“Rolling” Stoneflies (Insecta: Plecoptera) from Mid-Cretaceous Burmese amber

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ABSTRACT
This contribution describes seven new species of fossil stoneflies from Cretaceous Burmese amber, all of which are dedicated to present and past members of the Rolling Stones. Two species – Petroperla mickjaggeri sp. nov. and Lapisperla keithrichardsi sp. nov. – are placed in a new family Petroperlidae within the stemline of Systellognatha. The first Cretaceous larval specimen of Acroneuriinae, Electroneuria ronwoodi sp. nov., is also described along with another four new species that are placed within the Acroneuriinae genus Largusoperla Chen et al., 2018: Largusoperla charliewattsi sp. nov., L. brianjonesi sp. nov., L. micktaylori sp. nov., and L. billwymani sp. nov. Additional specimens of Acroneuriinae are mentioned without formal assignment to new species due to insufficient preservation. Implications for stonefly phylogeny and palaeobiogeography are discussed.

INTRODUCTION
Stoneflies (Plecoptera) is a small insect order with approximately 3,700 extant and 250 fossil species currently described (DeWalt et al., 2018). Extant stonefly diversity is highest in the temperate regions of the Northern Hemisphere (Fochetti & De Figueroa, 2008), a pattern probably consistently followed throughout their history (Sinitshenkova, 1997). Stoneflies in general have aquatic larvae and usually prefer cold streams with relatively high amount of dissolved oxygen (Zwick, 1973; Hynes, 1976), although there are both extant and extinct Jurassic taxa known from hypotrophic lakes (Brittain, 1990; Sinitshenkova & Zherikin, 1996).

Plecoptera is considered either as sister group to all other Neoptera or as one of the basal clades within Polyneoptera (Zwick, 2009; Misof et al., 2014, Wang et al., 2016). Phylogeny of individual lineages within the order was analysed by Zwick (1973, 1980). Sinitshenkova (1987) presented a phylogeny that also included fossil taxa. However, partly due to the limited number of characters visible in some fossil taxa, her topology is not supported by reliable apomorphies of individual clades. The most recent and widely accepted phylogeny of Plecoptera was published by Zwick (2000) based on morphological characters of extant species only.

The first molecular phylogeny was published by Thomas et al. (2000) using 18S gene only. A more complex study using six molecular markers (12S, 16S, 18S, 28S, COII, H3) and morphological data was performed by Terry (2003). Results of this study were largely congruent with Zwick (2000), recovering all major groups, i.e. Antarctoperlaria, Arctoperlaria, Systellognatha, Euholognatha (without Megaleuctra), and Perloidea as monophyletic. Recently, Chen et al. (2018b) proposed a molecular phylogeny of Systellognatha inferred from mitochondrial genome sequences.

Stoneflies are relatively rare in the fossil record, which might be related to their delicate bodies and their preferred lotic habitat preventing fossilization. Stoneflies date back to the Carboniferous, with the alleged stem-Plecoptera Gulou carpenteri Béthoux et al., 2011 from the Pennsylvanian of China (Béthoux et al., 2011), although there is only indirect evidence for its placement within Plecoptera. Numerous stonefly fossils attributed to the crown group are known from the Permian, with the diversity culminating in the Jurassic and declining in the Early Cretaceous (Sinitshenkova, 1997; Liu & Ren, 2006).

The best-preserved fossil specimens are found in amber, allowing the observation of even minute morphological details. However, amber inclusions of stoneflies are in general very rare. Only one species attributed to the Perlidae subfamily Acroneuriinae (Stark & Lenz, 1992) was
described from Miocene Dominican amber. Three species of Capniidae and Leuctridae were
recognized in Rovno amber (Sinitshenkova, 2009), and nineteen species out of five families
(Taeniopterygidae, Leuctridae, Nemouridae, Perlidae, Perlodidae) are described from Eocene
Baltic amber, all but two of which are attributed to extant genera (Caruso & Wichard, 2010;
Caruso & Wichard, 2011; Chen 2018a). The occurrence of Plecoptera in Upper Cretaceous
Siberian amber is also known (Wichard & Weitschat, 1996). Only recently, Chen et al. (2018a)
and Chen (2018b, c) reported the first Plecoptera from mid-Cretaceous Burmese amber with the
descriptions of the new genera *Largusoperla* Chen et al., 2018 (Perlidae: Acroneuriinae)
including four species, and *Pinguisoperla* Chen, 2018, including a single species *P.yangzhouensis*.

In this study, we add four new species of *Largusoperla* and describe the first larval
specimen of stoneflies in Burmese amber. More importantly, we report two new genera within a
new family of fossil stoneflies, which probably represent stem group representatives of
Systellognatha. We discuss their systematic affinities and evaluate possible implications for
Plecoptera phylogeny. We also provide novel insights into several aspects of the palaeocology
and palaeobiogeography of stoneflies.

**MATERIAL AND METHODS**

**Specimens**
All pieces of fossil-bearing Burmese amber originate from the type locality Hukawng Valley,
Kachin State, Myanmar. The exact outcrop among the various amber mines in this valley is
unknown, because the specimens were acquired from traders. A review of these amber deposits
and relative geological history is available in Zherikhin & Ross (2000), Grimaldi et al. (2002),
and Ross et al. (2010). UePb zircon dating (Shi et al., 2012) constrained this amber to a
maximum age of 98.79 ± 0.62 Ma, which is equivalent to the earliest Cenomanian (Gradstein et
al., 2004).

**Imaging**
The material was studied under a Leica M205 C (Leica Corporation, Wetzlar) and Olympus
SZX7 (Olympus Corporation, Tokyo) stereomicroscope. Leica Z16 APO Macroscope with Leica
Application Suite Version 3.1.8 and Helicon Focus Pro was used to obtain stacked photographs
with extended depth of field. Photographs were sharpened and adjusted in contrast and tonality
in Adobe Photoshop™ version CS6 (Adobe Systems Incorporated, San Jose).
High-resolution µ-CT scanning with a Bruker Skyscan 1272 tomograph was performed on
specimen SMNS BU-79, but yielded no sufficient contrast to produce any useful tomographic
image.

**Terminology**
Abbreviations for wing veins used throughout the text follow Béthoux (2005): C: costa; ScP:
subcosta posterior; R: radius; RA: radius anterior; RP: radius posterior; M: media; MA: media
anterior; MP: media posterior; Cu: cubitus; CuA: cubitus anterior; CuP: cubitus posterior; AA:
analis anterior; arc: arculus (secondarily strengthened cross vein between M and Cu).
All type specimens examined are housed in the State Museum of Natural History, Stuttgart, Germany (SMNS) and catalogue numbers are specified for individual species below. Further specimens of coll. P. Müller, Käshofen, Germany, were additionally investigated.

When discussing the affinities of individual taxa, we refer to the phylogenetic system of Plecoptera proposed by Zwick (2000).

**Nomenclature**

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:486E9A01-EF59-41D7-B001-4AD6D7FBB11F. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

**Etymology of “Rolling” Stoneflies**

Burmese amber is one of the oldest resins with insect inclusions, and stoneflies are one of the oldest pterygote lineages. What lies closer at hand than to link fossil stoneflies in ancient stones with the Rolling Stones and to name the new species after the members of the oldest and greatest Rock’n Roll Band in the World. The discerning reader will notice that the new family and genera are named after “the Stones”, and all present and former members of the Rolling Stones are honoured with their own species.

**SYSTEMATIC PALAEONTOLOGY**

Class Insecta Linnaeus, 1758
Subclass Pterygota Lang, 1888
Order Plecoptera Burmeister, 1839
Suborder Arctoperlaria Zwick, 1973
Infraorder Systellognatha Zwick, 2000

**Petroperlidae, fam. nov.**

*Petroperla* gen. nov.

**Type genus.** *Petroperla* gen. nov.

**Diagnosis.** Glossae and paraglossae of approximately same size (plesiomorphy of Systellognatha), rather stout labial palps (plesiomorphy of Systellognatha), short first tarsomere (apical tarsomere 3.5× longer than first tarsomere) (apomorphy of *Systellognatha*); euplantulae present on tarsi (plesiomorphy of *Systellognatha*); setose arolium (apomorphy of...
Systellognatha); forewing with numerous crossveins in costal field (plesiomorphy of Systellognatha); vein RA almost reaching wing apex (apomorphy of Petroperlidae), proximal origin of vein RP (just distal to 1/4 of wing length) (plesiomorphy of Systellognatha).

**Petroperla gen. nov.**

urn:lsid:zoobank.org:act:68557BD3-F4E1-43BB-A10B-68D796971769

**Type species.** Petroperla mickjaggeri, gen. et sp. nov.

**Diagnosis.** By monotypy, as for the type species.

**Etymology.** The first part of the compound noun refers to the Rolling Stones and is derived from Latin "petra", meaning "stone", the second part "perla", refers to the stonefly genus Perla.

