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Bizarre egg structure uncovers a new family of Plecoptera (Insecta) from mid-Cretaceous Burmese amber

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Abstract

A new fossil stonefly, *Perspicuusoperla lata* gen. et sp. nov., is described and illustrated based on a well-preserved female adult and its eggs in mid-Cretaceous Burmese amber. The new taxon exhibits a combination of diagnostic morphologies, such as two crossveins between anterior radius (RA) and posterior radius (RP), broad subgenital plate exceeding abdomen tip, and entirely membranous eggs that cannot be incorporated into any known stonefly families. Perspicuusoperlidae, fam. nov. is established based on *Perspicuusoperla* gen. nov. and its systematic position is preliminarily discussed based on morphological comparison with other stoneflies. Palaeobiological implications are inferred from the egg morphology. This study represents the earliest known and best-preserved fossil record of extinct stonefly eggs.

Key Words

Burmese amber, Perspicuusoperlidae, Plecoptera, stonefly

1. Introduction

Plecoptera, also called stoneflies, are a basal, aquatic insect order distributed on all continents and most major islands except Antarctica (Steward 2009). Stoneflies are hemimetabolous, with egg, nymph, and adult life stages. They are typically associated with running water and waterside microhabitats. Plecoptera is supported as a monophyletic order according to a series of anatomical characters and also molecular evidence (Zwick 2000; Terry and Whiting 2005). There are more than 4100 species recorded in Plecoptera, including over 300 fossil species (DeWalt et al. 2021). The current classification system of Plecoptera comprises 16 extant families under two suborders (Zwick 2000). The suborder Arctoperlaria is largely distributed in the Northern Hemisphere except the family Notonemouridae, which occurs in the Southern Hemisphere. Arctoperlaria is further divided into two groups/infraorders, Euholognatha (including six families: Capniidae, Leuctridae, Nemouridae, Taeniopterygidae, Scopuridae and Notonemouridae) and Systellognatha (including six families Pteronarcyidae, Peltoperlidae, Styloperlidae, Perlidae, Perlodidae and Chloroperlidae). The other suborder Antarctoperlaria is exclusively restricted to the Southern Hemisphere, containing four families: Austroperlidae, Diamphipnoidae, Eustheniidae, and Gripopterygidae. The 16 extant families of Plecoptera can be readily divided by their unique morphology concerning mouthparts, gills, wings, tarsi, genitalia, cerci, and other characters (Stewart and Stark 2008; Chen and Du 2018).

Plecoptera comprises relatively rich fossil record, with the oldest Pennsylvanian representative *Gulou carpenteri* Béthoux et al. (2011) from the Tupo Formation of China (Béthoux et al. 2011). Numerous younger fossils have been described with ages ranging from Permian to Pliocene (Liu and Ren 2006). In recent years, mid-Cretaceous Kachin amber is attracting lots of interest from the researchers. Three families of stoneflies are known from Kachin amber, including Perlidae, extinct family Petroperlidae, and Peltoperlidae (Latreille 1802; Claassen 1931; Sroka et al. 2018; Chen and Xu 2020). These extinct stoneflies have exhibited a series pf specially modified external structures which are probably associated with mating behavior (Chen and Xu 2021). Egg morphology of Plecoptera is very informative from species level to subordinal level delimitation and has obvious oviposition-related biological implications (Hynes 1976; Zwick 2000; Mtow and Machida 2018; Mtow et al. 2021). However, eggs are rarely reported from fossil materials, merely with simple egg description from Tertiary Dominican amber (Stark and Lentz 1992). In this study, a new stonefly that represents a new extinct family is described based on a well-preserved female specimen from the mid-Cretaceous Kachin amber. The description and analysis are provided for the female and its well-preserved egg mass.

2. Materials and methods

The Burmese amber studied in this study was obtained from Kachin, Hukawng Valley ($26^{\circ}20$ 'N, $96^{\circ}36$ 'E) of northern Myanmar (precise locality in Kania et al. 2015: fig. 1). The age was dated and widely accepted as the earliest Cenomanian (98.79 ± 0.62 Ma) of mid-Cretaceous (Shi et al. 2012; Yu et al. 2019). The amber is deposited in the Insect Collection of Jiangsu University of Science and Technology (**ICJUST**, No. CZT-PLE-MA11), Jiangsu Province, China. Examination and measurements were conducted with a SDPTOP SZM45 stereomicroscope. Photographs were taken by a Canon EOS 6D digital camera equipped with a Canon MP-E 65 mm 5× macro lens. Photographs and line drawings were adjusted and optimized with Adobe Photoshop CS6. Wing venation nomenclature follows Béthoux (2005).

