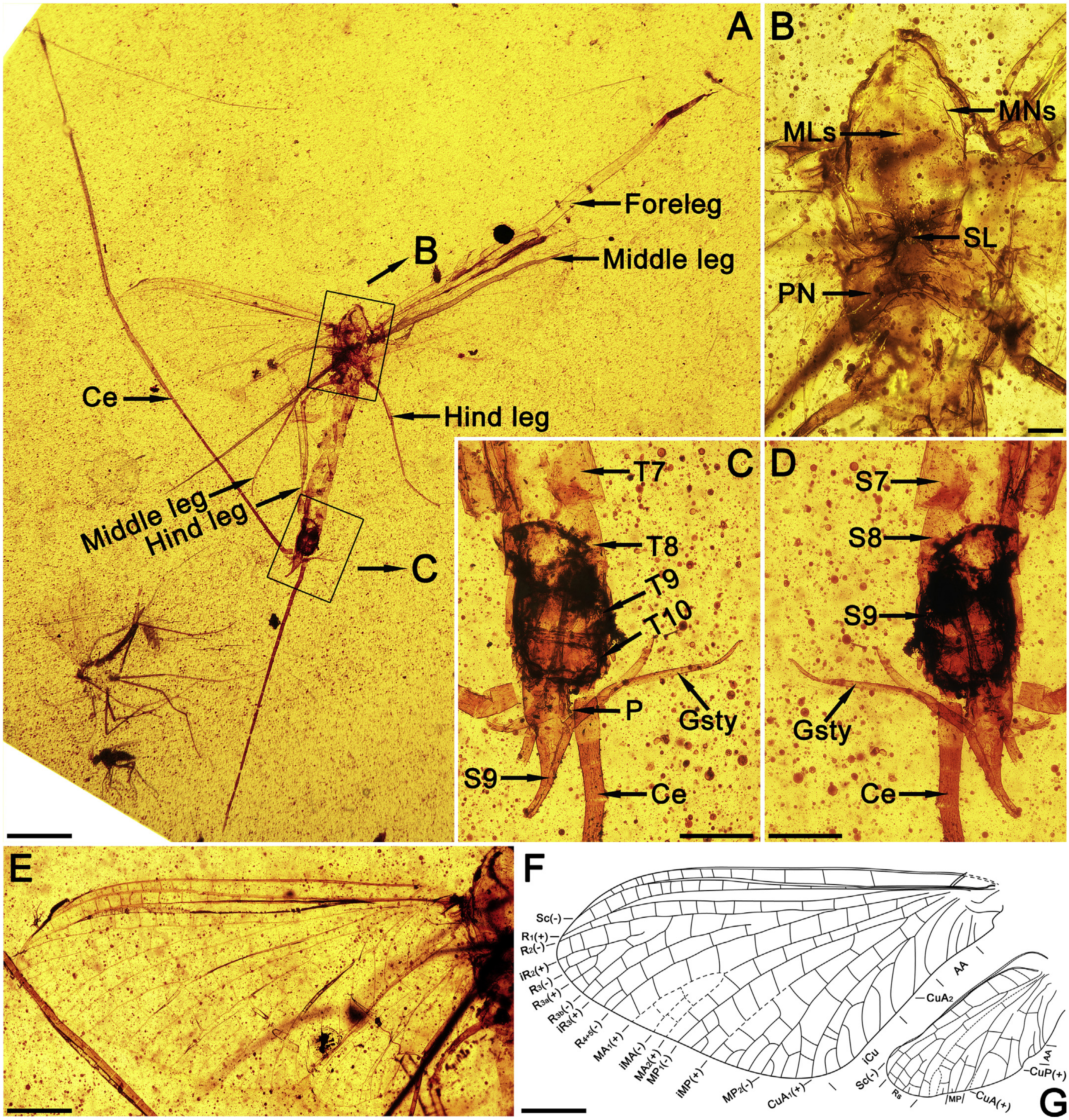

Fig. 5. *Hexameropsis elongatus* sp. nov. Paratype No. CNU-EPH-MA2018002. A, Photograph of habitus in dorsal view. B, Photograph of mesothorax and metathorax in dorsal view. C, Photograph of genitalia in dorsal view. D, Photograph of genitalia in ventral view. E, Photograph of forewing and hind wing. F, Forewing reconstruction. G, Hind wing reconstruction. Ce: Cerci; Gsty: Gonostylus; MLs: Median longitudinal suture; MNs: Mesonotal suture; P: Penis; PN: Postnotum; S7-S9: Abdominal sternum VII-IX; SL: Scutellum; T7-T10: Abdominal tergum VII-X. (Scale bar for A = 2 mm, scale bar for B = 0.25 mm, scale bars for C to D = 0.5 mm, scale bars for E to G = 1 mm).