**Petroperla mickjaggeri sp. nov.** (Figs 1–2)

urn:lsid:zoobank.org:act:838EDFF8-BD85-4F83-88F6-87E38701A941

**Diagnosis.** Thoracic gill remnants absent, abdominal segments not extended posterolaterally.

**Etymology.** The name refers to Sir Mick Jagger, founding member, harmonica player, and lead singer of the Rolling Stones.

**Material.** Holotype specimen: SMNS BU-79, female.

**Description.**

**Head.** Colour greyish, original cuticular colouration not preserved. All three ocelli fully developed. Median ocellus slightly subequal in size to lateral ocelli. Antennae 3.6 mm long (approximately 0.6× body length). Individual segments covered with short hair-like setae. Antennal segments in middle third of antenna approximately 2.2× longer than wide. Maxillary palps five-segmented, two basal palpomeres short, three distal palpomeres longer, of approximately same length. Labium with glossae and paraglossae of approximately same size, labial palps rather stout, three-segmented (Figs 1C, 2A). Two basal palpomeres short, apical palpomere longer. Other mouthparts not recognizable.

**Thorax.** Prothorax approximately quadrangular. Colour greyish, original cuticular colouration not preserved (Figs 1A, B).

**Forewings (Fig. 2E–F):** length 6.5 mm, width 2 mm; costal field with numerous crossveins (12 crossveins visible on right forewing and 17 on left forewing, including area distal to ScP, badly visible due to preservation); ScP reaching RA just distally to 1/2 of wing length; RA simple, almost reaching the wing apex; single crossvein between RA and RP; RP originating from R just distally to 1/4 of wing length; RP with 2 distal branches, originating at 2/3 of wing length; single crossvein between RP and M; M approximated to R basally, diverging close to origin of RP; M with 2 branches, originating just distally to 1/2 of wing length; occurrence of arculus and up to 6 additional crossveins between M and CuA; CuA branched distally, with 3
branches; up to 5 crossveins between CuA and CuP; CuP simple and straight; AA1 simple; AA2
with 2 branches.

Hind wings (Fig. 2G, venation visible only in apical portion): length 5.6 mm; RA simple,
almost reaching wing apex; single crossvein between RA and RP; RP with 2 distal branches,
originating at 2/3 of wing length; single crossvein between RP and M; M with 2 branches;
branching of Cu and AA not recognizable.

Thoracic sterna (Fig. 2C) with one pair of dark patches centrally on mesosternum and two
pairs on metasternum. Metasternum (Fig. 2C) with apparent arched furcal pits (not apparent on
pro- and mesosternum due to state of preservation). Thoracic gill remnants absent.

Legs slender, covered with very short spine-like setae (thicker setae near posterior margin
of femora and on dorsal surface of tibiae. Single tibial spur present apically (Fig. 2B). Tarsi with
first two tarsomeres short (approximately equal in size) and apical tarsomere long, approximately
1.5× longer than first two combined (Fig. 2B). Arolium present, approximately as wide as width
of apical tarsomere, with setae on arolium. Euplantulae present on tarsomeres 1 and 2.

Abdomen. Colour greyish, original colouration not preserved. Individual segments not
distinctly enlarged posteromedially. No abdominal gill remnants recognizable. Subgenital plate
poorly visible, probably triangular, without notch medially (Figs 1D, 2D). Cerci short, 1 mm in
length, covered with very short setae (Fig. 1A).

Lapisperla gen. nov.
urn:lsid:zoobank.org:act:05FAF13D-5548-4EFB-AFA1-CA30EA1A0B7B

Type species. Lapisperla keithrichardi, gen. et sp. nov.

Diagnosis. By monotypy, as for the type species.

Etymology. The first part of the name refers to the Rolling Stones and is derived from Latin
"lapis", meaning "stone", the suffix "perla" refers to the stonefly genus Perla.

Lapisperla keithrichardi sp. nov. (Figs 3–4)
urn:lsid:zoobank.org:act:586DF169-34E5-4E6F-89EC-58E7D67BF6CB

Diagnosis. prominent subgenital plate, abdominal segments extended posterolaterally, thoracic
gill remnants present.

Etymology. The name refers to Keith Richards, founding member and guitar player of the
Rolling Stones, master of the ancient art of weaving.

Material. Holotype specimen: SMNS BU-313, female.

Description.
Body length 6.1 mm (without head).

Head. Not preserved.
Thorax. Prothorax approximately quadrangular (Fig. 3A, B). Original cuticular colouration not preserved.

Forewings (Fig. 4A, B): right forewing present only as short basal fragment, 2.3 mm long. Left forewing almost complete, except for apical portion, length of preserved part approximately 6 mm, width 2.4 mm; costal field with 9 visible crossveins, including area distal to ScP with 2 visible crossveins; ScP reaching RA just proximally to RA–RP crossvein; RA simple; single crossvein between RA and RP; RP originating from R relatively basally, approximately 1.8 mm from wing base; RP with 2 visible distal branches, originating just distally to RA–RP crossvein; single crossvein between RP and M; M approximated to R basally; M with 2 visible branches, originating approximately 3.6 mm from wing base; occurrence of arculus and 5 additional crossveins between M and CuA; CuA branched distally, with 3 branches; 6 crossveins between CuA and CuP; CuP simple and straight; AA1 simple; AA2 with 3 branches.

Hind wings (Fig. 4C-E): apical portions missing, length of preserved parts approximately 5.7 mm (right hind wing) and 4.9 (left hind wing); costal field with 6 visible crossveins, including area distal to ScP with 3 crossveins; ScP reaching RA just proximally to RA–RP crossvein; RA simple, close to apex not approximated to C; single crossvein between RA and RP; RP with 2 branches, originating just distally to RA–RP crossvein; single crossvein between RP and M; M with 2 branches; CuA, CuP and AA1 simple. Venation pattern of AA2 not recognizable.

Visible gill remnants ventrolateral between meso- and metathorax. Legs slender, covered with very short spine-like setae. Single apical tibial spur present (Fig. 3D). Tarsi with first two tarsomeres short (approximately equal in size) and apical tarsomere long, approximately 1.6× longer than first two combined (Fig. 3D). Long hair-like setae near base of claws. Arolium present, approximately as wide as width of apical tarsomere. Arolium equipped with setae. Euplantulae present apically on tarsomeres 1 and 2 (Fig. 3D).

Abdomen. Individual segments with pronounced posterolateral extensions (Fig. 1C, D). No abdominal gill remnants recognizable. Prominent subgenital plate, rounded posteriorly, with slightly elevated notch posteromedially (Figs 3C, 4F). Cerci broken off, only short basal parts preserved, densely covered with short setae.

Remarks on generic composition of Petroperlidae. L. keithrichardsi sp. nov. differs from P. mickjaggeri sp. nov. in having a more prominent subgenital plate (badly visible, but much smaller in P. mickjaggeri sp. nov.). Abdominal segments of L. keithrichardsi sp. nov. are equipped with posterolateral projections (no projections in P. mickjaggeri sp. nov.), and meso- and metathorax of L. keithrichardsi sp. nov. ventrolaterally with gill remnants (apparently absent in P. mickjaggeri sp. nov.). We consider these differences pronounced enough to justify a placement of these species in two separate genera within Petroperlidae.

Order Plecoptera Burmeister, 1839
Suborder Arctoperlaria Zwick, 1973
Infraorder Systellognatha Zwick, 2000
Superfamily Perloidea Latreille, 1802
Family Perlidae Latreille, 1802
Subfamily Acroneuriinae Klapálek, 1914
**Electroneuria, gen. nov.**

urn:lsid:zoobank.org:act:3A4CA23C-2D23-4F8E-9492-93C490AE736C

**Type species.** Electroneuria ronwoodi, gen. et sp. nov.

**Diagnosis.** By monotypy, as for the type species.

**Etymology.** Latin “electrum” refers to both amber and electric guitars, the suffix “–neuria” to the stonefly subfamily Acroneuriinae.

**Electroneuria ronwoodi** sp. nov. (Figs. 5–6)

urn:lsid:zoobank.org:act:A52885BB-E2CF-49E8-871B-C4CE8577002C

**Diagnosis.** Larva with occipital spinule row complete medially; fringe of long thin setae laterally on pronotum; long hair-like setae on surface of wingpads and abdominal terga; posterior margin of abdominal terga with numerous very long thin setae; cerci long, with only short setae.

**Etymology.** The name of this immature specimen refers to Ronnie Wood, guitar player of the Rolling Stones since 1975, and thus the youngest member of the Rolling Stones.

**Material.** Holotype specimen SMNS BU-306, larva.

**Description.** Body length 8.1 mm (Figs 5A-B).

**Head.** Antennae 5.5 mm long (approximately 0.7× body length). Length of antennal segments in the middle third of antenna approximately equal to segment width. Mouthparts of predaceous type. Mandibles with only apical part of right mandible recognizable, with 4 rounded teeth. Left maxilla well visible (Figs 5C, 6F), with thin galea slightly shorter than lacinia. Lacinia with two long, prominent pointed teeth, apical tooth longer. Row of six long setae on inner margin of lacinia, situated basally from subapical tooth, on slightly elevated hump. Left maxillary palp with three recognizable elongated palpomeres, basal part not well visible. Distal palpomere probably missing. Sparse short setae present on all visible palpomeres, more dense on proximal palpomere. Other mouthparts not recognizable.

