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The Pangean journey of ‘south forestflies’ (Insecta: Plecoptera) revealed by their first fossils

Yingying Cui^a, Dong Ren^{b*} and Olivier Béthoux^a

^aSorbonne Universités, UPMC Univ Paris 06, MNHN, CNRS, Centre de Recherche sur la Paléobiodiversité et les Paléoenvironnements (CR2P), Paris, France; ^bCollege of Life Science, Capital Normal University, Beijing 100048, China

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The ‘south forestflies’ (Notonemouridae) are known from the southern hemisphere. However, their successive closest sister-groups all occur in the northern hemisphere, suggesting a north-to-south migration at some stage of their evolution. No reliable fossil remains that would provide age constraints for this event have been identified. According to previously published divergence date estimates, the group arose recently (65–98 Ma), implying a late transcontinental dispersal. Here, we describe a new fossil insect, *Paranotonemoura zwicki* Cui & Béthoux sp. nov. (Daohugou, China), and revise *Paranotonemoura fidelis* Sinitshenkova, 1987 comb. nov. (Bakhar, Mongolia), both of Jurassic age (c. 165 Ma). Based on the study of their wing venation pattern and of that of extant ‘south forestflies’, we demonstrate that the fossils belong to this group, and therefore are its first fossils. Our discovery demonstrates that the lineage is much more ancient than previously estimated. Plausible scenarios on the origin, migration and partial extinction are proposed based on the dispersal abilities of these insects and palaeogeographical reconstructions during the Mesozoic. We assume that the north-to-south migration took place between 220 and 160 Ma.

<http://zoobank.org/urn:lsid:zoobank.org:pub:66E22602-FE0D-4641-AB14-D8CB129D8F67>

Keywords: new taxon; Insecta; divergence date estimate; Jurassic; biogeography

Introduction

The two suborders of Plecoptera, Arctoperlaria and Antarctoperlaria, have been named after their current geographical distribution, in northern and southern hemispheres, respectively, with few exceptions. While the antarctoperlarian families are strictly distributed in the southern hemisphere, some arctoperlarian lineages occur also in the southern hemisphere. The Notonemouridae (‘south forestflies’) occur in South America, South Africa, Australia and New Zealand; and some lineages within Perlidae occur also in South America, and Southeast Asia (Fochetti & Tierno de Figueroa 2008).

The Notonemouridae are closely related to Nemouridae (Zwick 2000), and therefore derive from a northern hemisphere lineage. Since the complete lack of definite fossil record of the Notonemouridae, the timing and biogeographical context of their dispersal (if so) is poorly understood. McCulloch *et al.* (2016), relying on a set of comparatively recent fossil calibration points, have proposed a very recent origin of the group, c. 76 million years ago (Ma), with a large confidence interval (65 to 98 Ma). Thus the scenario best explaining the current distribution

of Notonemouridae is long-distance dispersal, which appears dubious, given the biology of stoneflies in general.

Herein, we describe a new fossil species from the famous Daohugou locality (Inner Mongolia, China; Middle Jurassic), that can be confidently identified as a Notonemouridae. We also discuss affinities of previously described fossil species in the light of our discovery, and reconsider the systematics of the corresponding lineage under the cladotypic nomenclatural procedure. The age of the fossils indicates an origin of the group much earlier than previously, this having important implications on the ancient biogeography of this lineage, and of stoneflies in general.

Material and methods

Material and data production

The fossil specimen PIN 3791/1220 (Figs 1A, 2A, F) was unearthed at the Bakhar locality (Central Mongolia; Middle (Late?) Jurassic; Rasnitsyn & Zherikhin 2002). It is housed at the Palaeontological Institute of the Russian

*Corresponding author. Email: rendong@mail.cnu.edu.cn

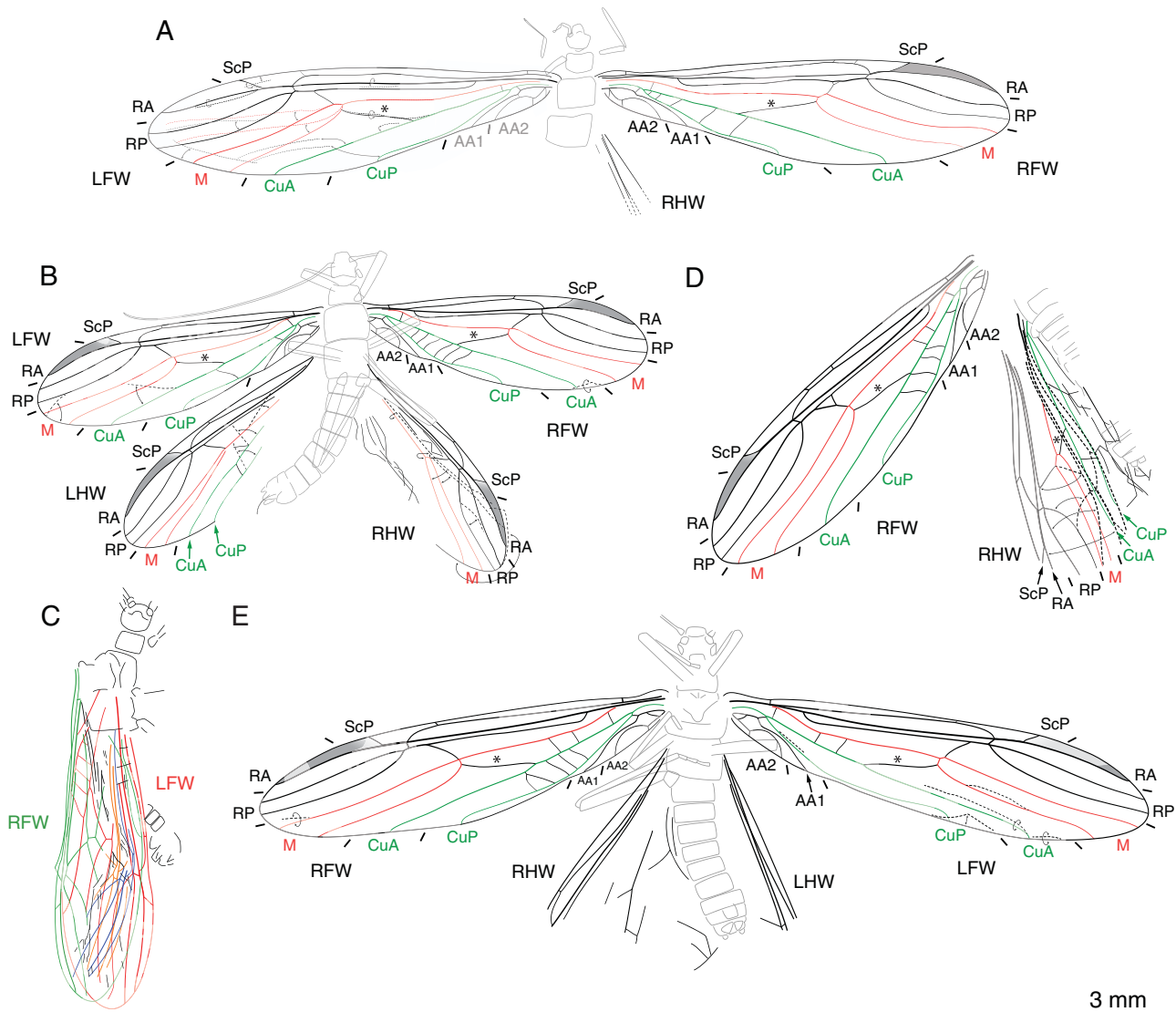


Figure 1. Drawings of *Paranotonemoura fidelis* Sinitshenkova, 1987 (A) and *Paranotonemoura zwicki* Cui & Béthoux sp. nov. (B–E). A, PIN No. 3791/1220; B, CNU-PLE-NN-2016103; C, CNU-PLE-NN-2016106; D, CNU-PLE-NN-2016101; E, CNU-PLE-NN-2016102. The * indicates the mp-cua cross-vein.

