



# New fossil stoneflies (Plecoptera: Arctoperlaria) from Australia testify ancient dispersal across Pangea

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## Abstract

The stonefly suborders Arctoperlaria and Antarctoperlaria reflect the current division of the diversity of this insect order between the Northern and Southern Hemispheres. However, there are several exceptions to this pattern, the most notable being the family Notonemouridae, which is phylogenetically deeply subordinate within the northern Arctoperlaria, but distributed in South Africa, South America, and Australia. Various hypotheses have been proposed regarding the circumstances of their dispersal to the south. Some estimated their origin as relatively recent, with long-distance dispersal to the southern continents in the Late Cretaceous or early Paleogene. On the other hand, fossils of Notonemouridae have been dated to the Middle Jurassic, proving the lineage is very ancient. However, all known notonemourid fossils originate from Asia and the timing of their dispersal to the south cannot be precisely estimated. Here we report new fossil stoneflies from the Late Jurassic Talbragar Fish Beds, Australia, described as *Talbragaria australis* **gen. et sp. nov.** and attributed to Notonemouridae. This finding represents the first fossil evidence of the northern suborder Arctoperlaria in the Southern Hemisphere, and confirms the north-to-south dispersal of Notonemouridae across Pangea prior to the continental break-up.

## Key words

Arctoperlaria, biogeography, new species, Notonemouridae, Upper Jurassic, Talbragar, taxonomy

## 1. Introduction

Plecoptera have an unusual antitropical distribution, being much more speciose in high latitude environments than in tropical regions (Zwick 2000). The current higher-level classification of the order also reflects this division, as is implied by the names of two suborders, Antarctoperlaria and Arctoperlaria. These two major clades are widely agreed upon and strongly supported as monophyletic by several approaches (Zwick 2000; Ding et al. 2019). Antarctoperlaria are restricted to the Southern

Hemisphere, whereas Arctoperlaria are restricted to the Northern Hemisphere, albeit with a few exceptions.

Those exceptions are represented by three lineages of originally Laurasian Arctoperlaria found in the Southern Hemisphere, namely the genus *Neoperla* (Perlidae) in Africa, subfamily Acroneuriinae (Perlidae) in South America, and family Notonemouridae, which shows a disjunct South African (included Madagascar), South American, and Australian (including New Zealand) distribution

(Zwick 2000). The timing and circumstances under which these three lineages reached the Southern Hemisphere differ. The originally Asian genus *Neoperla* probably reached Africa relatively recently during the Paleogene (Zwick 2000). For South American Acroneuriinae, Stark and Gaufin (1976) hypothesized that recent representatives arose from a now extinct Asian or European group which dispersed across Northern Africa in the Cretaceous and became established in South America. This hypothesis is partly supported by the presence of Acroneuriinae in Late Cretaceous Burmese amber (Sroka et al. 2018).