Occipital row of short spinules medially regular, in lateral parts scattered goups of longer spinules present (Figs 5D, 6E).

**Thorax.** Pronotum covered with minute, hair-like setae on surface. Longer setae along margins (Fig. 6C). Pronounced wingpads (same size on meso- and metathorax), posterior notal contour not apparent. Thoracic gills badly preserved, indistinctly visible on left side between meso- and metathorax. Legs covered with numerous setae of various size and shape (Fig. 6G).

Regular row of long, hair-like setae along outer margin of femora (length approximately 0.5× femur width) and tibiae (length approximately 1.5× tibia width). Tarsi with first two tarsomeres very short, third one approximately 2× longer than first two combined. Two claws with indistinctly pronounced denticles (Figs 5E, 6H).

**Abdomen.** Posterior margin of terga with long setae (posterior tergal spinule fringe sensu Stark & Gaufin, 1976). Numerous long, intercalary setae on surface of terga (Fig. 5F, 6D).

Sterna with short spine-like setae along posterior margin; row of these setae complete in two last...
segments (Fig. 6A). No abdominal gill remnants recognizable. Paraprocts bluntly pointed apically. Cerci 6 mm long (approximately 0.7× body length). Individual segments with short, spine-like setae (Fig. 6B).

Order Plecoptera Burmeister, 1839
Suborder Arctoperlaria Zwick, 1973
Infraorder Systellognatha Zwick, 2000
Superfamily Perloidea Latreille, 1802
Family Perlidae Latreille, 1802
Subfamily Acroneuriinae Klapálek, 1914
Genus Largusoperla Chen et al., 2018

Largusoperla charliewattsi sp. nov. (Figs 7–8)
urn:lsid:zoobank.org:act:43BA0BA8-7818-47FE-BA37-E38F140A457C

Diagnosis. Large paraprocts; hammer knob-shaped, elongated transversally; pronotum not distinctly widened anteriorly.

Etymology. The name refers to Charlie Watts, drummer of the Rolling Stones, which is most adequate in regard of the pronounced drumming apparatus of the new species.

Material. Holotype specimen: SMNS BU-10, male.

Description. Body length 8.1 mm (Fig. 7A).

Head. Colour brown, marginal areas paler. Three fully developed ocelli. Median ocellus slightly subequal in size to lateral ocelli. Antennae 5.4 mm long (approximately 0.7× body length). Individual segments covered with short hair-like setae. Antennal segments in the middle third of antenna length approximately 2.5× longer than wide.

Maxillary palps slender, five elongated palpomeres covered with short hair-like setae (Fig. 7B). Labial palps rather elongated, three palpomeres present. First palpomere short (Fig. 7B). Other mouthparts not recognizable.

Thorax. Prothorax approximately quadrangular. Colour brown with pale median longitudinal line.

Forewings (Fig. 8C): length 8 mm, width 2.6 mm; costal field with 15 visible crossveins (including 2 crossveins distal to ScP); ScP reaching RA just proximally to 2/3 of wing length; RA simple; two crossveins between RA and RP; RP originating from R just distally to 1/3 of wing length; RP with 4 distal branches; single crossvein between RP and M; M slightly approximated to R basally; M with 2 branches, originating just distally to 1/2 of wing length; occurrence of arculus and 4 additional crossveins between M and CuA; CuA branched distally, with 4 branches; 5 crossveins between CuA and CuP; CuP simple and straight; single cubito-anal crossvein reaching anal cell; A1 simple; AA2 with 2 branches, originating directly from anal cell.

Hind wings (Fig. 8D, venation details observable only in apical portion): length 6.9 mm; costal field with 5 visible crossveins (including 3 crossveins distal to ScP); ScP reaching RA
distal to 1/2 of wing length; RA simple; single crossvein between RA and RP; RP originating from common stem with M at 1/4 of wing length; RP with 3 distal branches; branching of M, Cu and AA not recognizable.

Thoracic sterna (Figs 7C, 8A) with apparent oblique furcal pits, converging anteriorly. Transverse meso- and metasternal ridge connecting anterior corners of respective furcal pits. Longitudinal median ridge apparent on mesofurcasternum. Y-ridge connecting posterior corners of furcal pits absent. Gill remnants recognizable on all thoracic segments (Fig. 8A).

Legs slender, covered with very short hair-like setae. Two thickened tibial spurs present apically on tibia, along with several additional long spine-like setae (Fig. 7E). Tarsi with first two tarsomeres short (approximately equal in size) and apical tarsomere long, approximately 1.5× longer than first two combined. Arolium present, slightly wider than width of last tarsomere. Euplantulae present on tarsomeres 2 and 3 (Fig. 7E-F).

Abdomen. Colour brown, ventral side paler. Individual segments not distinctly enlarged posteromedially. Elevated, knob-shaped and transversally elongated hammer near posterior margin of sternum IX (Figs 7D, 8B). Enlarged dark brown hook-like paraprocts between cerci (Figs 7D, 8B). Cerci short, 2.1 mm in length (approximately 0.3× body length). Slightly moniliform in shape; segments covered with short hair-like setae (Fig. 7D).

Affinities. L. charliewattsi sp. nov. exhibits a combination of morphological characters allowing attribution to the family Perlidae (presence of long and slender palps, vestiges of thoracic gills, euplantulae, short first tarsomere, and forewings with numerous crossveins in the basal half of the costal field, see Zwick, 1980; Zwick, 2000). The presence of sclerotized and strongly recurved paraprocts and well-developed hammer allow a placement into the subfamily Acroneuriinae (Stark & Gaufin, 1976; Zwick, 1980; Zwick, 2000).

Within Acroneuriinae, L. charliewattsi sp. nov. can be attributed to the recently described genus Largusoperla, as defined by Chen et al. (2018a), based on the following diagnostic characters: triocellate; pronotum with pale median area; sternum IX with a small elevated lobe; large paraprocts sclerotized and strongly upcurved; short cerci, no longer than 1/2 of the abdomen length. Some characters stated by Chen et al. (2018a) as diagnostic for the genus are not visible in L. charliewattsi sp. nov., possibly due to the state of preservation (head with dark stigma covering ocelli; abdominal terga with darker lateral markings). Another diagnostic character (abdominal segments posteromedially extended) is not very pronounced in L. charliewattsi sp. nov. and is probably variable within the genus.

In Pinguisoperla Chen, 2018, the second Perlidae genus described from Burmese amber, the subfamilial attribution is uncertain (Chen, 2008b), and it might also belong to Acroneuriinae. Nevertheless, any affinity of L. charliewattsi sp. nov. to Pinguisoperla can be excluded based on the absence of enlarged, plump basal segment of the cercus, which constitutes the main diagnostic character of Pinguisoperla.

Up to now, four species of Largusoperla have been described, all based on male specimens from the Burmese amber, namely Largusoperla acus Chen et al., 2018, Largusoperla flata Chen et al., 2018, Largusoperla arcus Chen et al., 2018, and Largusoperla difformitatem Chen, 2018. L. charliewattsi sp. nov. differs from L. acus in having less prominent posterolateral extensions on abdominal segments, pronotum not distinctly widened anteriorly, and paraprocts without needle-like apices. L. flata can be discriminated from L. charliewattsi sp. nov. by having entirely different shape of paraprocts (see Chen et al., 2018a, figs 12, 13 and Figs 7D, 8B). L. arcus possesses a more circular hammer on sternum IX, compared to a transversally rather
elongated hammer in *L. charliewattsi* sp. nov. and paraprocts with apices distinctly diverging,
contrary to more parallel oriented paraprocts in *L. charliewattsi* sp. nov. *L. difformitatem* differs
by longer, highly divergent paraprocts and smaller hammer.

*Largusoperla billwymani* sp. nov. (Figs 9–10)
urn:lsid:zoobank.org:act:4AB77845-FAB5-4440-8440-8496-935CBD1249B0

**Diagnosis.** Very large paraprocts, knob-shaped, circular hammer, slender body, trapezoidal
pronotum.

**Etymology.** The name refers to Bill Wyman, former bass player of the Rolling Stones until
1991.

**Material.** Holotype specimen: SMNS BU-229, male.

**Description.** Body length 10.2 mm (Fig. 9A).

**Head.** Colour brown without distinct markings. Surface of head capsule with numerous short
hair-like setae. Three fully developed ocelli. Median ocellus subequal in size to lateral ocelli.
Antennae 7.6 mm long (approximately 0.7× body length). Individual segments covered with
short hair-like setae. Antennal segments in the middle third of antenna length approximately 2.5×
longer than wide.
Maxillary palps slender, with 5 elongated palpomeres covered with short hair-like setae
(Figs 9B, 10E). Palpomeres 1 and 5 short, palpomeres 2–4 approximately equal in length.
Labium with glossae much smaller than paraglossae. Labial palps elongated, palpomere 2
longest, palpomeres 1 and 3 slightly shorter (Figs 9B, 10C, E). All palpomeres covered with
short hair-like setae. Other mouthparts not recognizable.