Academy of Science (PIN; Moscow, Russia). The fossil specimens CNU-PLE-NN-2016101, -02, -03, -06 (Figs 1B–E, 2B–E, G, 3) were unearthed at the Daohugou locality (Inner Mongolia, China; Middle Jurassic; Jiulongshan Formation; Gao & Ren 2006; Liu *et al.* 2006a). These are housed at the Capital Normal University (CNU; Beijing, China).

Except for the specimen PIN 3791/1220, the fossil material was examined using a Leica MZ12.5 microscope and illustrated with the aid of a drawing tube, under dry and ethanol conditions. Final drawings were prepared with Adobe Illustrator CC using both draft drawings and photographs. The final drawing of the specimen PIN 3791/1220 was based on photographs only.

Extant material was investigated for a comparative analysis (see Fig. 4). Collecting data are provided in the Supplemental material. Wings were cut off and mounted in white Euparal medium (Asco Laboratories, Manchester, UK). Extant specimens mentioned herein were given a number under the acronym ‘MNHN-EP’, with the exception of the specimens illustrated in Figure 4D, belonging to the private collection of OB (acronym ‘IWC OB’).

Photographs of specimens CNU-PLE-NN-2016101, -2016102, -2016103, -2016106 were taken using a digital camera Canon EOS 5D Mark III coupled to a Canon MP-E 65 mm macro lens equipped with a polarizing filter. The light-mirror technique was employed (see Béthoux &

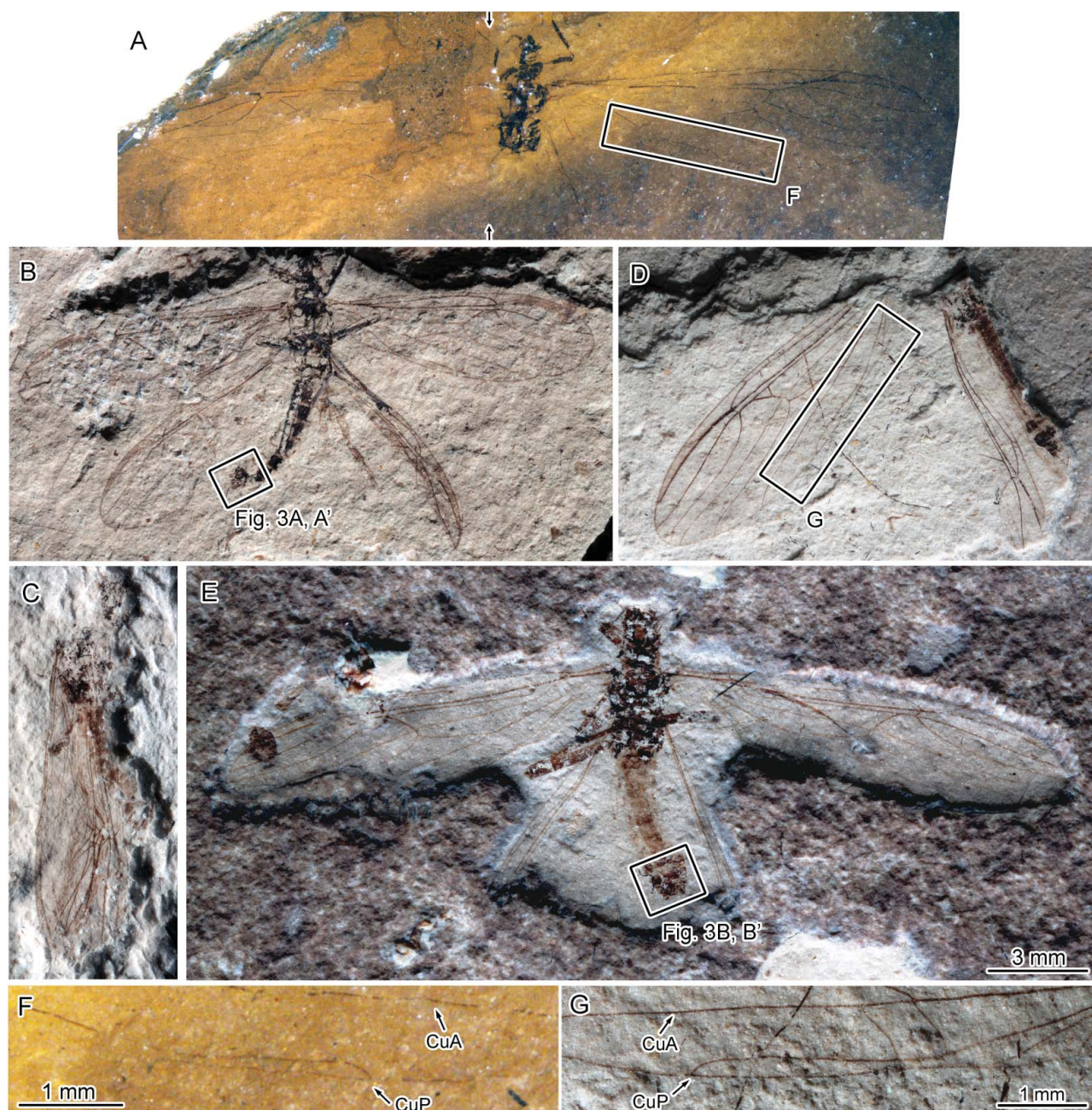


Figure 2. Photographs of *Paranotonemoura fidelis* Sinitshenkova, 1987 (A, F) and *Paranotonemoura zwicki* Cui & Béthoux sp. nov. (B–E, G); A, PIN 3791/1220 (ethanol; two photographs stitched – arrows indicate their delimitation); B, CNU-PLE-NN-2016103 (positive imprint, dry-ethanol composite); C, CNU-PLE-NN-2016106 (negative imprint, dry-ethanol composite); D, CNU-PLE-NN-2016101 (negative imprint, light-mirrored, dry-ethanol composite); E, CNU-PLE-NN-2016102 (negative imprint, light-mirrored, dry-ethanol composite); F, detail of PIN 3791/1220 as located on A; G, detail of CNU-PLE-NN-2016101 as located on D.

Briggs 2008), and the rock matrix was used as white balance (see Cui *et al.* 2015). Resulting photographs were optimized using Adobe Photoshop CS6. We used various combinations of composites (sides-composite; dry-ethanol composite, etc.; see Béthoux 2015), as indicated in the figure captions.

Specifics of the camera used to produce photographs composing Figure 2A are unknown to us. We produced a panorama from the two photographs kindly provided by N. Sinitshenkova to obtain a single, complete overview of the specimen. The original photographs were taken with the specimen under ethanol.