3. Systematic palaeontology

Order Plecoptera Burmeister, 1839 Suborder Arctoperlaria Zwick, 1973

Perspicuusoperlidae, fam. nov.

http://zoobank.org/3B3C915F-BB52-4A6B-BAF0-BAB42239D696

Type genus. Perspicuusoperla gen. nov.

Etymology. The first part of the compound noun refers to the transparent egg and is derived from Latin 'perspicuus'; the second part 'perlidae' refers to the stonefly family Perlidae Latreille, 1802.

Diagnosis. Triocellate; maxillary palp slender, apical segment unmodified; labial palp short, apical segment slightly shortened; cervical gills invisible. Legs with two giant apical tibial spurs; first two tarsal segments shortest, with developed euplantulae; arolium without setae. In forewings, ScP joining into RA after ra-rp; h stout and with regular obliquity; RA not reaching wing apex; RP originating at basal ¹/₃ of RA and with three branches; two crossveins present between RA and RP; CuA with four branches, two posterior branches fused basally; CuP and AA1 simple; AA2 appears unforked and abruptly curved backwards at apical half; hind wings with extremely broad and multifolded anal area. Abdominal segments unmodified; paraprocts sclerotized and thumb-shaped; subgenital

plate broad, exceeding posterior margin of tergum 10. Cerci slender, membranous and with multiple segments. Egg mass with dozens of uniformly oriented cylindrical eggs; each egg with very short collar, membranous and transparent chorion, without anchor and pedicel.

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Perspicuusoperla gen. nov.

http://zoobank.org/D44F3A06-90E9-49FC-A85C-5F35D2C36C2D

Type species. Perspicuusoperla lata gen. et sp. nov.

Etymology. The genus name is a combination of the words *Perspicuuso* and *perla*; the first word is derived from Latin 'perspicuus', meaning 'transparent' and refers to the transparent egg; the second word refers to the stonefly genus *Perla* Geoffroy, 1762.

Diagnosis. By monotypy, as for the type species.

Perspicuusoperla lata sp. nov.

http://zoobank.org/D6B8C72C-2175-49E4-9B03-56C4DDDA509A Figs 1–5

Etymology. The specific epithet means 'broad' and is derived from Latin 'lata', refers to the broad female subgenital plate.

Type material. Holotype male (No. CZT-PLE-MA11), deposited in the Insect Collection of Jiangsu University of Science and Technology (ICJUST). The specimen is well preserved, but its hindwings are covered by forewings.

Type locality. Hukawng Valley, southwest Maingkhwan, Kachin State (26°20N, 96°36E), Myanmar, uppermost Albian-lowermost Cenomanian (mid-Cretaceous).

Description. Macropterous (Fig. 1A–C); body long and stout, length (excluding antennae and cerci) ca. 7.5 mm, generally brown.

Head (Figs 1, 2A–C) short and wide, width three times longer than length, mostly dark brown, anterolateral and posterior margins pale. Triocellate, anterior ocellus large and elevated. Compound eye large, oval and strongly protruded laterad. Antenna brown and filiform, with 25 segments preserved, basal segments much shorter than wide, each antennal segment covered with dense short hairs. Maxillary palp slender, with five segments, apical segment unmodified. Labial palp short, length near 2/3 of maxillary palp, three-segmented, apical segment slightly shorter than second segment. Cervical gills invisible.

Pronotum (Figs 1A–B, 2A–B) slightly narrower than head, transversely kidney-shaped, anterior margin longer than posterior margin, surface densely pubescent, with thick rugosity. Meso- and metanota mostly sclerotized, nearly as wide as pronotum. Legs mostly dark brown, femur longer and thicker than tibia (Fig. 1); two giant tibial spurs present ventrally; first two tarsal segments shortest (Fig. 2D–F), euplantulae developed; third tarsal segment apically with long bristles; arolium without setae.