**Thorax.** Prothorax trapezoidal, distinctly wider anteriorly. Surface of pronotum with
numerous short hair-like setae. Colour brown with pale longitudinal median band, poorly visible
due to state of preservation.
Forewings (Fig. 10A-B): length 9.3 mm, width 2.5 mm; costal field with up to 13
crossveins (single crossvein distal to ScP faintly visible on right forewing); ScP reaching RA
approximately at 2/3 of wing length; RA simple; single crossvein between RA and RP; RP
originating from R distal to 1/3 of wing length; RP with 4 distal branches; single crossvein
between RP and M; M approximated to R basally; M with 2 branches, originating proximally to
2/3 of wing length; occurrence of arculus and 5 additional crossveins between M and CuA; CuA
branched distally, with 3 branches; 5–6 crossveins between CuA and CuP; CuP simple and
straight; single cubito-anal crossvein reaching anal cell; AA1 simple; AA2 with 2 branches
originating directly from anal cell.

Hind wings (Fig. 10D): length 7.8 mm; costal field with 5 visible crossveins (including
single crossvein distal to ScP); ScP reaching RA proximal to 2/3 of wing length; RA simple;
single crossvein between RA and RP; RP originating from common stem with M at 1/3 of wing
length; RP with 4 distal branches; single crossvein between RP and M; branching of M, Cu and
AA not recognizable.
Thoracic sterna (Fig. 10C) with apparent oblique furcal pits, converging anteriorly. Transverse meso- and metasternal ridge connecting anterior corners of respective furcal pits. Longitudinal median ridge apparent on mesofurcasternum, bifurcated and connecting anterior corners of furcal pits. Y-ridge connecting posterior corners of furcal pits absent. Gill remnants recognizable on all thoracic segments (Fig. 10C). Legs slender, covered with short hair-like setae. Several longer and thicker spine-like setae occasionally on tibia. Two thickened tibial spurs and several setae apically on tibia (Fig. 9D-E). Very long hair-like setae subapically on tarsomere 3, approximately as long as claw length. Tarsi with first two tarsomeres short (approximately equal in size) and apical tarsomere long, approximately 1.6× longer than first two combined. Arolium present, slightly wider than width of last tarsomere. Euplantulae present on tarsomeres 2 and 3 (Fig. 9E).

Abdomen. Colour brown, ventral side paler. Individual segments not distinctly enlarged posteromedially. Elevated, knob-shaped and circular hammer near posterior margin of sternum IX (Figs 9C, 10F). Enlarged hook-like paraprocts between cerci (Figs 9C, 10F). Paraprocts with convex lateral margins, not diverging apically. Number of hair-like setae apparent on sterna VIII, IX (Fig. 9C). Cerci very short, consisting of 13 segments, 1.7 mm in length (approximately 0.2× body length). Slightly moniliform in shape; segments covered with long hair-like setae (Fig. 9C).

Affinities. *L. billwymani* sp. nov. share all the diagnostic characters of the Perlidae subfamily Acronurinae and the genus *Largusoperla*, as discussed above. *L. billwymani* sp. nov. clearly differs from *L. charliewattsi* sp. nov. based on the general shape of body and wings (more slender with narrower wings in *L. billwymani* sp. nov.) and pronotum shape (distinctly trapezoidal in *L. billwymani* sp. nov., more oblong-shaped in *L. charliewattsi* sp. nov.). *L. billwymani* sp. nov. also exhibits larger paraprocts in comparison with *L. charliewattsi* sp. nov. contrary to transversally elongated in *L. charliewattsi* sp. nov.). The paraprocts of *L. billwymani* sp. nov. are similar to *L. flata*, but slightly differ in shape, lateral contour being concave in *L. flata* (Chen et al., 2018a, figs 12, 13) and convex in *L. billwymani* sp. nov. (Figs 9C, 10F). *L. billwymani* sp. nov. also exhibits narrower pronotum and more circular hammer compared to *L. flata*. Another difference can be found in the forewing venation, vein RP in *L. flata* is three-branched with bifurcation on the posterior branch (Chen et al., 2018a, fig 11), whereas *L. billwymani* sp. nov. has a four-branched RP with bifurcations on anterior branches (Fig. 10A-B). Nevertheless, wing venation characters must be taken cautiously, since they are subject to large intraspecific variability (Béthoux et al., 2011). Another two species *L. acus* and *L. arcus* have differently shaped paraprocts compared to *L. billwymani* sp. nov. (*L. acus* with strongly constricted, needle-shaped apices and *L. arcus* with apices distinctly curved outward). *L. difformitatem* can be distinguished from *L. billwymani* sp. nov. by having a smaller, transversally elongated hammer and also highly divergent paraprocts.

*Largusoperla micktaylori* sp. nov. (Figs 11–14) urn:lsid:zoobank.org:act:17E6ED82-03C8-4824-9176-51C34EFDF66F

Diagnosis. Posterior margin of subgenital plate with three long, narrow, apically pointed processes.
Etymology. The name refers to Mick Taylor, guitar player of the Rolling Stones between 1969 and 1975 with unmatched virtuosity and dexterity, which is reflected by the finger-like, three-lobed subgenital plate of the new species.

Material. Holotype specimen SMNS BU-227, female; paratype specimen SMNS BU-312, female.

Description. Body length 8.6–10.5 mm (Figs 11A-B, 13A-B, 15A-B).

Head. Colour brown without distinct markings. Three fully developed ocelli. Median ocellus slightly subequal in size to lateral ocelli. Antennae 7.2–7.4 mm long (approximately 0.8× body length). Individual segments covered with short hair-like setae. Antennal segments in the middle third of antenna length approximately 2.2× longer than wide.

Maxillary palps slender, with 5 elongated palpomeres covered with short hair-like setae (Figs 11C, 13C). Palpomeres 1 and 5 short, palpomeres 2–4 approximately equal in length.

Labium with glossae much smaller than paraglossae. Labial palps elongated, three-segmented. All palpomeres of approximately same length (Figs 11C, 13C). All palpomeres covered with short hair-like setae. Other mouthparts not recognizable.

Thorax. Pronotum trapezoidal, anteriorly slightly wider. Colour brown with central longitudinal pale band.

Forewings (Figs 12B-C, 14B-C): length 10–10.7 mm, width 3.1–3.5 mm; costal field with 9–14 crossveins, including 1–2 crossveins distal to ScP; ScP reaching RA just proximally to 2/3 of wing length; RA simple; single crossvein between RA and RP; RP originating from R just distally to 1/3 of wing length; RP with 3–4 distal branches; single crossvein between RP and M; M slightly approximated to R basally; M with 2 branches, originating proximal to 2/3 of wing length; occurrence of arculus and 3–5 crossveins between M and CuA; CuA branched distally, with 4 branches; 3–7 crossveins between CuA and CuP; CuP simple and straight; single cubito-anal crossvein reaching anal cell; AA1 simple; AA2 with 3 branches originating directly from anal cell.

Hind wings (Figs 12D, 14D): length 8.7–8.8 mm; costal field with 7–8 crossveins, including 1–2 crossveins distal to ScP; ScP reaching RA distal to 1/2 of wing length; RA simple; single crossvein between RA and RP; RP originating from common stem with M at approximately 1/4 of wing length; RP with 3–4 distal branches; single crossvein between RP and M; M with 2 branches originating distal to 1/2 of wing length; CuA with 2 branches; CuP and A recognizable only partially.

Thoracic sterna (Fig. 12A) with apparent oblique furcal pits, converging anteriorly. Longitudinal median ridge apparent on mesofurcasternum, bifurcated in the middle of its length and connecting anterior corners of furcal pits. Y-ridge connecting posterior corners of furcal pits absent. Transverse meso- and metasternal ridge connecting anterior corners of respective furcal pits indistinct. Remnants of thoracic gills recognizable.

Legs slender, covered with short hair-like setae. Two thickened tibial spurs apically on tibia. Very long hair-like setae subapically on tarsomere 3, approximately as long as claw length. Tarsi with first two tarsomeres short (approximately equal in size) and apical tarsomere long, approximately 1.5× longer than first two combined. Arolium present, slightly wider than width of last tarsomere. Euplantulae prominent, present on tarsomeres 2 and 3.
Abdomen. Individual segments not distinctly enlarged posteromedially. Cerci short, 2.2 – 2.3 mm in length (approximately 0.2× body length), covered with short setae (Figs 13E, 14A).