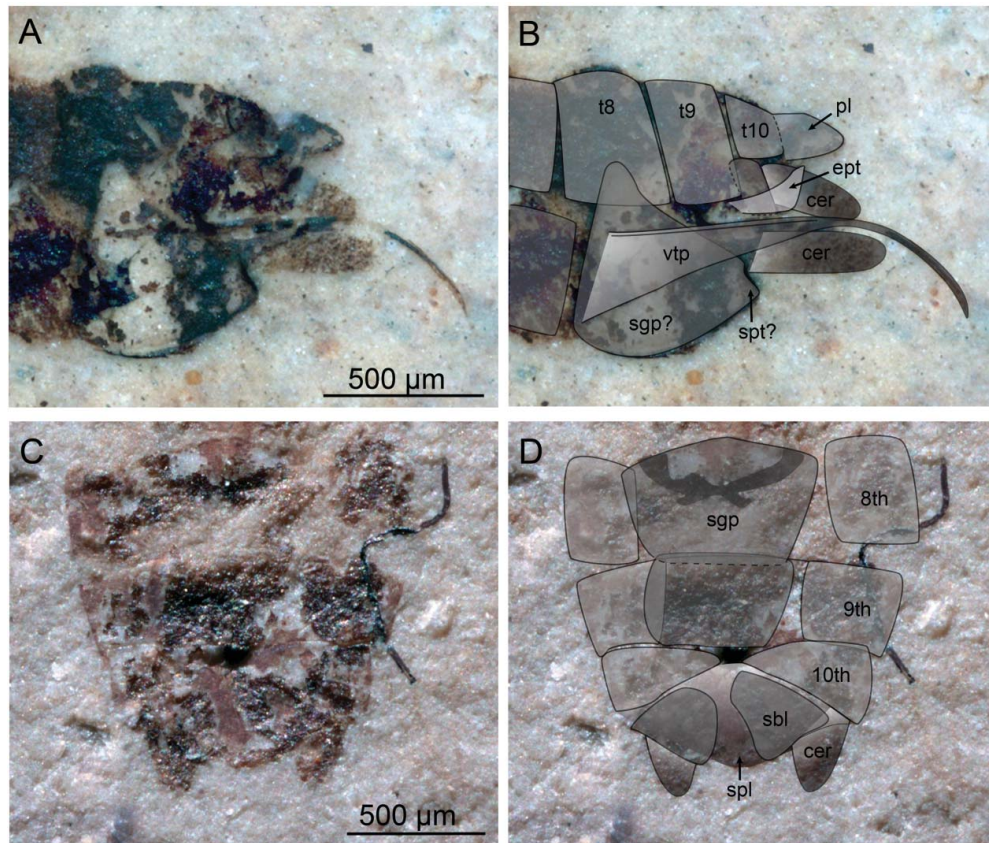


Figure 3. Genitalia of *Paranotonemoura zwicki* sp. nov. **A, B**, genitalia of CNU-PLE-NN-2016103 (male), lateral view, photograph (sides composite, ethanol) (**A**) and interpretation (**B**), as located on [Figure 2B](#); **C, D**, genitalia of CNU-PLE-NN-2016102 (female), ventral view, photograph (composite of positive imprint under ethanol and negative imprint under dry conditions, flipped) (**C**) and interpretation (**D**), as located on [Figure 2E](#).

Nomenclature

We provide a formal description of the new species under the traditional nomenclatural procedure as well as a treatment under the cladotypic procedure (Béthoux 2007a, b, 2010; Béthoux *et al.* 2015) in the Appendix. In order to facilitate comparison between the outcomes of the two procedures, we provide a dual representation in [Figure 5](#).

Elsewhere in the manuscript, we mainly use the cladotypic nomenclatural procedure. Under this procedure, all the taxon names are written in italics, with a capital letter, just as names of genera under the traditional, ICZN-governed procedure. In the body of the paper we also use traditional names, for example for suborders and families. They can easily be differentiated from cladotypic names as they are written in regular style (as opposed to italics) and, for familial names, have a typical ending. Generic names are also mentioned, but their nature is always specified to prevent confusion with cladotypic names. We also provide an Appendix with an ICZN-compliant nomenclatural treatment.

Wing venation terminology and homologies

We follow the serial insect wing venation ground plan (Lameere 1922, 1923). Wing venation nomenclature is repeated here for convenience: **ScP**: posterior subcosta; **RA**: anterior radius; **RP**: posterior radius; **M**: media; **MA**: anterior media; **MP**: posterior media; **Cu**: cubitus; **CuA**: anterior cubitus; **CuP**: posterior cubitus; **AA**: anterior analis; **AA1**: first anterior analis; **AA2**: second anterior analis; **ra-rp**: cross-vein between RA and RP; **rp-ma**: cross-vein between RP and MA; **mp-cua**: the last cross-vein between MP and CuA. Right and left forewings are indicated as **RFW** and **LFW** respectively, and right and left hind wings as **RHW** and **LHW**, respectively.

Other abbreviations are as follows: **s9**: sternite 9; **t8,9,10**: tergite 8,9,10; **sgp**: subgenital plate; **sbl**: subanal lobe; **spl**: supra-anal lobe; **cer**: cercus; **ept**: epiproct; **pl**: posterior lobe of tergite 10; **vtp**: ventral process; **spt**: tongue of subgenital plate.

We follow wing venation homologies proposed for Plecoptera and *Nemouromorpha* by Béthoux (2005) and Béthoux *et al.* (2015), respectively. Some previous

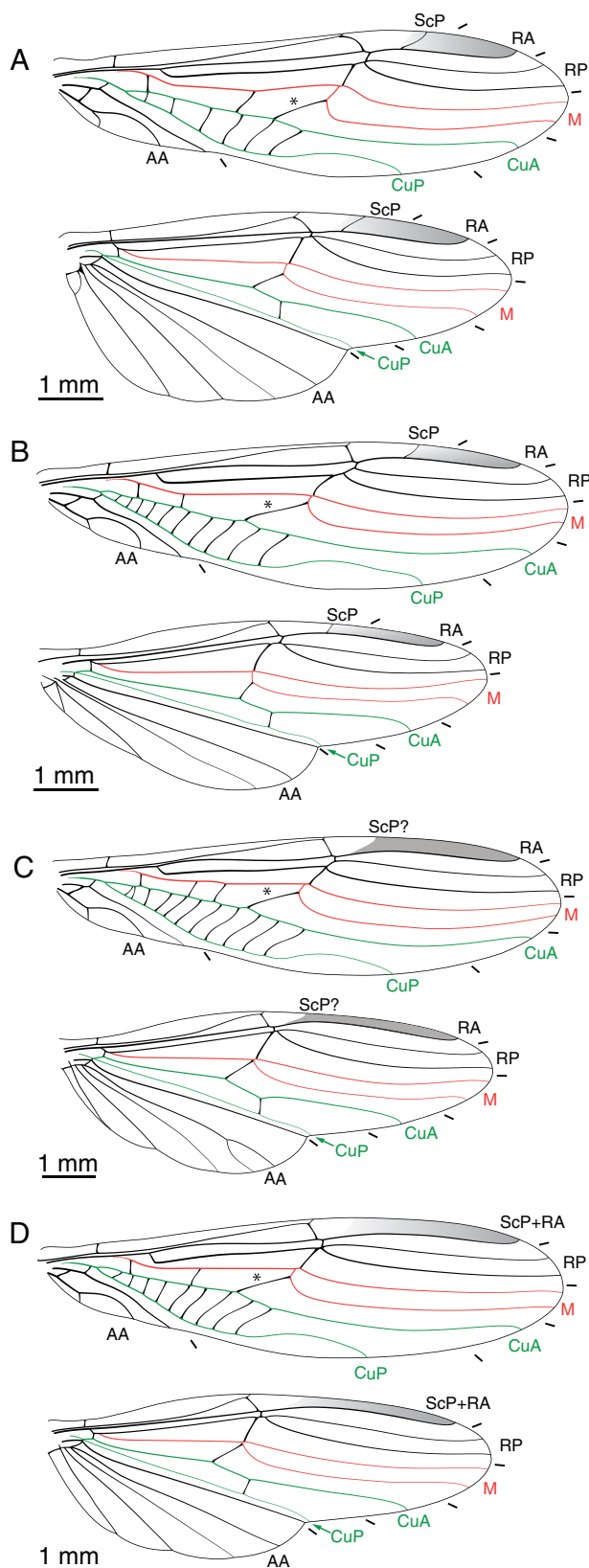


Figure 4. Forewing and hind wing venation patterns in extant species of Notonemouridae; **A**, *Spaniocerca zelandica* Tillyard, 1923, PlecoEvol-113 (right pair); **B**, *Neonemura illiesi* Zwick,