Wings (Figs 1, 3) hyaline, veins dark brown. Forewings length ca. 10.0 mm. In right forewing (Fig. 3), ScP



Figure 1. *Perspicuusoperla lata* gen. et sp. nov., holotype female (CZT-PLE-MA11): A. Habitus photo, dorsal view; B. Drawing of habitus, dorsal view; C. Habitus photo, ventral view. Scale bars: 1.0 mm.



Figure 2. *Perspicuusoperla lata* gen. et sp. nov., holotype female (CZT-PLE-MA11): A. Head and thorax, dorsal view; B. Head and thorax, ventral view; C. Head, ventral view; D. Tarsi of left foreleg, ventral view; E. Tarsi of left midleg, ventral view; F. Tarsi of left hindleg, ventral view. Scale bars: 0.5 mm (A, B), 0.1 mm (D–F).



Figure 3. *Perspicuusoperla lata* gen. et sp. nov., holotype female (CZT-PLE-MA11): drawing of forewings, dorsal view. Abbreviations: RFW, right forewing; LFW, left forewing; h, humera; ScP, posterior subcosta; RA, anterior radius; RP, posterior radius; M, media; CuA, anterior cubitus; CuP, posterior cubitus; AA1, first anterior analis; AA2, second anterior analis; ra-rp, crossvein between RA and RP. Scale bar: 1.0 mm.

reaching RA after ra-rp; h stout and with regular obliquity, another 12 crossveins present between Sc and the anterior margin; one extra crossvein present beyond ScP; RA not reaching wing apex; RP originating at basal 1/3 of RA and with three branches; two crossveins present between RA and RP; M forked at near half of wing length; at least six crossveins present between M and CuA; other longitudinal veins invisible. In left forewing (Fig. 3), RA, RP and M similar to right forewing; two crossveins present between RA and RP; single crossvein present between RP and M; area between M and CuA with seven crossveins; CuA with four branches, two posterior branches fused basally; three crossveins present between CuA and CuP; CuP and AA1 simple; AA2 seems unforked and abruptly curved backwards at apical half. Hind wings length ca. 9.0 mm, veins invisible; anal area extremely broad, with multiple folds.

Abdomen (Figs 1, 4) length ca. 4.5 mm, stout, generally brown. Abdominal terga unmodified; posterior margin of tergum 10 near truncate (Fig. 1A–B). Paraproct strongly sclerotized, thumb-shaped, two times longer than wide, apex blunt and curved (Fig. 4A–C). Subgenital plate originating



Figure 4. *Perspicuusoperla lata* gen. et sp. nov., holotype female (CZT-PLE-MA11): A. Photo of abdomen and egg mass, ventral view; B. Photo of terminalia, ventral view; C. Drawing of terminalia, ventral view. Scale bars: 0.5 mm (A), 0.1 mm (B, C).



Figure 5. *Perspicuusoperla lata* gen. et sp. nov., holotype female (CZT-PLE-MA11): A. Photo of egg mass, dorsal view; B. Photo of egg mass, ventral view; C. Drawing of single egg, lateral view; D. Drawing of single egg, anteriolateral view; E. Drawing of single egg, anterior view. Scale bars: 0.2 mm (A, B), 0.1 mm (C–E).

from sternum 8, broad and rounded, lateral margins near parallel at anterior half; posterior margin of subgenital plate extended beyond posterior margin of tergum 10 (Fig. 4A–C). Cerci (Fig. 4A) membranous and dark brown, with 12 segments preserved; each segment covered with dense, moderately long bristles; boundaries of segments clear.

Egg mass (Figs 1, 4A, 5A–B) composed of dozens of cylindrical eggs, diameter ca. 1.2 mm; posterior poles of all eggs stuck together in the center of egg mass, whereas collars of anterior poles pointing outward. Egg length ca. 0.75 mm, slender, slightly enlarged at middle (Fig. 5A–E). Chorion entirely membranous, transparent and smooth. Collar very short, narrow, simple and weakly sclerotized, boundary with chorion inconspicuous, inner area circular and medially depressed, forming a funnelform median channel (Fig. 5C–E). Anchor and pedicel absent.