Individual segments not distinctly enlarged posteromedially. Cerci short, 2.2 – 2.3 mm in length (approximately 0.2× body length), covered with short setae (Figs 13E, 14A). Subgenital plate with three long, narrow, apically pointed processes on posterior margin (Figs 11D, 13E, 14A). All three processes of same length, one situated medially and two laterally.

Affinities. Largusoperla micktaylori sp. nov. shares with male representatives of the genus Largusoperla traits typical for the Perlidae (presence of long and slender palps, vestiges of thoracic gills, euplantulae, short first tarsomere, and forewings with numerous crossveins in the basal half of the costal field). Relative size of glossae and paraglossae is apparent in the holotype and paratype only, with paraglossae distinctly larger (Figs 11C, 13C) and thus congruent with the assignment to Perlidae. The placement to the subfamily or tribe within Perlidae can be done only based on characters of male genitalia, which is inapplicable for L. micktaylori sp. nov. However, based on the presence of key generic diagnostic characters of Largusoperla (triocellate; pronotum with pale median area; short cerci, no longer than 1/2 of the abdomen length) together with overall high similarity in the arrangement of tarsi, mouthparts, wing venation and simultaneous occurrence with Largusoperla males, we include L. micktaylori sp. nov. into Largusoperla. From Pinguisoperla Chen, 2018, another Perlidae genus described from the Burmese amber, L. micktaylori sp. nov. clearly differs by the absence of an enlarged, plump basal segment of the cercus, which constitutes the main diagnostic character of Pinguisoperla.

The subgenital plate in L. micktaylori sp. nov. with three pronounced extensions on posterior margin is rather unusual and unique among known stoneflies and represents a crucial diagnostic character of L. micktaylori sp. nov. Since the shape of the subgenital plate is exactly the same in all three specimens from the type series and since they also share other morphological characteristics (body size, arrangement of mouthparts, general wing venation pattern), we consider these specimens to represent a single new species.

Individual specimens of L. micktaylori sp. nov. differ from each other in the wing venation details such as number of crossveins and RP branches (Figs 12B-C, 14B-C). However, these differences correspond with common intraspecific variability, as documented for recent Perlidae by Béthoux et al. (2011). In holotype, the number of RP branches even differs between right and left forewing, being four and three, respectively, a phenomenon not uncommon in extant taxa.

**Largusoperla brianjonesi** sp. nov. (Figs 15–16) urn:lsid:zoobank.org:act:3FF737E9-D935-48D7-901A-A1F5FBF61CE9

**Diagnosis.** Posterior margin of subgenital plate with two broadly rounded lobes, medial longitudinal pale band on pronotum.

**Etymology.** The name refers to Brian Jones, founding member and former guitar player of the Rolling Stones until 1969.

**Material.** Holotype specimen SMNS BU-311, female.

**Description.** Body length 10.3 mm (Fig. 15A-B).
Head. Colour brown, with distinct pale areas (Fig. 16C). Median ocellus slightly subequal in size to lateral ocelli. Antennae 6.4 mm long (approximately 0.6× body length). Individual segments covered with short hair-like setae. Antennal segments in the middle third of antenna length approximately 2× longer than wide.

Maxillary palps with three visible elongated palpomeres of approximately same length. Two basal palpomeres not visible, presumably shorter than three distal palpomeres. Glossae and paraglossae not recognizable. Postmentum large. Labial palps rather elongated, three-segmented. First palpomere shortest, second slightly longer, apical palpomere longest (Fig. 16F).

Thorax. Pronotum slightly trapezoidal, wider anteriorly (Fig. 15A). Colour brown, pale longitudinal band medially.

Forewings (Fig. 16B-C): length 10.8 mm, width 3.1 mm; costal field with 14 crossveins visible (including single crossvein distal to ScP); ScP reaching RA approximately at 2/3 of wing length; RA simple; single crossvein between RA and RP; RP originating from R distal to 1/3 of wing length; RP with 3 distal branches; single crossvein between RP and M; M approximated to R basally; M with 2 branches, originating proximal to 2/3 of wing length; occurrence of arculus and 6 additional crossveins between M and CuA; CuA branched distally, with 3 branches; 3 crossveins between CuA and CuP; CuP simple and straight; AA1 simple; AA2 with 2 branches originating directly from anal cell.

Hind wings (Fig. 16D, details of venation only visible in apical portion): length 8.9 mm; costal field with 7 visible crossveins (including 2 crossveins distal to ScP); ScP reaching RA distal to 1/2 of wing length; RA simple; single crossvein between RA and RP; RP originating from common stem with M approximately at 1/4 of wing length; RP with 4 distal branches; single crossvein between RP and M; course and branching of M, CuP and AA unrecognizable.

Thoracic sterna (Fig. 16A) with apparent oblique furcal pits, converging anteriorly. Transverse meso- and metasternal ridge connecting anterior corners of respective furcal pits. Longitudinal median ridge apparent on mesofurcasternum, connecting anterior corners of furcal pits. Y-ridge connecting posterior corners of furcal pits absent. Remnants of thoracic gills recognizable on all thoracic segments.

Legs slender, covered with short hair-like setae. One thickened tibial spur and several setae apically on tibia (Fig. 16E). Tarsi with first two tarsomeres short (approximately equal in size) and apical tarsomere long, approximately 1.5× longer than first two combined. Arolium present, slightly wider than width of last tarsomere. Euplantulae present on tarsomeres 2 and 3 (Fig. 16E).

Abdomen. Individual segments not distinctly enlarged posteromedially. Cerci very short, 1.9 mm in length (approximately 0.2× body length). Subgenital plate bilobed with wide rounded notch in middle of posterior margin (Fig. 15D, 16G).

Affinities. Largusoperla brianjonesi sp. nov. is very similar to L. micktaylori sp. nov., sharing all the diagnostic characters for the family Perlidae and genus Largusoperla as discussed above. At the same time, L. brianjonesi sp. nov. clearly differs from L. micktaylori sp. nov. based on the shape of the subgenital plate (with two broad lobes on the posterior margin in L. brianjonesi sp. nov. in contrast to the presence of three narrow projections in L. micktaylori sp. nov.).

Largusoperla spp. (Figs 17–18)

Material. SMNS BU-228 (Figs 17-18)
Perlidae: Acronuriinae spp. (Fig. 19)

Material. SMNS BU-99 (Fig. 19).

Remarks to species descriptions. We refrain from associating males and females described in _Largusoperla_, since any association would be purely speculative. Clearly, multiple similar species lived in the common palaeohabitat.

The larva described above as _E. ronwoodi_ sp. nov. is attributable to the subfamily Acronuriinae, as all the adults described here in _Largusoperla_ and possibly also adults of _Pinguisoperla_, described by Chen (2018b). However, we refrain from assigning _E. ronwoodi_ sp. nov. into one of these two genera, based on the difference in the length of cerci. Usually there is a correlation between the length of cerci in larvae and adults in Systellognatha (Zwick, 1980). _E. ronwoodi_ sp. nov. exhibits much longer cerci than _Largusoperla_ and _Pinguisoperla_, therefore we prefer assigning this species to a separate genus at this time. As _E. ronwoodi_ has an age of about 100 million years, we also exclude its placement within an extant genus of Acronuriinae.

Discriminating species characters for males of Acronuriinae are the mainly detailed shape of hammer and paraprocts (Stark et al., 2009). For females, the crucial structure is the shape of subgenital plate. Therefore, we designate species only for the specimens with these structures well visible. We studied another male specimen (SMNS BU-228) attributable to _Largusoperla_, but with hammer and/or paraprocts insufficiently visible to allow detailed comparisons. Yet another investigated specimen (SMNS BU-99) is assignable to Acroneuriinae, but without visible genitalia and generally poorly preserved to allow generic attribution.

DISCUSSION

**Phylogenetic position of Petroperlidae**

The absence of crossveins in the distal half of (ScP+) RA–RP area allows the placement of Petroperlidae in the suborder Arctoperlaria (Cui et al., 2015).

Among characters of phylogenetic significance, segmentation of tarsi is well visible in the specimens. The first two tarsomeres are short, approximately equal in size and the apical tarsomere is long, approximately 3.5× longer than first tarsomere (Figs 2B, 3D). A short basal tarsomere is either considered an autapomorphy of Perloidea (Zwick, 1973), a synapomorphy of Perloidea + Peltoperlidae + Styloperlidae (Zwick, 1980), or as a character independently derived in these lineages (Zwick, 2000; Nelson, 2009). In any case, it points to the placement of Petroperlidae in the infraorder Systellognatha. Any assignment to the infraorder Euholognatha is excluded because of the presence of euplantulae on tarsomeres 1 and 2, absent in the Euholognatha (Nelson, 2009). Further diagnostic characters of Systellognatha are the apomorphic presence of setae on the arolium (see Figs 2B, 3D) (Nelson, 2009) and the plesiomorphic presence of numerous crossveins in the costal field, both of which also accounts for Petroperla gen. nov. and Lapisperla gen. nov. (Figs 2E, 4A)

Moreover, in the forewing of _L. keithrichardsi_ sp. nov., the basal crossvein in the costal field (Fig. 4B) is stronger than the remaining crossveins, short, and of opposed obliquity (in _P.
mickjaggeri sp. nov. the view onto this character is obstructed). This character has been proposed as diagnostic for Systellognatha by Cui et al. (2015).