authors have recognized a ‘costal cross-vein’ which, if occurring, is located in the distal third of wing length, between the anterior wing margin and RA. It actually is the ultimate portion of ScP, diverging from ScP+RA (Béthoux *et al.* 2015). If the structure is absent, it implies that ScP remains fused with RA until both reach the wing margin. It must be mentioned here that the distal part of ScP can be a very weak structure, best observed under ideal light settings (for the record, this reduction of ScP was acquired multiple times among *Nemouromorpha*; Béthoux *et al.* 2015).

Plecoptera fossil record

We carried out a critical review of the fossil record of Plecoptera to prepare Figure 6. We relied on Jell & Duncan (1986), Sinitshenkova (2002), Grimaldi & Engel (2005), Béthoux *et al.* (2011, 2015) and Cui *et al.* (2016). The taxonomic assignment of many fossils proved insufficiently established and/or would have to be re-evaluated in the light of recent discoveries (and see herein). We only considered fossil species for which affinities are well ascertained (narrow selection). Among important fossils, the Jurassic species *capniomimus* Ansoerge, 1993 (genus *Dobbertiniopteryx* Ansoerge, 1993), represents the earliest Capniidae (see original description and Liu *et al.* 2009) and, incidentally, the earliest crown-Euholognatha.

Systematic palaeontology

Family Notonemouridae Ricker, 1950

Amendment to diagnosis. In forewing, CuP closely approaching posterior wing margin (just distal of the end of AA1), then diverging from it, until it reaches it more distally (as opposed to ‘in forewing, distal the end of AA1, area between CuP and posterior wing margin tapering uninterruptedly’).

Remarks. The character state listed above as diagnostic of the family defines the taxon *Arcuonemourida* (see Appendix).

Subfamily Notonemourinae Ricker, 1950

Amendment to diagnosis. In forewing, end of CuA opposite or distal to the end of RA (as opposed to ‘in forewing, end of CuA basal to the end of RA’).

1972, PlecoEvol-111 (right pair); **C**, *Austronemoura chilena* Aubert, 1960, PlecoEvol-27 (left pair); **D**, *Austronemoura quadrangularis* Aubert, 1960, IWC OB 1173 (right pair). The * indicates the mp-cua cross-vein.

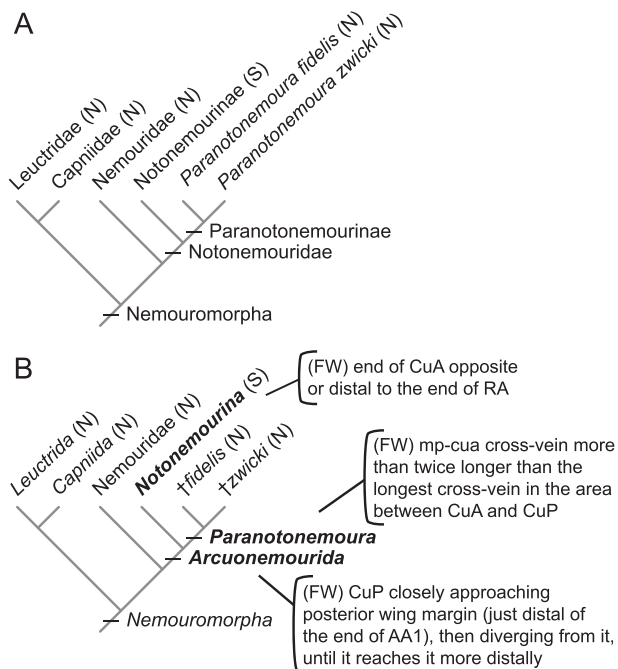


Figure 5. Summary of the assumed phylogenetic relationships of the taxa and species considered in this contribution. (N), (S), occurring in northern or southern hemisphere, respectively. **A**, systematic treatment under the traditional, Linnaean nomenclatural procedure. **B**, systematic treatment under the cladotypic procedure (newly erected supra-specific taxa indicated in bold and associated with defining character state).

Remarks. The character state listed above as diagnostic of the subfamily defines the (cladotypic) taxon *Notonemourina* (see Appendix).

Subfamily **Paranotonomourinae** Cui & Béthoux
subfam. nov.

Diagnosis. That of the type genus.

Type genus. †*Paranotonomoura* Cui & Béthoux gen. nov.

Genus ***Paranotonomoura*** Cui & Béthoux gen. nov.

Diagnosis. In forewing, the mp-cua cross-vein more than twice longer than the longest cross-vein in the area between CuA and CuP.

Type species. *Paranotonomoura zwicki* sp. nov.

Other species. *Paranotonomoura fidelis* (Sinitshenkova, 1987) comb. nov.

Etymology. A combination of ‘para’ (‘beside’ in ancient Greek) and ‘*Notonemoura*’, type genus of the Notonemouridae, to which the new genus belongs. The gender is feminine.

Remarks. The character state listed above as diagnostic of the genus defines the (cladotypic) taxon *Paranotonomoura* (see Appendix).

Paranotonomoura fidelis (Sinitshenkova, 1987)
(Figs 1A, 2A, F)

1987 *Perlariopsis fidelis* Sinitshenkova: 56, fig. 52.

Diagnosis. In forewing, CuP reaching the posterior wing margin basal to the fork of M (it is distal to the fork of M in *Paranotonomoura zwicki* sp. nov.).

Description. Specimen PIN 3791/1220: comparatively well-preserved specimen, nearly complete pair of forewings, few veins of right hind wing, and part of body preserved; RFW nearly completely preserved, with length about 12.0 mm, width about 3.0 mm; ScP ended at RA and diverged from RA after 0.5 mm long (not complete?) fusion; in the area between anterior wing margin and ScP with three cross-veins: one in the very basal part, the other two in distal part of ScP (before the fusion with RA); basal part coloration between anterior wing margin and ScP in distal part of the wing clearly visible; rp-ma not simple; LFW poorly preserved, with posterior part partly folded with anterior part (see reconstruction drawing in Fig. 1A).

Remarks. The defining character state of Notonemouridae/*Arcuonemourida* (viz. bent CuP in forewing; Fig. 2F) was not documented in the original description of the species (Sinitshenkova 1987, fig. 52). Based on photographs provided by N. Sinitshenkova, we could assess that it occurs in the holotype specimen. Note that its occurrence could not be interpreted in any of the four paratypes, because they are too incomplete and/or poorly preserved. The identification of the species as a stem-Notonemouridae is not indicative of the affinities of other species assigned to the Perlariopseidae.

Paranotonomoura zwicki Cui & Béthoux sp. nov.
(Figs 1B–E, 2B–E, G, 3)

Diagnosis. In forewing, CuP reaching the posterior wing margin distal to the fork of M (it is basal to the fork of M in *Paranotonomoura fidelis* comb. nov.).