4. Discussion

4.1. Systematic position

The monophyly of Arctoperlaria is supported by drumming behavior and related male abdominal structures such as ventral lobe, hammer, vesicle or hair brush (Zwick 2000). However, the female holotype does not allow a convenient subordinal assignment by drumming related male structures.

Antarctoperlaria: Egg structure and wing venation of Perspicuusoperlidae apparently distinguish from those of the four antarctoperlarian families. The completely membranous egg chorion of Perspicuusoperlidae differs from the sclerotized chorion in most Antarctoperlaria except for Austroperlidae (Hynes 1974; Zwick 2000; Mtow et al. 2021). The absence of net-like venation, namely

Euholognatha of Arctoperlaria: Although the soft egg chorion is considered apomorphic in the infraorder Euholognatha (Zwick 2000), the assignment of Perspicuusoperlidae to Euholognatha is easily excluded by the presence of euplantulae on first two tarsal segments and the multiple branches of CuA in forewings (Nelson 2009; Cui et al. 2014). The presence of well-developed wings and absence of thoracic notal projections exclude Perspicuusoperlidae from the apterous family Scopuridae (Jin and Bae 2005). The two shortest basal tarsomeres and absence of setiform basipulvilli on pretarsus exclude Perspicuusoperlidae from superfamily Nemouroidea (Zwick 2000; Nelson 2009). The presence of more than one crossvein in the distal half of RA-RP area in forewings also denied the assignment of Perspicuusoperlidae to most Nemouroidea except some Taeniopterygidae (Chen 2021).

Systellognatha of Arctoperlaria: The absence of setae on the arolium, the completely membranous egg chorion, and the basal crossvein of the costal field equal in size to the remaining crossveins and with normal regular obliquity all together excluded Perspicuusoperlidae from the infraorder Systellognatha (Zwick 2000; Nelson 2009; Cui et al. 2014). Specifically, Perspicuusoperlidae differs from Pteronarcyidae by absence of numerous crossveins in wings and absence of gill remnants on abdominal segments (Nelson 1988; Chen and Du 2018); from Peltoperlidae by the presence of two crossveins between RA and RP (Chen and Xu 2020); from Styloperlidae by the presence of three well-developed ocelli, giant tibial spurs, and absence of numerous crossveins between RA and M (Uchida and Isobe 1989); from Perlidae by absence of thoracic gill remnants (Zwick 2000) and presence of sclerotized paraprocts in female; from the three recognized tribes (Arcynopterygini, Diploperlini, Perlodini) of perlodid subfamily Periodinae by the apparently different shape and structure of eggs (Stark and Szczytko 1984), from another perlodid subfamily Isoperlinae by the extremely large female subgenital plate exceeding end of sternum 10 in combination with the three-branched RP in forewing (Zwick and Surenkhorloo 2005; Szczytko and Kondratieff 2015a, 2015b); from Chloroperlidae by the stout body, broad anal region in forewing and unmodified apical maxillary palpal segment (Zwick 2000, 2006); from the recently proposed Kathroperlidae by absence of strongly elongated head, and by two crossveins between RA and RP (South et al. 2021).

The wing venation, especially the presence of two crossveins between RA and RP in forewings of Perspicuusoperlidae apparently differs from all other extinct stoneflies described from mid-Cretaceous Kachin amber, but is reminiscent of the Late Permian fossil family Palaeoperlidae (Sinitshenkova 1987, 2013). However, the combination of wing characters, including ScP reaching RA after ra-rp, RP with three branches and CuA with four branches can separate Perspicuusoperlidae from Palaeoperlidae (Sinitshenkova 1987, 2013).