Within Systellognatha, a labium with glossae only slightly smaller than paraglossae and with rather stout labial palps (Figs 1C, 2A) excludes a closer relationship of P. mickjaggeri sp. nov. to Perloidea, the latter characterized by apomorphic shape of labium with glossae much shorter than paraglossae (Zwick, 2000). Therefore, based on the shape of labium, a relationship to the other systellognathan superfamily, Pteronarcoyoidea, would seem more probable. However, neither Petroperla nor Lapisperla possess any of the wing venation characters known to represent traits of individual Pteronarcoyoidea lineages (Cui et al., 2016), which are numerous.

crossveins between M and CuA in distal half of wing; AA2 with more than three branches; and M with more than two branches. Moreover, Petroperlidae feature several wing venation characters not present in Systellognatha. These include a vein RA almost reaching the wing apex, and a plesiomorphic origin of vein RP in the forewing close to wing base (Figs 2E-F, 4A). Vein RA almost reaching the wing apex is absent in Carboniferous stem-stonefly Gulou carperteri and is not known for any other stonefly taxa, both extant and fossil, except of the genus Kargalopera Sinitschenkova, 1987 from the Upper Permian of Ural (Palaeoperlidae, see Sinitschenkova, 1987, fig. 10). It is unlikely that it represents a plesiomorphic character that was independently lost in several other basal stonefly lineages (including G. carpenteri). It is more parsimonious to assume that it is either an autapomorphy of Petroperlidae, or even a synapomorphy of Petroperlidae and Kargalopera.

An origin of RP close to the wing base presumably represents a plecopteran ground plan character known already from Paleozoic stoneflies. It is also present in G. carpenteri, and according to Béthoux et al. (2011) it is a diagnostic character of early stoneflies, also supporting the affinity of G. carpenteri to Plecoptera. It is also present in Permian Palaeoperla exacta Sharov, 1961 (Palaeoperlidae) and Perlopsis filicornis Martynov, 1940 (Perlopseidae) and can be observed in Euholognatha as well, e.g. Recent Leuctridae or fossil Perlariopseidae (Sinitschenkova, 1992, fig. 2). Probably the origin of RP in the forewing situated close to the wing base is also retained in Petroperlidae and lost in all other Systellognatha.

Based on available evidence, we propose the phylogenetic position of Petroperlidae as a distinct stem lineage of Systellognatha. The presence of a short first tarsomere is evaluated here as potential apomorphic character of Systellognatha and was already early present in the stemline of Systellognatha. Further support for a placement in Systellognathan stemline is the apomorphic presence of an arrolum with setae. Tarsal euplantulae and numerous crossveins in the costal field are plesiomorphies shared with remaining Systellognatha. The plesiomorphic proximal origin of RP excludes the position of Petroperlidae in the crown group Systellognatha, and RA reaching the wing apex might be an autapomorphic character of Petroperlidae. Vein RA almost reaching the wing apex is not completely preserved in L. keithrichardsi sp. nov. due to the missing wing apices. However, from the course of RA in right hind wing approximating the wing apex (Fig. 4D), we assume a similar pattern in P. mickjaggeri sp. nov. Therefore, as L. keithrichardsi sp. nov. and P. mickjaggeri sp. nov. share the same unique combination of characters, we assign them to the same family Petroperlidae.

Relationships with several fossil groups considered as stem-Systellognatha (Illies, 1965; Stark & Gaufin, 1976) cannot be reliably analysed. Permian Tshekardoperlidae Sinitschenkova, 1987 and Jurassic Platyperlidae Sinitschenkova 1982 are known in the larval stage only (Sinitschenkova, 1987; Carpenter, 1992). The family Palaeoperlidae Sharov, 1961, whose members sometimes exhibit aforementioned wing venation characters, represent a very vaguely
733 defined Permian group known only from larvae and isolated forewings and thus many other
734 characters (tarsi, mouthparts) cannot be compared. Association of larvae and adults described as
735 Palaeoperlidae is also uncertain. In Sinitshenkova (2002), Palaeoperlidae was considered as a
736 sister group of Perlina (containing Zwick’s Systellognatha + Antarctoperlaria), in other words
737 one of the most basal branches within Plecoptera. However, wing venation indicates at least
738 some members of Palaeoperlidae (genus Kargaloperla) might be related to Petroperlidae, and
739 Palaeoperlidae might not constitute a monophyletic group.
740
741 **Systematic position of Electroneuria ronwoodi gen. nov. sp. nov.**
742 Predaceous mouthparts with long and slender palps are diagnostic for larvae of the superfamily
743 Perloidea within the arctoperlariid group Systellognatha (Zwick, 1980).
744
745 Of the three families of Perloidea (Perlidae, Perlodidae, and Chloroperlidae), the wing pad
746 arrangement of *E. ronwoodi* rather resembles Perlidae and Chloroperlidae, since the “rounded
747 shape of larval wing-pads whose edges meet medially, without leaving a separate notal contour”
748 is mentioned as a possible synapomorphy of these two families within Perloidea by Zwick
749 (2000).
750
751 *E. ronwoodi* can be excluded from Chloroperlidae, as larvae of this family exhibit a slender
752 body with usually an oval pronotum and cerci distinctly shorter than the abdomen (see examples
753 in Brittain & Saltveit, 1996; Stewart & Stark, 2002), presumably apomorphic features of the
754 family (Zwick, 2000). On the contrary, the body of *E. ronwoodi* is relatively robust bearing long
755 cerci. Another apomorphic character of Chloroperlidae (except for subfamily Paraperlinae) is a
756 thin, asymmetrically inserted, terminal maxillary palpmere (Zwick, 1973; Zwick, 1980; Zwick,
757 2000; Surdick, 1985), which is not present in *E. ronwoodi*.
758
759 Thus more likely is a placement within Perlidae, also supported by the presence of thoracic
gills (Zwick, 1980). Thoracic gills are difficult to identify in *E. ronwoodi* due to its poor
760 preservation. The specimen most probably is an exuvia, as only the exoskeleton is preserved.
761 Furthermore, respective body regions corresponding with the insertion points of thoracic gills are
762 obscured by mineral particles, but the remains of thoracic gills might be visible at least on the
763 left side of the body, between meso- and metathorax. Its affinity to Perlidae is further confirmed
764 by the presence of an occipital row of short spinules (Stark & Gauvin, 1976; Sivec et al., 1988;
765 Zwick, 2000). The arrangement of this row represents the larval key character distinguishing
766 Perlidae subfamilies Perlinae and Acroneuriinae (Stark & Gauvin, 1976). In *E. ronwoodi*, the row
767 is slightly sinuate, regular medially, in lateral parts disintegrate into scattered goups of longer
768 spinules (Figs 5D, 6E), an arrangement present in Acroneuriinae, in contrast to the straight and
769 complete occipital row of Perlinae (Stark & Gauvin, 1976; Sivec et al., 1988).
770
771 There are also two Permian families, Palaeoperlidae and Tshekardoperlidae, which might
772 be candidates for a closer relationship to *Electroneuria* gen. nov., but both of them are rather
773 poorly defined. Diagnoses are mostly based on the length ratios of body parts (Sinitshenkova,
774 1987). Both Palaeoperlidae and Tshekardoperlidae differ from *E. ronwoodi* (apart from the
775 marked difference in geological layer) in the shape of thoracic segments with clearly visible
776 notal contour between wingpads (figs 8, 25–27 in Sinitshenkova, 1987). Furthermore,
777 Tshekardoperlidae are characterized by prolonged antennal segments, 2–3 times longer than
778 wide in the middle third of the antenna (Sinitshenkova, 1987). *E. ronwoodi* exhibits much shorter
779 antennal segments (Fig. 5C). Jurassic Platyperlidae most notably differ by the presence of a
780 median projection on the posterior margin of terminal abdominal segment (Carpenter, 1992;
781 Sinitshenkova, 1987) which is missing in *E. ronwoodi*. 
Based on the combination of characters as presented above, we attribute *E. ronwoodi* to the Perlidae subfamily Acroneuriinae. There are no larval diagnostic characters for the three Acroneuriinae tribes (Stark & Gaufin, 1976; Murányi & Li, 2016), but from all described genera of Acroneuriini, Anacroneuriini, and Kiotinini, the larval specimen *E. ronwoodi* can be diagnosed by the combination of characters as follows: (1) occipital spine row complete medially, (2) fringe of long thin setae laterally on pronotum (most of them broken, but bases clearly visible), (3) long hair-like setae on surface of wing pads and abdominal terga, (4) posterior margin of abdominal terga with numerous very long thin setae, and (5) long setae on cerci absent.