Material. Holotype: CNU-PLE-NN-2016103 (Figs 1B, 2B, 3A, B); paratypes: CNU-PLE-NN-2016101 (Figs 1D, 2D, G), -2016102 (Figs 1E, 2E, 3C, D), -2016106 (Figs 1C, 2C); additional specimens, CNU-PLE-NN-2016104, -2016105.

Description. Small size, length of forewing about 12.0/8.6 mm long (female and male respectively); in forewing, near to two-thirds of wing length, ScP fused with RA for some distance, then diverging from it and

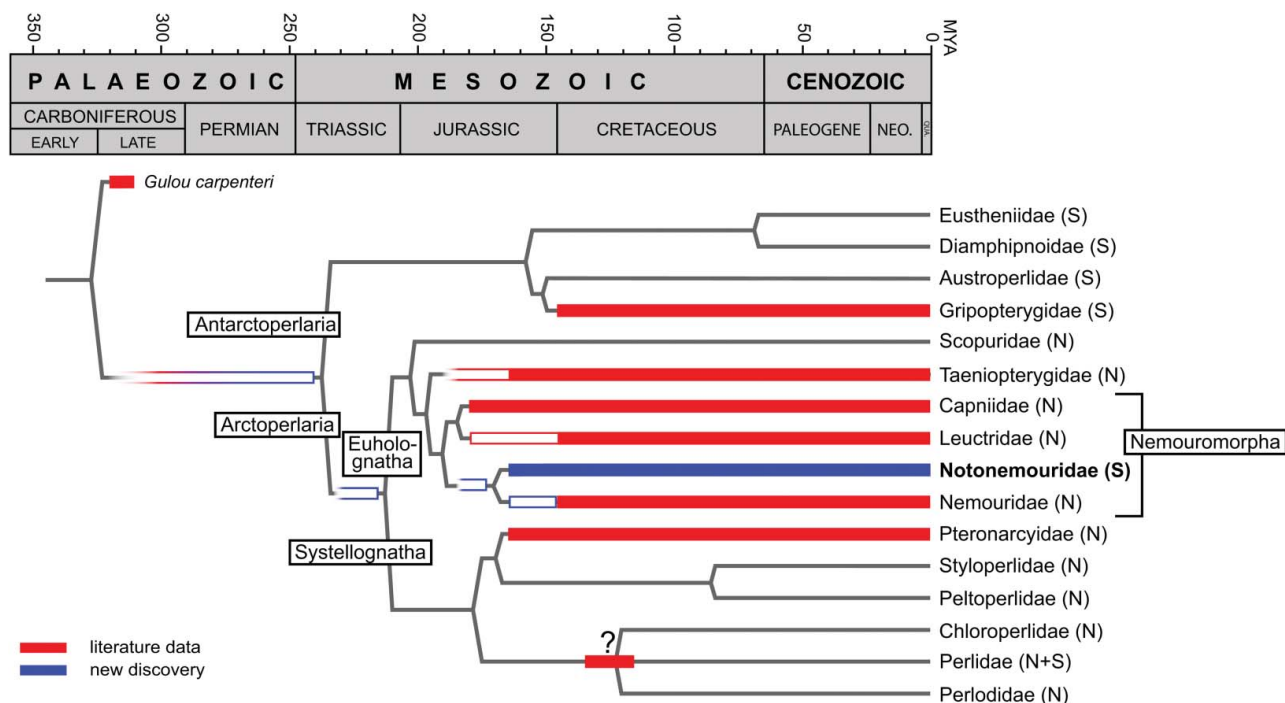


Figure 6. Phylogeny and fossil record of Plecoptera (narrow selection), modified from Zwick (2000), based on literature data and the new discovery. Full bars indicate observed fossil occurrence, empty bars predicted occurrence; question mark accounts for uncertainty on the placement of *Sinisharperla zhaoi* Liu, Sinitshenkova & Ren, 2007 (see Cui *et al.* 2015).

reaching the anterior wing margin; area between anterior wing margin and ScP usually with two cross-veins (possibly three, see Fig. 1D); the basal-most one very near the wing base ('humeral cross-vein'), and the distal one (or two) in the narrowest area between anterior wing margin and ScP; in the area delimited by the anterior wing margin and RA, and distal to the distal free part of ScP, occurrence of dark coloration; R forked into RA and RP in the basal fifth of wing length; RA simple; RP forked near the ending point of ScP on RA; in the area between RA and RP, only one cross-vein (ra-rp) exists exactly/slightly before the fork of RP; M forked into MA and MP in the middle of the wing length; only one cross-vein (rp-ma) in area between RP and M/MA; area between M/MP and CuA with 3–4 cross-veins, including the very curved, oblique and long mp-cua; CuP closely approaching posterior wing margin (just distal of the end of AA1), then diverging from it, until it reaches it more distally; distal half of the area between CuA and CuP without cross-veins; first branch of AA2 simple, strongly bent, delimiting a large cell. Hind wings with nearly the same venation as that of forewing; m-cua cross-vein shorter than in forewing (* on Fig. 1D, RHW); only one cross-vein in the area between CuA and CuP (Fig. 1D, RHW); vannus comparatively large (incompletely known; Fig. 1E).

CNU-PLE-NN-2016103. (holotype; Figs 1B, 2B, 3A, B): nearly complete male individual, LFW, LHW and RHW partly creased; posterior margin of head 0.9 mm long; right antenna 5.1 mm long as preserved; prothorax 0.9 mm wide, 0.5 mm long; mesothorax 1.3 mm wide, 1.0 mm long; metathorax 1.2 mm long; legs slender, with estimated length of hind legs longer than the abdomen; LFW 8.2 mm long, 2.5 mm wide; RFW 8.5 mm long, 2.5 mm wide; RHW with anal area not visible, 7.3 mm long as preserved, 2.3 mm wide opposite the end of CuP; coloration in the distal part of the area between anterior wing margin and RA well visible in all four wings; abdomen about 23.0 mm long; genitalia (Fig. 3A, B) preserved in lateroventral view; tergite 8 (t8) preserved much bigger than t9, t10; subgenital plate (sgp) produced to form a long ventral process (vtp), which is preserved downturned; epiproct (ept) with a well-developed triangular hook; cerci (cer) one-segmented.

CNU-PLE-NN-2016106. (paratype; Figs 1C, 2C): nearly completely preserved specimen, probably a male, in resting position, with body partly visible and four wings overlapping; LFW 9.1 mm long as preserved, 2.5 mm wide; RFW 9.4 mm long, 2.5 mm wide; hind wings with only the distal portions of R identifiable.

CNU-PLE-NN-2016101. (paratype; Figs 1D, 2D, G): partly preserved specimen, probably a female, with LFW

very well preserved and LHW partly creased; part of abdominal segments visible; LFW estimated length 11.2 mm, 3.1 mm wide; LHW 7.4 mm long as preserved, 2.6 mm wide as reconstructed; m-cua cross-vein visible (* on Fig. 2D); area between CuA and CuP nearly completely preserved, with a single cross-vein.