In the case of Notonemouridae, conflicting hypotheses have been proposed. Phylogenetically, Notonemouridae is a sister lineage to Laurasian Nemouridae, nested within Euholognatha (Zwick 2000; Ding et al. 2019), and despite their current distribution range being restricted to the Southern Hemisphere they are certainly of Laurasian origin (Illies 1965; Zwick 2000; Ding et al. 2019). Some authors have considered that the present distribution of notonemourids is attributable to Gondwanan vicariance (Illies 1965; Zwick 2000) and results from dispersal across Antarctica (Zwick 1981, 1990). On the contrary, McCulloch et al. (2016) estimated the age of Notonemouridae as postdating the continental break-up and hypothesized a later colonization of Gondwana by Notonemouridae by long-distance dispersal. Similar results were presented by Ding et al. (2019), who dated the divergence of Notonemouridae at 71 Ma, suggesting that the ancestors of this family spread to the Southern Hemisphere during the Late Cretaceous. An important piece of fossil evidence was presented by Liu et al. (2011), who described the family Pronemouridae, supposedly representing the stem group of Notonemouridae + Nemouridae clade, occurring already in the Middle Jurassic of China. Based on this finding, Liu et al. (2011) suggested the dispersal of Notonemouridae to the Southern Hemisphere took place by at least the Early Cretaceous. Other fossil evidence for the antiquity of Notonemouridae was brought forward by Cui et al. (2018), who attributed *Paranotnemoura zwicki* Cui and Béthoux, 2018, also from the Middle Jurassic of China, to the crown group Notonemouridae. The same authors also transferred another species to Notonemouridae, *Perlariopsis fidelis* Sinitshenkova, 1987, described earlier from the same epoch of Mongolia and originally attributed to the family Perlariopseidae by Sinitshenkova (1987). With the discovery of Notonemouridae in the Jurassic of China and Mongolia, Cui et al. (2018) proved that the age of this family is much older than hypothesized by other authors. Nevertheless, they did not prove that the dispersal of this lineage to the Southern Hemisphere is also ancient, since their fossils originated from Asia. Cui et al. (2018) nevertheless assumed that the north-to-south migration of Notonemouridae took place between 220 and 160 Ma.

Therefore, the colonization of Southern Hemisphere by Notonemouridae might have been possible prior to the main continental break-up. This scenario seems to be more plausible than a later long-distance dispersal overseas given the restricted flight ability and short adult lifespan of stoneflies (Zwick 1980). Nevertheless, there has

been no fossil evidence of Notonemouridae being present in the Southern Hemisphere. Therefore, the time of dispersal of this lineage to the south could not be confirmed.

We report new Late Jurassic stonefly fossils from the Talbragar Fish Beds in Australia, which we attribute to Notonemouridae. Our findings represent the only fossil evidence of Arctoperlaria in the Southern Hemisphere in deep time, and therefore are of considerable value for understanding the dispersal of stoneflies to Gondwana and the historical biogeography of this insect order in general.