**Palaeodiversity, Paleoecology, and Paeeobiogeography of Perlidae**

The family Perlidae, despite being very abundant and diversified today, was so far only scarcely found in the fossil record. Several specimens of the extant genus *Perla* are known from Eocene Baltic amber (Pictet & Hagen, 1856; Carpenter, 1992). A single immature larva of *Perla cf. burmeisteriana* Claassen, 1936 was described by Prokop (2002) from Lower Miocene deposits of the Czech Republic. An adult specimen of *Dominiperla antigua* Stark & Lenz, 1992 was described from Dominican amber (dated between upper Eocene to lower Miocene) and attributed to Acroneuriinae (subfamily "Anacroneuriinae", as stated in Stark & Lenz, 1992 probably represents a spelling error). Affinities were evaluated based on the course of M1 vein, only slightly divergent from R until the origin of Rs (present in some Perlidae), and small, spindle-shaped eggs similar to the Neotropical genus *Anacroneuria*. A young larva is also known from Oligocene of SW Montana, attributed to *?Acroneuria* (Lewis & Gundersen, 1987). Another larva was described as *Euperlida parvicercifera* Cifuentes-Ruiz, 2007 from Oligocene of Mexico (Cifuentes-Ruiz et al., 2007) and tentatively attributed to Perlidae subfamily Acroneuriinae based on general body resemblance (the shape and size of the head, wing pads, body pattern, foreleg and pronotum shape).

The oldest Perlidae species *Archaeoperla rarissimus* Liu, Ren & Sinitshenkova, 2008 described by Liu et al. (2008) from Jurassic/Cetaceous of China, was later synonymized by Cui et al. (2015) with *Sinosharaperla zhaoi* Liu et al., 2007, which probably represents stem-Systellognatha, although attribution to Perlidae was not excluded by Cui et al. (2015). If we do not consider *S. zhaoi* as a genuine Perlidae, the genera *Largusoperla*, *Pinguisoperla*, and *Electroneuria* from the mid-Cretaceous represent the oldest record of the family Perlidae. At the same time, they represent fossils attributed to Perlidae without doubt and based on multiple characters. Previously published Perlidae records were assigned to this family mostly based on a limited number of characters, often only on a superficial resemblance.

Three tribes were proposed within Perlidae subfamily Acroneuriinae based on adult male characters (Acroneuriini, Anacroneuriini and Kiotinini, see Stark & Gaufin, 1976; Stark et al., 2009; Murányi & Li, 2016). Regarding the position of *Largusoperla*, we concur with Chen et al. (2018a) that the form of the hammer, an elevated knob rather than a low callus, suggests affinity to Anacroneuriini, whereas the well-developed anterior ocellus and short cerci represent plesiomorphies within Perlidae and suggest a possible position of *Largusoperla* in the stemline of Acroneuriini + Anacroneuriini.

Out of 10 stonefly specimens described in the present study, 8 are attributed to the subfamily Acroneuriinae and, apart from one larval specimen, belong to the single genus *Largusoperla*, as the four species described recently by Chen et al. (2018a) and Chen (2018c). A single specimen described by Chen (2018b) in the genus *Pinguisoperla* probably also belongs to
the same subfamily. From such a pattern (even taking into consideration a fragmentary nature of the fossil record), we might assume that the stonefly community in the Burmese amber forest streams was dominated by representatives of a limited number of higher taxa. This might be caused by the nature of the original habitat, which has been assumed to be a tropical Araucaria forest (Grimaldi et al., 2002). Present stonefly diversity is concentrated in the temperate regions, a pattern probably consistently followed throughout their history (Sinitshenkova, 1997).

However, as demonstrated by our data, some groups like Acroneuriinae had been adapted to the warmer streams of the Cretaceous Burmese amber palaeohabitat. Although the adults might be speculated to represent allochthonous material in the inclusions, our finding of a larva of the same taxonomic placement rather corroborates the occurrence of Acroneuriinae in the Burmese amber forest streams.

With more than 1,000 described species, Perlidae is the most diverse extant family. The most diverse perlid areas are Asia, and Central and South America. At present, the Chinese perlid species represent about 25% of the world Perlidae, making the Oriental region one of the most important areas of the world for perlid diversity (Fochetti & De Figueeroa, 2008). We assume placement of all Acroneuriinae adult material dealt with in the present study into the tribe Anacroneuriini sensu Stark & Gaufin (1976). At present, all extant Anacroneuriini are restricted to the Neotropics and southern portion of the Nearctic (Muráni & Li, 2016). Stark & Gaufin (1976) hypothesized recent Anacroneuriini arose from a now extinct Oriental group which dispersed across Northern Africa in Early Cretaceous and became established in South America. Largusoperla and Electroneuria might actually represent such a stem-Anacroneuriini group, still to be found in the Oriental region during the late Cretaceous and subsequently becoming extinct.

Close relations between Neotropic and Oriental fauna dating back to the Cretaceous were already known in other groups of aquatic and terrestrial insects, e.g. the Burmese amber damselfly family Mesomegaloprepidae, related to extant Neotropical taxa (Huang et al., 2017) or the psocid family Compsocidae, known from Burmese amber and the extant fauna of Central America (Azar et al., 2016; Sroka & Nel, 2017). Our study thus provides support for the hypothesis of Stark & Gaufin (1976) claiming oriental origin of Anacroneuriini.

CONCLUSIONS

Our findings report with the fossil family Petroperlidae the presence of a new taxon in the stem lineage of Systellognatha in the Cretaceous. It reveals new insights into the character evolution within this group: Petroperlidae have shortened tarsomeres 1 and 2, which consequently must now be assumed as ground plan character of Systellognatha. Otherwise, the Burmese Cretaceous stonefly fauna was dominated by species of the Anacroneuriini (Perlidae: Acroneuriinae), a taxon, which today is restricted to the Nearctic realm. This points to an oriental origin of Anacroneuriini, thus confirming the respective hypothesis of Stark & Gaufin (1976).

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**Figure legends**

**Fig. 1:** *Petroperla mickjaggeri* gen. nov. sp. nov., holotype SMNS BU-79, photographs. (A) Dorsal view. (B) Ventral view. (C) Head in frontoventral view. Abbreviations: gl, glossa; pgl, paraglossa; pmx, maxillary palp; plb, labial palp. (D) Ventral tip of abdomen with subgenital plate: sgl.

**Fig. 2:** *Petroperla mickjaggeri* gen. nov. sp. nov., holotype SMNS BU-79, line drawings. (A) Head in frontoventral view. Abbreviations: ant, antenna; gl, glossa; lbr, labrum; pgl, paraglossa; pmx, maxillary palp; plb, labial palp. (B) Tarsus in ventral view. (C) Head and thorax in ventral view. (D) Subgenital plate; sgp. (E) Right forewing. (F) Left forewing. (G) Left hind wing.

**Fig. 3:** *Lapisperla keithrichardsi* gen. nov. sp. nov., holotype SMNS BU-313, photographs. (A) Dorsal view. (B) Ventral view. (C) Abdomen in ventral view. (D) Tarsus of right middle leg in lateral view. Abbreviations: ar, arolium; eu, euplantula.
Fig. 4. *Lapisperla keithrichardsi* gen. nov. sp. nov., holotype SMNS BU-313, line drawings. (A) Left forewing. (B) Right forewing base. (C) Left hind wing. (D) Right hind wing. (E) Right hind wing from ventral side. (F) Tip of ventral abdomen with subgenital plate, sgp.

Fig. 5. *Electroneuria ronwoodi* gen. nov. sp. nov., holotype SMNS BU-306, photographs. (A) Dorsal view. (B) Ventral view. (C) Head with exposed maxilla, mx. (D) Head, occipital row of spines, marked by arrows. (E) Tarsus of left foreleg. (F) Setae on abdominal terga.

Fig. 6. *Electroneuria ronwoodi* gen. nov. sp. nov., holotype SMNS BU-306, line drawings. (A) Abdominal sterna. (B) Detail of right cercus (C) Anterior margin of pronotum (D) Setation of abdominal terga. (E) Head, occipital row of spines. (F) Maxilla. (G) Right middle leg. (H) Tarsus of right middle leg.

Fig. 7. *Largusoperla charliewattsi* sp. nov., holotype SMNS BU-10, photographs. (A) Dorsal view, arrows marks rounded pronotum. (B) Head in ventral view. (C) Meso-and metathorax in ventral view with furcal pits, fp. (D) Ventraltip of abdomen with hammer, paraprocts, pp, and cercus, ce. (E) tarsus of right hind leg. (F) Tarsus of left hind leg with euplantulae, eu.

Fig. 8. *Largusoperla charliewattsi* sp. nov., holotype SMNS BU-10, line drawings. (A) Head and thorax in ventral view with furcal pits and gill remnants. (B) Ventraltip of abdomen with hammer and paraprocts, pp. (C) Left forewing. (D) Left hind wing.