segment; abdominal tergum X short and small, a paired cerci situated at the terminal of abdominal tergum X (Fig. 4A, B); length of abdominal sternum IX more than three times as long as abdominal tergum X; a pair of gonostyli situated at posterior of abdominal sternum IX where it beginning to taper, gonostyli with 4 segments, 3rd segment the longest, then 1st segment, 4th segment slender and sharp, 2nd segment the shortest; a pair of penis, slender and small, visible between abdominal tergum X and abdominal sternum IX (Fig. 4A–C).

Paratype. No. CNU-EPH-MA2018002. Male, probably a subimago due to its right fore leg, middle legs and left hind leg having obvious transparent part just like cuticles of a subimago. However, it does not have setae on wing margin and wing membrane transparent without granular tubercles.

Moderate size. Head, prothorax and right foreleg without preservation (Fig. 5A). Metathorax and mesothorax preserved well, mesothorax a bit shorter than two times of metathorax (Fig. 5B).

Forewing and hind wing almost complete. Forewing (Fig. 5E, F) almost as long as that of the holotype. Hind wing (Fig. 5E, G) less than half of forewing. In forewing, first curved loop-like triad slightly wider than second one and much wider than third one, no cross-veins between CuA and anal veins.

Each abdominal segment with the same width, abdominal sternum IX (Fig. 5C, D) more than four times as long as abdominal tergum X and tapered to acute at the base of gonostyli, the apical part longer and more slender than that of the holotype; a pair of penis visible as small and slender as that of the holotype.

Other characters in paratype are similar to those of holotype.

Measurements. Holotype: No. CNU-EPH-MA2018001; Body length (excluding long cerci) 9.4 mm, forewing length 7.8 mm, width 3.3 mm at the widest point, hind wing length 3.8 mm, width 1.9 mm at the widest point, mesothorax 1.3 mm, metathorax 0.9 mm, length of abdominal sternum IX 1.2 mm, length of abdominal tergum X 0.3 mm.

Paratype. No. CNU-EPH-MA2018002; Body length (excluding long cerci) 9.1 mm, forewing length 6.9 mm, width 3.1 mm at the widest point, hind wing length 2.7 mm, width 1.6 mm at the widest point, mesothorax 1.4 mm, metathorax 0.9 mm, length of abdominal sternum IX 1.2 mm, length of abdominal tergum X 0.3 mm.

Key characters for identification of genera and species in Hexagenitidae imagoes

1 Moderate size, forewing length 6.9–23 mm, forewings length less than two times of hind wings.......................................**2**

1′ Large size, forewing length 35–43 mm, forewings more than two times of hind wings...**7**

2 Six curved loop-like triads in cubital field, without intercalary veins in triads, length of forewing 18 mm [Lower Cretaceous] .... ***Mongologenites laqueatus***

2′ Fewer than six curved loop-like triads in cubital field, with intercalary veins in triads..**3**

3 Three curved loop-like triads in cubital field, R_2 unbranched..***Hexameropsis*, 4**

3′ Four curved loop-like triads in cubital field, R_2 branched.........**5**

4 Numerous cross-veins and intercalary veins, R_{3b} approaching to R_{4+5}? the third curved loop-like triad wider than other two curved loop-like triads, length of forewing 20 mm [~~Upper Jurassic~~]..***Hexameropsis selini***

4′ Much fewer cross-veins and intercalary veins, R_{3b} in contact with R_2, the first curved loop-like triad wider than other two curved loop-like triads, length of forewing 6.9–7.8 mm [mid-Cretaceous]................................***Hexameropsis elongates* sp. nov.**

5 Veins express weaker symmetrical in MA, CuA straight in apical half, numerous cross-veins exist in cubital field, hind wing much smaller than forewing length, length of forewing 13 mm [Lower Cretaceous]...............***Cratogenitoides*, *Cratogenitoides delclosi***

5′ Veins express obvious symmetrical in some place as MA, CuA strongly curved in apical half, cross-veins in cubital field not developed, hind wing almost as long as forewing length...... .... ***Hexagenites*, 6**

6 R_2 branched, MA straight in apical half, length of forewing 16 mm [Upper Jurassic]...........................***Hexagenites weyenberghi***