## 2. Material and methods

### 2.1. Locality

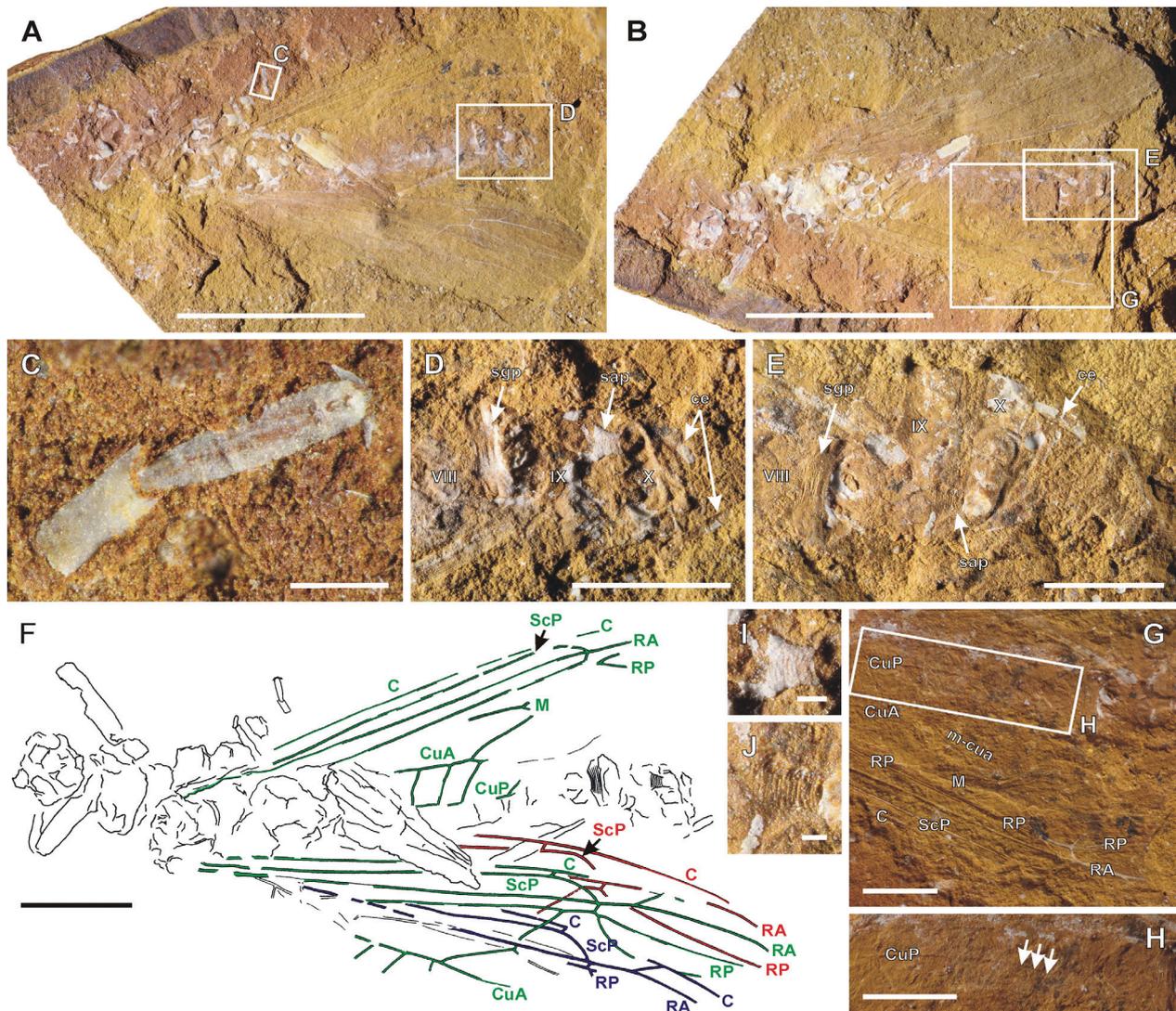
The material originates from the Talbragar Fossil Fish Beds, situated north of Gulgong in central New South Wales, Australia. A recent analysis of zircon crystals from this strata dates it to the very late Oxfordian–Tithonian (Late Jurassic), ca 157.3–145.0 Ma (Turner et al. 2009). The deposit represents a shallow-water-lake palaeoenvironment at the northern end of the deposit, grading to a shoreline palaeoenvironment towards the southern end of the deposit. It was part of a productive lake supporting a large population of fish and a diverse aquatic/shoreline and terrestrial woodland fringe palaeoecosystem, which has produced a significant number and variety of insect fossils (Beattie and Avery 2012). Several new insect taxa have recently been described, comprising members of the orders Odonata (Beattie and Nel 2012), Hemiptera (Chen et al. 2019; Li et al. 2022), Coleoptera (Fikáček et al. 2014; Ashman et al. 2015; Oberprieler et al. 2016), Hymenoptera (Oberprieler et al. 2012), and Diptera (Oberprieler and Yeates 2012, 2014; Oberprieler et al. 2015).

### 2.2. Material processing

The material was examined dry and under a film of ethyl alcohol using Olympus SZX7 and Leica M205 C stereomicroscopes. The photographs were taken using a Canon EOS 550D and a Canon EOS 1200D digital camera equipped with MP-E 65 mm and EF-S 60 mm macro-lenses or attached to the Leica M205 C stereomicroscope. Original photographs were processed by stacking and editing using Adobe Photoshop™ version CS6 (Adobe Systems Incorporated, San Jose, U.S.A.). The measurements of individual body parts were inferred from the photographs taken with a calibration scale.

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.

All the material is deposited in the Australian Museum, Sydney, Australia under the accession numbers as specified below.