Fig. 9. *Largusoperla billwymani* sp. nov., holotype SMNS BU-229, photographs. (A) Dorsal view, arrow marks trapezoid pronotum. (B) Head in ventral view. (C) Ventraltip of abdomen with hammer, paraprocts, pp, and cercus, ce. (D) Tarsus of left hind leg. (E) Tarsus of right hind leg.

Fig. 10. *Largusoperla billwymani* sp. nov., holotype SMNS BU-229, line drawings. (A) Left Forewing. (B) Right forewing. (C) Head-and thorax in ventral view. (D) Right hind wing. (E) Head in ventral view. (F) Ventraltip of abdomen with hammer and paraprocts, pp.

Fig. 11. *Largusoperla micktaylori* sp. nov., holotype SMNS BU-227, photographs. (A) Dorsal view. (B) Ventraltip of abdomen with mess and gill remnants. (C) Tarsus of right hind leg. (D) Ventraltip of abdomen with subgenital plate, paraprocts, and cerci. (F) Three-lobed (arrows) subgenital plate.

Fig. 12. *Largusoperla micktaylori* sp. nov., holotype SMNS BU-227, line drawings. (A) Head-and thorax in ventral view. (B) Left forewing. (C) Right forewing. (D) Right hind wing.

Fig. 13. *Largusoperla micktaylori* sp. nov., paratype SMNS BU-312, photographs. (A) Dorsal view. (B) Ventraltip of abdomen with subgenital plate, paraprocts, and cerci. (E) Ventraltip of abdomen with subgenital plate, paraprocts, and cerci. (F) Three-lobed (arrows) subgenital plate.

Fig. 14. *Largusoperla micktaylori* sp. nov., paratype SMNS BU-312, line drawings. (A) Ventral tip of abdomen with subgenital plate, paraprocts, and cerci. (B) Left forewing. (C) Right forewing. (D) Left hind wing (ventral view). (E) Right hind wing.
Fig. 15. *Largusoperla brianjonesi* sp. nov., holotype SMNS BU-311, photographs. (A) Dorsal view. (B) Ventral view. (C) Head in dorsal view. (D) Bi-lobed (arrows) subgenital plate.

Fig. 16. *Largusoperla brianjonesi* sp. nov., holotype SMNS BU-311, line drawings. (A) Head-and thorax in ventral view. (B) Left forewing. (C) Right forewing. (D) Right hind wing (ventral view). (E) Tarsus in ventral view. (F) Head in ventral view. (G) Bi-lobed subgenital plate.

Fig. 17. *Largusoperla* sp., SMNS BU-228, photographs. (A) Dorsal view. (B) Head in ventral view. (C) Ventral tip of abdomen with hammer, paraprocts, pp, and cercus, ce. (D) Tarsus of left hind leg.

Fig. 18. *Largusoperla* sp., SMNS BU-228, line drawings. (A) Head-and thorax in ventral view. (B) Left forewing. (C) Right forewing. (D) Left hind wing. (E) Right hind wing.

Fig. 19. *Acroneuriinae* spp., SMNS BU-99, photograph. Dorsal view.
Figure 1

*Petroperla mickjaggeri* gen. nov. sp. nov., holotype SMNS BU-79, photographs.

(A) Dorsal view. (B) Ventral view. (C) Head in frontoventral view. Abbreviations: gl, glossa; pgl, paraglossa; pmx, maxillary palp; plb, labial palp. (D) Ventral tip of abdomen with subgenital plate: sgl.
Figure 2

*Petroperla mickjaggeri* gen. nov. sp. nov., holotype SMNS BU-79, line drawings.

(A) Head in frontoventral view. Abbreviations: ant, antenna; gl, glossa; lbr, labrum; pgl, paraglossa; pmx, maxillary palp; plb, labial palp. (B) Tarsus in ventral view. (C) Head and thorax in ventral view. (D) Subgenital plate; sgp. (E) Right forewing. (F) Left forewing. (G) Left hind wing.
Figure 3

*Lapisperla keithrichardsi* gen. nov. sp. nov., holotype SMNS BU-313, photographs.

(A) Dorsal view. (B) Ventral view. (C) Abdomen in ventral view. (D) Tarsus of right middle leg in lateral view. Abbreviations: ar, arolium; eu, euplantula.
Figure 4

*Lapisperla keithrichardsi* gen. nov. sp. nov., holotype SMNS BU-313, line drawings.

(A) Left forewing. (B) Right forewing base. (C) Left hind wing. (D) Right hind wing. (E) Right hind wing from ventral side. (F) Tip of ventral abdomen with subgenital plate, sgp.
Figure 5

*Electroneuria ronwoodi* gen. nov. sp. nov., holotype SMNS BU-306, photographs.

(A) Dorsal view. (B) Ventral view. (C) Head with exposed maxilla, mx. (D) Head, occipital row of spines, marked by arrows. (E) Tarsus of left foreleg. (F) Setae on abdominal terga.
Figure 6

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(A) Abdominal sterna. (B) Detail of right cercus (C) Anterior margin of pronotum (D) Setation of abdominal terga. (E) Head, occipital row of spines. (F) Maxilla. (G) Right middle leg. (H) Tarsus of right middle leg.
Figure 7

*Largusoperla charliewattsi* sp. nov., holotype SMNS BU-10, photographs.

(A) Dorsal view, arrows marks rounded pronotum. (B) Head in ventral view. (C) Meso-and metathorax in ventral view with furcal pits, fp. (D) Ventral tip of abdomen with hammer, paraprocts, pp, and cercus, ce. (E) tarsus of right hind leg. (F) Tarsus of left hind leg with euplantulæ, eu.
Figure 8

*Largusoperla charliewattsi* sp. nov., holotype SMNS BU-10, line drawings.

(A) Head and thorax in ventral view with furcal pits and gill remnants. (B) Ventral tip of abdomen with hammer and paraprocts, pp. (C) Left forewing. (D) Left hind wing.
Figure 9

*Largusoperla billwymani* sp. nov., holotype SMNS BU-229, photographs.

(A) Dorsal view, arrow marks trapezoid pronotum. (B) Head in ventral view. (C) Ventral tip of abdomen with hammer, paraprocts, pp, and cercus, ce. (D) Tarsus of left hind leg. (E) Tarsus of right hind leg.
Figure 10

*Largusoperla billwymani* sp. nov., holotype SMNS BU-229, line drawings.

(A) Left Forewing. (B) Right forewing. (C) Head-and thorax in ventral view. (D) Right hind wing. (E) Head in ventral view. (F) Ventral tip of abdomen with hammer and paraprocts, pp.
Figure 11

*Largusoperla micktaylori* sp. nov., holotype SMNS BU-227, photographs.

(A) Dorsal view. (B) Ventral view. (C) Head in ventral view. (D) Three-lobed (arrows) subgenital plate.
Figure 12

*Largusoperla micktaylori* sp. nov., holotype SMNS BU-227, line drawings.

(A) Head and thorax in ventral view. (B) Left forewing. (C) Right forewing. (D) Right hind wing.
Figure 13

*Largusoperla micktaylori* sp. nov., paratype SMNS BU-312, photographs.

(A) Dorsal view. (B) Ventral view. (C) Head in ventral view. (D) Tarsus of right hind leg. (E) Ventral tip of abdomen with subgenital plate, paraprocts, and cerci. (F) Three-lobed (arrows) subgenital plate.
**Figure 14**

*Largusoperla micktaylori* sp. nov., paratype SMNS BU-312, line drawings.

(A) Ventral tip of abdomen with subgenital plate, paraprocts, and cerci. (B) Left forewing. (C) Right forewing. (D) Left hind wing (ventral view). (E) Right hind wing.
Fig. 15. *Largusoperla brianjonesi* sp. nov., holotype SMNS BU-311, photographs.

(A) Dorsal view. (B) Ventral view. (C) Head in dorsal view. (D) Bi-lobed (arrows) subgenital plate.
Figure 16

Fig. 16. *Largusoperla brianjonesi* sp. nov., holotype SMNS BU-311, line drawings.

(A) Head-and thorax in ventral view. (B) Left forewing. (C) Right forewing. (D) Right hind wing (ventral view). (E) Tarsus in ventral view. (F) Head in ventral view. (G) Bi-lobed subgenital plate.
Manuscript to be reviewed

A

B

C

D

E

F

G
Figure 17

Fig. 17. *Largusoperla* sp., SMNS BU-228, photographs.

(A) Dorsal view. (B) Head in ventral view. (C) Ventral tip of abdomen with hammer, paraprocts, pp, and cercus, ce. (D) Tarsus of left hind leg.
Figure 18

Fig. 18. *Largusoperla* sp., SMNS BU-228, line drawings.

(A) Head-and thorax in ventral view. (B) Left forewing. (C) Right forewing. (D) Left hind wing. (E) Right hind wing.
Figure 19

Fig. 19. Acroneuriinae spp., SMNS BU-99, photograph.

Dorsal view.