CNU-PLE-NN-2016102. (paratype; Figs 1E, 2E, 3C, D): nearly completely preserved female individual, hind wings poorly preserved and damaged; head small, 1.1 mm wide, with large eyes; prothorax 1.1 mm wide, 0.9 mm long; mesothorax 1.7 mm wide, 1.2 mm long; metathorax 1.5 mm wide, 1.1 mm long; legs slender, with 3-segmented tarsus; LFW 12.2 mm long, 2.9 mm wide; coloration between anterior wing margin and RA in the distal part of wing partly visible in LFW, not preserved in RFW; RFW 11.9 mm long, 2.9 mm wide; both hind wings with only few vein portions visible; RHW preserved parts of a large vannus; abdomen completely preserved; genitalia (Fig. 3C, D) with subgenital plate (sgp) well visible; tongue of subgenital plate (spt) probably very short, if present (not visible here); subanal lobe (sbl) simple; cerci (cer) one-segmented.

Remarks. It is clear that at least some fossil insects recovered from the Daohugou locality experienced plastic deformation, but to a very variable extent (pers. obs.). The minor difference in lengths of the forewings of specimen CNU-PLE-NN-2016103 (Figs 1B, 2B) can be attributed to such deformation. Also, the forewings of the specimen CNU-PLE-NN-2016102 (Figs 1E, 2E) appear elongated if compared to that of the specimen CNU-PLE-NN-2016101 (Figs 1D, 2D). This alteration can also be the consequence of a minor plastic deformation. In both cases the resulting deformation is of minor importance.

The specimens CNU-PLE-NN-2016103 and CNU-PLE-NN-2016102 can be confidently identified as male and female, respectively. The former possesses an elongated ventral process, an epiproct (identified according to its location and shape), and a posterior lobe of tergite 10 (Fig. 3A, B). Although the genitalia of the specimen CNU-PLE-NN-2016102 are viewed ventrally (only slightly laterally), it can be assessed that they have a fundamentally different organization, without elongated elements such as the ventral processes. We could identify the subgenital plate, but it could not be delimited confidently (yet it clearly does not form a stylet-like ovipositor). As one could expect with stoneflies, which display a female-biased sexual size dimorphism (Guillermo-Ferreira *et al.*, 2014; and references therein), the male is significantly smaller than the female in the news species. This allows us to assume that the specimen CNU-PLE-NN-2016106 (Figs 1C, 2C) and CNU-PLE-NN-2016101 (Figs 1D, 2D) are male and female, respectively, owing to their size.

Compared with other Arctoperlaria from Daohugou (Liu *et al.* 2006b, 2009, 2011; Cui *et al.* 2016), the

Paranotonemoura are very rare in this locality: the six specimens of *Paranotonemoura zwicki* sp. nov. we discovered were noticed after a survey of more than a thousand specimens of Plecoptera, mostly belonging to Euholognatha.

Phylogenetic considerations

The assumed phylogenetic relationships of the various taxa and species considered above are summarized in Fig. 5: the *Paranotonemoura* are sister-group related to all extant Notonemouridae (i.e. they are stem-Notonemouridae), the latter composing the Notonemourinae/*Notonemourina*. As expected from such ancient species, they exhibit several plesiomorphies, such as a well-developed free distal portion of ScP. This state is present in Nemouridae (the presumed sister-group of *Arcuonemourida*; see Needham & Claassen (1925); Baumann (1975); Stewart & Stark (2008), while it is reduced in many *Notonemourina* (i.e. crown-Notonemouridae; Fig. 4C, D). Similarly, a well-developed hind wing vannus (Fig. 1E) is, at the level of Plecoptera, a plesiomorphy (the vannus is reduced in most *Notonemourina*; Fig. 4B–D; note that a reduction of the vannus likely occurred multiple times within *Nemouromorpha*, but also, more generally, within Plecoptera).

Discussion

The fossil record of *Arcuonemourida*

The current contribution is not the first one claiming the discovery of stem-Notonemouridae. Sinitshenkova (1982) described fossil material of *gracilis* Brauer *et al.* 1889 (genus *Mesoleuctra* Brauer *et al.* 1889) and assigned the species to this family on the basis of the lack of gills, and the presence of long subgenital plates in males and of long abdominal segments. However, representatives of other families share these characters. Later Sinitshenkova (1987) erected the family Mesoleuctridae to accommodate *gracilis* and newly discovered species assigned to the genus *Mesoleuctra*, as well as the genus *Mesoleuctroides* Sinitshenkova, 1985. The genera *Mesoleuctrisca* Sinitshenkova, 1998 and *Capitiperla* Lin, 1992 were further added to this family. Given that all species ever assigned to the Mesoleuctridae are nymphs, the family is certainly not a natural assemblage.

In regard to the supposed phylogenetic affinities of its constituent species, the ‘Mesoleuctridae’ is considered by Sinitshenkova (1987, 2002) as an early side branch of the stem-group Nemouroidea *sensu* Zwick (2000). In other words, the corresponding fossils would be remotely related to the Notonemouridae. Whichever actual relationships these ‘nymphal species’ have with ‘other’ stonefly species, the hypothesis of close affinities of *gracilis* with