6′ R_2 unbranched, MA strongly curved in apical half, length of forewing 19–23 mm [Upper Jurassic]... ***Hexagenites cellulosus***

7 R_{4+5} in contact with R_2 to form a triad, several intercalary veins existing between MP_2 and CuA_1, longitudinal veins almost straight in apical half, only MP slightly curved, four to six curved loop-like triads in cubital field....................***Epicharmeropsis*, 8**

7′ R_{4+5} detached with R_2, without intercalary veins between MP_2 and CuA_1, longitudinal veins curved in different degree in apical half, Sc and CuA strongly curved, four to five curved loop-like triads in cubital field..................................***Ephemeropsis*, 9**

8 Six curved loop-like triads in cubital field, length of forewing 34 mm [Lower Cretaceous]......***Epicharmeropsis hexavenulosus***

8′ Four curved loop-like triads in cubital field, length of forewing 37–38.5 mm [Lower Cretaceous].................................. ....***Epicharmeropsis quadrivenulosus***

9 R_3 in contact with R_{4+5}, branched at middle of forewing and located toward the base from MA branch point, five curved loop-like triads in cubital field, apex of hind wing strongly extended, length of forewing 40–43 mm [Upper Jurassic].............. ....***Ephemeropsis trisetalis***

9′ R_3 in contact with R_{4+5}, branched at two fifth length of forewing and located almost the same level as MA branch point, four curved loop-like triads in cubital field, apex of hind wing less extended, length of forewing 35 mm [Upper Jurassic]......... .... ***Ephemeropsis martynovae***

4. Discussion

In this paper, we described a new species of *Hexameropsis* Tshernova and Sinitshenkova, 1974 in Hexagenitidae based on two male mayflies in Myanmar amber. The new taxon, owing to their well-preserved characters in amber, provides more complete morphological characters of wings and body of *Hexameropsis* to enhance our understanding of morphological characters and relationships of Hexagenitidae. We provide a Key with important venation characters to help identifying all imago species of Hexagenitidae recorded in winged stage.

In the winged stage of Ephemeroptera, each abdominal segment from I to IX has tergum and sternum distinctly separated by soft pleura while abdominal segment X only has tergum. Abdominal sternum IX in males is produced posteriorly in the form of a plate, bearing a pair of gonostyli. Abdominal sternum IX in females is quite simple and without any other appendages (Kluge, 2004). However, abdominal sternum IX for other species in Hexagenitidae imagoes is covered by abdominal tergum X.

The distinctly elongated abdominal sternum IX of *Hexameropsis elongatus* is quite unique in Hexagenitidae, which is long and tapering from the base of gonostyli to the apical and gonostyli emerging from the middle point of abdominal sternum IX. Abdominal sternum IX (including apical part) is more than three times as long as abdominal tergum X. So far, only two species *Epicharmeropsis hexavenulosus* and *Epicharmeropsis quadrivenulosus* in *Epicharmeropsis* Huang, Ren & Shih, 2007 (Huang et al., 2007b) are recorded with abdominal sternum IX in Hexagenitidae hitherto. But abdominal sternum IX of *Epicharmeropsis* has normal length, covered by abdominal tergum X, but the posterolateral projections of the ninth segment are long and sharp, nearly as long as abdominal tergum X. In addition, an extant genus *Brasiliocaenis* Puthz, 1975 of Caenidae in Ephemeroptera also has elongated abdominal sternum IX between the base of one-segmented gonostyli, but main part of abdominal sternum IX is still covered by abdominal tergum X (Malzacher, 1986, 1990; 1998; Kluge, 2004). Therefore, this is the first and earliest fossil record

Lower Cretaceous

with elongated abdominal sternum IX and tapered toward the apical, and variable shapes of abdominal sternum IX demonstrate the diversity of abdominal sternum IX in Ephemeroptera.

5. Conclusion

The new mayfly species, *Hexameropsis elongatus* sp. nov., in Hexagenitidae is documented by two male specimens from the mid-Cretaceous Myanmar amber. This is not only the first Hexagenitid in Myanmar amber but also the latest record in Hexagenitidae hitherto. Comparing to other genera attributed to Hexagenitidae, the well-preserved new mayflies provide important morphological information about wings and body. In addition, the new finding of the strongly elongated abdominal sternum IX not only broaden the diversity of Hexagenitidae, but also enhance our understanding of the development and early evolution of abdominal sternum IX for Hexagenitidae in the mid-Cretaceous.

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