**Figure 1.** *Talbragaria australis* gen. et sp. nov. **A** Holotype specimen, part F.136 856, general view. **B** Holotype specimen, counterpart F.136 857, general view. **C** Distal part of tarsus (F.136 856). **D** Posterior part of abdomen (F.136 856). **E** Posterior part of abdomen (F.136 857). **F** Drawing with reconstruction of the venation pattern (F.136 856). **G** Detail of forewing (F.136 857). **H** Course of CuP vein in forewing (F.136 857); arrows indicate curve diverging from posterior wing margin. **I** Detail of subanal plate (F.136 856). **J** Detail of subanal plate (F.136 857). Rectangles in **A**, **B** and **G** mark positions of detailed figures. Abbreviations: ce – cercus, sap – subanal plate, sgp – subgenital plate. Roman numbers indicate abdominal segments. Scale bars: 5 mm (**A**, **B**), 2 mm (**D**), 1 mm (**F–H**), 0.2 mm (**C**, **I**, **J**).

### 3. Results: systematic palaeontology

Class Insecta Linnaeus, 1758

Subclass Pterygota Lang, 1888

Order Plecoptera Burmeister, 1839

Suborder Arctoperlaria Zwick, 1973

Family Notonemouridae Ricker, 1950

#### 3.1. Genus *Talbragaria* gen. nov.

<https://zoobank.org/C1F3FF17-A78C-4A32-8F74-B2405341-3798>

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

**Type species.** *Talbragaria australis* sp. nov. by present description.

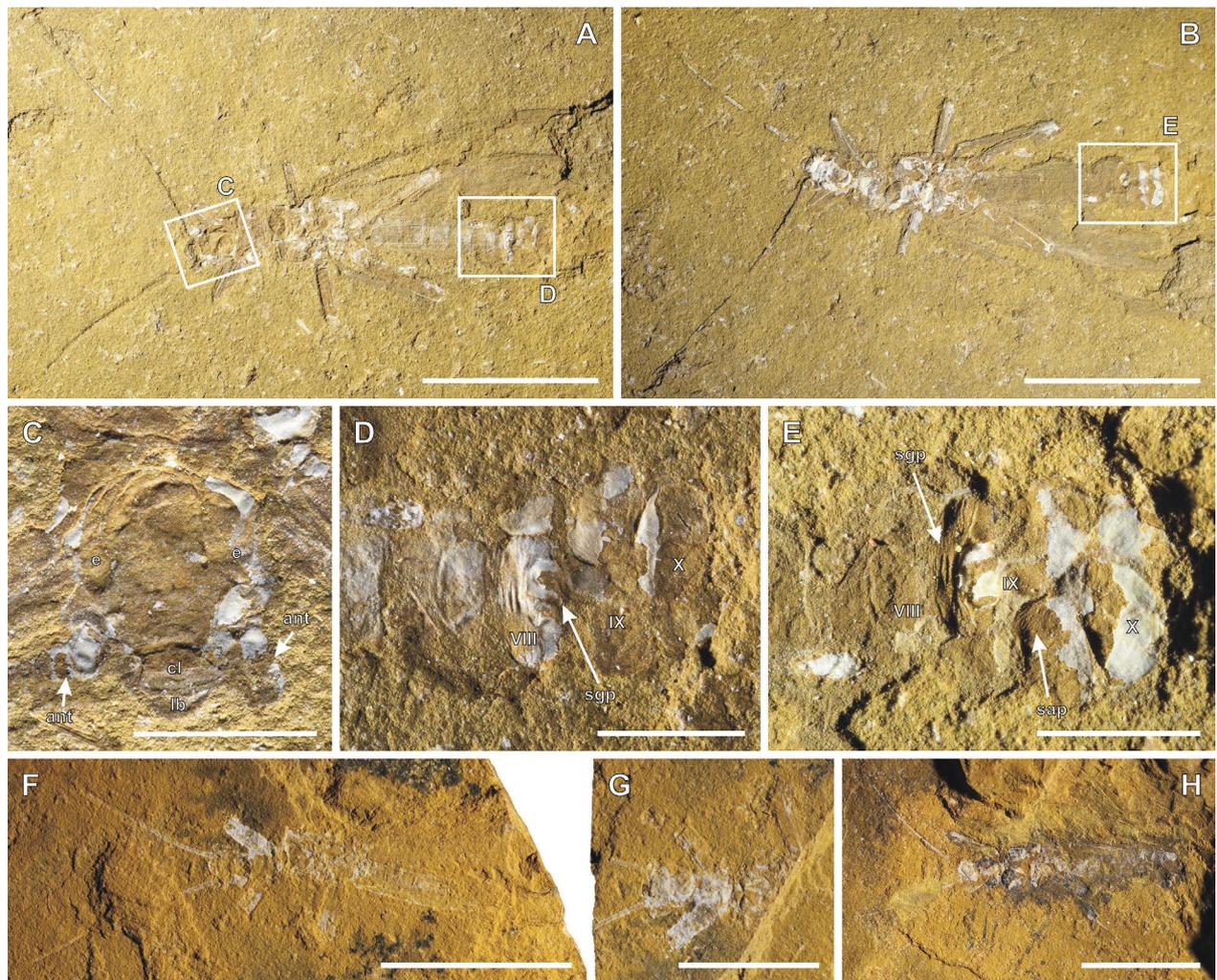
**Etymology.** Named after the locality Talbragar where the holotype and paratype specimens were found.