As a result, it's currently difficult to conclude the exact systematic position of Perspicuusoperlidae in lack of male characters. Perspicuusoperlidae is confidently excluded from suborder Antarctoperlaria by exhibiting no resemblance concerning body pattern and shape to any of the four extant families; the completely membranous egg chorion further suggests that Perspicuusoperlidae is not an antarctoperlarian group. Similarly, in Arctoperlaria, Perspicuusoperlidae cannot be reliably placed in any of the two infraorders (Euholognatha and Systellognatha) nor any of the families according to the characters discussed above. The general body characters (body shape, color, wing venation, tarsal structures, etc.) of Perspicuusoperlidae resemble those of Systellognatha, whereas the soft egg chorion is more close related to Euholognatha. Zwick (2000) suggested that sclerotized hard egg chorion is a groundplan character of Plecoptera whereas the soft chorion is probably apomorphy for Euholognatha. Perspicuusoperlidae is herein proposed as the stem group of Euholognatha + Systellognatha based on the following characters: soft egg chorion (apomorphy of Euholognatha); absence of anchor plate in eggs (opposed to the apomorphy of Systellognatha); presence of collar in eggs (apomorphy of Systellognatha), although not well defined; short first tarsomere (apomorphy of Systellognatha); presence of euplantulae on basal two tarsomeres (plesiomorphy of Systellognatha); absence of setae on arolium (opposed to the apomorphy of Systellognatha); forewing with numerous crossveins in costal field (plesiomorphy of Systellognatha); basal crossvein in the costal field of forewing similar to the remaining crossveins (opposed to the apomorphy of Systellognatha).

4.2. Palaeobiological implications

The eggs of Plecoptera are too small to be noticed and can hardly be preserved in fossil impressions, leaving the merely available description for *Dominiperla antigua* Stark & Lentz, 1992 (Plecoptera: Perlidae) from Tertiary Dominican amber (Stark and Lentz 1992). The eggs of *D. antigua* were bullet-shaped with one pole sharp and another pole enlarged. Herein, we reported the oldest stonefly's eggs, which perfectly preserved details for the extinct Plecoptera.

Several interesting characters are found in these eggs of Perspicuusoperlidae. Firstly, the egg mass comprises only dozens of eggs. The number of stonefly eggs in a mass is highly variable, ranged from only a few hundred in large species to over 1400 in small winter species (Jewett 1959). The egg masses immediately disintegrate very quickly under water (Hynes 1976). In Perspicuusoperlidae, the egg mass is considerably small, with no more than 100 eggs. According to the study of *Taeniopteryx nebulosa* (Linnaeus, 1758) in Brittain (1977), the low number of eggs per egg mass might suggest a low water temperature (lower than 10 °C) in the habitat area.

Whereas in the biological study of *Nemoura cinerea* (Retzius, 1783), the number of eggs per mass has no significant relationship with temperature (Ebrittain and Lillehammer 1987). A fixed level of available natural resource could lead to a tradeoff between egg size and egg number (Smith and Fretwell 1974), the apparently large individual eggs of Perspicuusoperlidae might result in the less number in the mass (Berrigan 1991). Another plausible hypothesis proposed by the author is that, the ancient Burmese forest streams were small in size, slow-flowing or even fragmented, which could not bear a high-density population as big rivers or streams and partially contributed to the low number of eggs in Perspicuusoperlidae.

Secondly, the eggs of Perspicuusoperlidae are completely membranous in lack of complicated external structures, and the egg mass is composed of uniformly arranged individual eggs. Eggs of stoneflies are highly variable in size, shape, and chorionic modification. Several main types of eggs are introduced by Hynes (1976): eggs with an anchor plate to adhere firmly to substrates under water (as in some Systellognatha); eggs with sticky membranous or gelatinous surface coverings that swell rapidly in water and stick to substrates (as in Euholognatha and some Systellognatha); eggs with filament-like projections with hooked tips (as in Perlesta Banks, 1906); eggs not sticky and simply fall into interstices of stream bed (as in most Antarctoperlaria). However, the eggs of Perspicuusoperlidae have no anchor plates, sticky membranous or gelatinous surface, or any filament-like projections. Dissolution of these structures during the fossil formation is less possible since the surface and outline of all visible eggs are uniformly clearly recognized without any remnants of above mentioned structures. Two potential strategies might be used by eggs of Perspicuusoperlidae: simply fall and scatter in water; or use the multiple concave collar areas arranged outside the egg mass as sucking discs to adhere to substrates. The latter assumption seems more reasonable since the egg masses of extant stoneflies usually stick together with random orientation for each egg, whereas the eggs of Perspicuusoperlidae uniformly project the collar areas outward. Such ordered arrangement of eggs should be functional.

Data availability

All material included in this paper is deposited in the Insect Collection of Jiangsu University of Science and Technology, Jiangsu Province, China.

Author contributions

ZTC produced the photos and prepared the paper.

Competing interests

The authors declare that they have no conflict of interest.

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