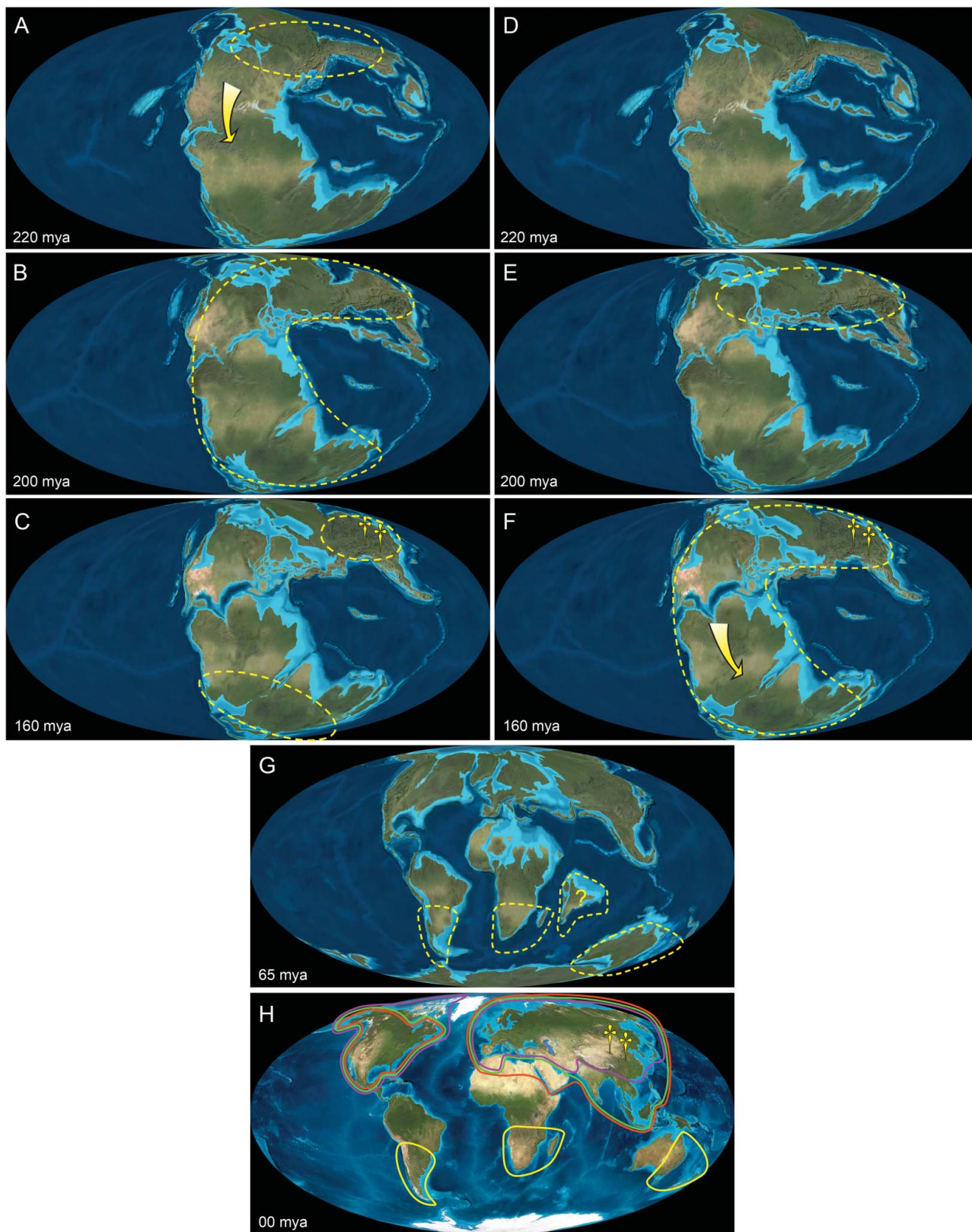


Figure 7. Palaeogeographical reconstructions during the Mesozoic, distribution of *Arcuonemourida* (A–G), and current distribution of other *Nemouromorpha* (H). Ancient distribution of *Nemouromorpha* as derived from their extant distribution (DeWalt *et al.* 2016). Purple, area of *Capniida*; green, area of *Leuctrida*; red, area of *Nemouridae*; yellow, area of *Arcuonemourida*, and location of *Paranotonemoura* (†). Maps are from Global Paleogeography and Tectonics in Deep Time 2016 Colorado Plateau Geosystems Inc., with permission.

the Notonemouridae/*Arcuonemourida* can be considered unsubstantiated and should be rejected.

Therefore, this is the first time that fossil *Arcuonemourida* are unambiguously identified. Our discovery demonstrates that the previous divergence date estimate of the corresponding lineage at 76 Ma (confidence interval, 65–98 Ma; McCulloch *et al.* 2016) is significantly underestimated: *zwicki* is, like other fossils from Daohugou (Selden *et al.* 2008; Cui 2012; Cui *et al.* 2015), 165 Ma. Concurring with recent discoveries (Cui *et al.* 2016), the current one demonstrates that most of the main extant lineages of Arctoperlaria were well differentiated by the Middle Jurassic (Fig. 6), at least, suggesting an Arctoperlaria–Antarctoperlaria split in the Early Mesozoic or latest Late Palaeozoic.

Ancient biogeography of *Arcuonemourida*

The various hypotheses on the origin and ancient biogeography of *Arcuonemourida* have been summarized by Zwick (2000), who, taking into consideration doubts on the monophyletic nature of the Notonemouridae, and at that time a complete lack of known fossils, reasonably remained cautious about scenarios explaining the current distribution of the taxon. Herein, we provide a defensible apomorphic character state, and associated systematic classification, suggesting that species currently assigned to the Notonemouridae, all occurring in the southern hemisphere, form a natural taxon, *Arcuonemourida*, and that this taxon occurred in the northern hemisphere as early as in the Middle Jurassic. The two scenarios can now be better proposed (Fig. 7), taking into account the distribution of continents from the Mesozoic onwards.

First, it is parsimonious to assume that the *Notonemourina* (extant southern hemisphere inhabitants) diverged from *Paranotonemoura* (known only from northern hemisphere fossils) while inhabiting the northern hemisphere, where the later, and all closely related taxa (Nemouridae, *Leuctrida* and *Capniida*), presently occur (Fig. 7H). The fossils suggest that this divergence took place, or had already taken place, 165 Ma. Given these assumptions, we propose four steps in the evolution of the distribution of *Arcuonemourida*: (1) divergence from their sister-group, somewhere in the northern hemisphere; (2) the *Notonemourina* (and their closest relatives) originated and dispersed in the southern hemisphere; (3) the *Notonemourina* and the *Paranotonemoura* became fully isolated; and (4) the *Paranotonemoura* became extinct.

A scenario implying an early divergence date (step 1), *c.* 220 Ma, can be considered (Fig. 7A, B). At this time the peneplanation of the Variscan mountain range, which resulted from the accretion of Gondwana and Laurussia during the Late Palaeozoic (Kroner & Romer 2013; Stampfli *et al.* 2013), is reaching completion. During the Triassic the area is characterized by remaining mountain

highlands and fluvio-lacustrine environments (Golonka & Ford 2000), likely involving connected drainages. Such environments are suitable for dispersal (step 2) of stoneflies at the larval stage, a mechanism favoured by some authors (Schultheis *et al.* 2002; and references therein). If this scenario is followed, during the Middle Jurassic (Fig. 7C), *fidelis* and *zwicki* are representatives of the group still inhabiting the northern hemisphere, but, possibly, already represent a relict of it. At this time the split of the Pangea is sufficiently advanced to isolate the *Notonemourina* and the *Paranotonemoura* (step 3).

An alternative scenario predicts a late colonization of the southern hemisphere. The *Arcuonemourida* have not yet diverged 220 Ma (Fig. 7D). Step (1) takes place at *c.* 200 Ma and steps (2) and (3) occur during a short interval, around 160 Ma. Taking into account the current distribution of Perlidae (DeWalt *et al.* 2016), suggesting some capacity of dispersal across narrow seas by stoneflies at the adult stage (on such dispersal mechanism in Plecoptera, see Knighton *et al.* (2014), and references therein), and possible temporary decrease in sea level during the corresponding periods, the continental distribution 160 Ma appears to be the latest opportunity for step (2).

In summary, the north-to-south dispersal of *Arcuonemourida* probably took place between 200 and 160 Ma. The date of complete extinction of the group in the northern hemisphere (step 4) is unknown. Also, the occurrence of *Arcuonemourida* in India remains an open and interesting question. Given that the stonefly fauna of Madagascar includes *Notonemourina*, it can be reasonably assumed that the group similarly occurred in India 160 Ma (Fig. 7C, F). If so, the group had to have experienced extinction as the subcontinent moved northwards, as already suggested by Fochetti & Tierno de Figueroa (2008). Indeed, the Deccan volcanism, which took place during the Cretaceous–Tertiary transition (continents distribution represented in Fig. 7G), rendered the subcontinent very inhospitable (Punekar *et al.* 2014), inducing a so-called ‘mock’ aridity (Harris & Van Couvering 1995; Khadkikar *et al.* 1999) and uncertainty of freshwater environments (Bajpai *et al.* 2013), resulting in no or few typical habitats where stoneflies could survive.

Conclusions

Our analysis of the wing venation allowed us to confirm that extant species of Notonemouridae form a monophyletic taxon (McCulloch *et al.* 2016), herein defined and named *Arcuonemourida*. The subsequent identification and discovery of the first fossils provide indications of previously unproposed stonefly palaeobiogeography, namely the origin and distribution of a novel taxon: its phylogenetic origin is to be found among the group of ‘northern hemisphere stoneflies’ (Arctoperlaria), but

presently restricted to the southern hemisphere. Firstly, the *Arcuonemourida* are at least *c.* 90 Myr older than estimated by McCulloch *et al.* (2016), a notable incongruity for stoneflies, for which the earliest record is 320 Ma (Béthoux *et al.* 2011), but which is not uncommon (Cui *et al.* 2016). Secondly, the fossil record demonstrates that *Arcuonemourida* occurred in the northern hemisphere 165 Ma, but with subsequent extinction in this area. A north-to-south dispersal probably took place between 220 and 160 Ma, when Laurussia and Gondwana elements were not fully differentiated.

Despite our discovery, knowledge of the history of *Arcuonemourida* remains very limited. The timing of the north-to-south dispersal is poorly defined. Also, it is probable that *Arcuonemourida* once occurred in India and experienced extinction during the intense volcanism that took place in the subcontinent during the Cretaceous–Tertiary transition, but records are lacking. We anticipate that the systematic framework we provide will allow for identifications of further fossil *Arcuonemourida*.

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Supplemental data

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Appendix

Taxon *Nemouromorpha* nom. Zwick, 2000, dis.-typ. Béthoux & Kondratieff, 2015 in Béthoux *et al.* (2015)

Comments. The fossil species herein (re-)described can be assigned to the taxon *Nemouromorpha*, as they possess its defining character state (viz. simple CuA). According to Béthoux *et al.* (2015), *Nemouromorpha* includes *Leuctrida* Béthoux & Kondratieff in (Béthoux *et al.* 2015), *Capniida* Béthoux & Kondratieff in (Béthoux *et al.* 2015), some fossils, and extant species assigned by Zwick (2000) to ‘Nemouridae s.l.’. The Notonemouridae is regarded by Zwick (2002) as belonging to the latter.

Taxon *Arcuonemourida* Cui & Béthoux, tax. nov.

Definition. Species that evolved from the hypothetical ancestral species in which the character state ‘in forewing, CuP closely approaching posterior wing margin (just distal of the end of AA1), then diverging from it, until it reaches it more distally’ (as opposed to ‘in forewing, distal the end of AA1, area between CuP and posterior wing margin tapering uninterruptedly’), as exhibited by *zelandica* Tillyard, 1923 and *quadrangularis* Aubert, 1960.

Cladotypes. Specimen MNHN-EP671, male of *zelandica* Tillyard, 1923; and specimen MNHN-EP675, male of *quadrangularis* Aubert, 1960.

Paracladotypes. Specimens MNHN-EP672, -EP673 and -EP674, male, female, and female of *zelandica* Tillyard, 1923, respectively; and specimens MNHN-EP676, -EP677 and -EP678, male, male, and female of *quadrangularis* Aubert, 1960, respectively.

Etymology. A combination of ‘arcuo’ (‘arched’ in Latin) and ‘Nemourida’, derived from the family name

Nemouridae, which extant species compose the sister-group of the defined taxon.

Composition. The taxa *Notonemourina* tax. nov. and *Paranotemoura* tax. nov. (see below).

Comments. We did not acknowledge the above defining character state in previous publications. The defining character state, is unique among all Plecoptera, and possibly among all Pterygota, and therefore is clearly derived. It occurs in all extant Notonemouridae (Fig. 4; see also Aubert (1960); Illies (1961, 1975); Winterbourn (1968); McLellan (1972, 1987, 1991, 2000a, 2000b); Hynes (1981); Stark *et al.* (2009); Zwick (2015); including the two cladotypic species (Fig. 4A, D)). Therefore, the character state confirms the monophyly of extant Notonemouridae (McCulloch *et al.* 2016), which was not apparent to Zwick (2000). Note that this character state could be related to the lack of cross-veins in the distal half of the area between CuA and CuP.

Taxon *Notonemourina* Cui & Béthoux, tax. nov.

Definition. Species that evolved from the hypothetical ancestral species in which the character state ‘in forewing, end of CuA opposite or distal to the end of RA’ (as opposed to ‘in forewing, end of CuA basal to the end of RA’), as exhibited by *zelandica* Tillyard, 1923 and *quadrangularis* Aubert, 1960.

Cladotypes. Specimen MNHN-EP671, male of *zelandica* Tillyard, 1923; and specimen MNHN-EP675, male of *quadrangularis* Aubert, 1960.

Paracladotypes. Specimens MNHN-EP672, -EP673 and -EP674, male, female, and female of *zelandica* Tillyard, 1923, respectively; and specimens MNHN-EP676, -EP677 and -EP678, male, male, and female of *quadrangularis* Aubert, 1960, respectively.

Etymology. Derived from the family name ‘Notonemouridae’ (all species currently assigned to this family belong to the *Notonemourina*). The name ‘Notonemouridae’ is an explicit reference to the geographical distribution of the corresponding species (Notos was the Greek god of the *south* wind). Therefore, if geographic distribution is considered a phylogenetically relevant character, the name is pre-occupied. In order to avoid confusion, we opted for spelling inspired from Notonemouridae but without particular meaning.

Composition. Species currently assigned to the family Notonemouridae (see DeWalt *et al.* (2016)).

Comments. We did not acknowledge the above defining character state in previous publications. The character state is unique among all Plecoptera. Based on literature and unpublished, we found that the defining character state also occurs in Gripterygidae. In addition, in

Eustheniidae and Austroperlidae, the anterior-most branch of CuA reaches the wing margin opposite the end of RA. However, these three families are only remotely related to the *Nemouromorpha* (Zwick 2000). The immediate sister-groups *Notonemourina*, namely the *Paranotonemoura*, the *Leuctrida* and the *Capniida*, all possess a CuA reaching the wing margin basal to the end of RA (Béthoux *et al.* 2015; and references therein). Therefore the proposed defining character state is likely derived.

We noticed some exceptions in the occurrence of the character in the species we assign to this taxon (see figs 2, 3, 57 in Aubert (1960); fig. 24 in McLellan (1972); fig. 6 in Illies (1975); fig. 11 in McLellan (1991)). Many lack a distal portion of ScP (forewing) or have a reduced vannus (hind wing), suggesting that their most recent common ancestor is more recent than that of all *Notonemourina*. Therefore, they still belong to *Notonemourina*.

Taxon *Paranotonemoura* Cui & Béthoux, tax. nov.

Definition. Species that evolved from the hypothetical ancestral species in which the character state ‘in forewing, the mp-cua cross-vein is more than twice longer than the longest cross-vein in the area between CuA and CuP’ (as opposed to ‘in forewing, the mp-cua cross-vein is equal to, or less than, twice longer than the longest cross-vein in the area between CuA and CuP’), as exhibited by † *Paranotonemoura zwicki* **sp. nov.** and † *fidelis* Sinitshenkova, 1987.

Cladotypes. Specimen PIN 3791/1220, † *fidelis* Sinitshenkova, 1987 (sex unknown); and specimen CNU-PLE-NN-2016103, male of † *Paranotonemoura zwicki* **sp. nov.**

Paracladotypes. Specimens CNU-PLE-NN-2016106, -101, and -102, male, female, and female of † *Paranotonemoura zwicki* **sp. nov.**, respectively.

Etymology. A combination of ‘para’ (‘beside’ in ancient Greek) and *Notonemourina*, the sister-group of the defined taxon; referring to the proximity of the new taxon with *Notonemourina*.

Composition. Species † *Paranotonemoura zwicki* **sp. nov.** and † *fidelis* Sinitshenkova, 1987.

Comments. We did not acknowledge the above defining character state in previous publications. The species † *fidelis* Sinitshenkova, 1987 was assigned to the genus † *Perlariopsis* Ping, 1928 (and to the family † *Perlariopseidae* Sinitshenkova, 1985). Based on our comparative analysis and observations (see below), the holotype of † *fidelis* exhibits the defining character of *Arcuonemourida*. In other words, it is a genuine stem-*Notonemouridae*. This is also the case of the newly described fossil species (see below). The *Paranotonemoura* therefore are *Arcuonemourida*.