#### 3.2. *Talbragaria australis* sp. nov.

<https://zoobank.org/B1FCB40F-D5C4-4784-A3B2-4CEA-4035D2FF>

Figs 1, 2

Plecoptera sp. in Beattie and Avery (2012: fig. 8D, F)



**Figure 2.** *Talbragaria australis* gen. et sp. nov. and additional stonefly specimens from Talbragar Fish Beds. **A** *T. australis* sp. nov., paratype specimen, part F.137 576, general view. **B** *T. australis* sp. nov., paratype specimen, counterpart F.137 577, general view. **C** detail of head (F.137 576). **D** Posterior part of abdomen (F.137 576). **E** Posterior part of abdomen (F.137 577). **F**, **G** Plecoptera sp., part and counterpart (both F.136 851). **H** Plecoptera sp. (F.137 324). Rectangles in **A** and **B** mark positions of detailed figures. Abbreviations: ant – antenna, cl – clypeus, e – compound eye, lb – labrum, sap – subanal plate, sgp – subgenital plate. Roman numbers indicate abdominal segments. Scale bars: 5 mm (**A**, **B**, **F**, **H**), 3 mm (**G**), 1 mm (**C**–**E**).

**Diagnosis.** The new species is distinguishable from all other known fossil Notonemouridae by the combination of the following characters: crossvein mp-cua ca  $1.2 \times$  longer than rp-ma; mp-cua crossvein ca  $1.6 \times$  longer than the longest crossvein in the area between CuA and CuP (on contrary, mp-cua crossvein more than twice as long as the longest crossvein in the area between CuA and CuP in closely related genus *Paranotonemoura* Cui and Béthoux, 2018); length of second tarsomere subequal to two thirds of third tarsomere length; female with pronounced corrugated subgenital plate on abdominal sternite VIII and corrugated anal plates on segment IX, narrowed posteriorly.

**Etymology.** The name refers to country where holotype and paratype specimens were found.

**Type material.** **Holotype:** F.136 856 (part) and F.136 857 (counterpart), female imago. — **Paratype:** F.137 576 (part) and F.137 577 (counterpart), female imago.

**Type locality and strata.** The Talbragar Fossil Fish Bed site is approximately 25 km northeast of Gulgong in New South Wales, Australia (Beattie and Avery 2012). Stratigraphically the unit is correlated with the Purlawaugh Formation of the Surat Basin and corresponding to the latest Oxfordian–Tithonian, Upper Jurassic.

**Description.** Body length ca 10–12.5 mm. — **Head:** Prognathous, ca  $1.2 \times$  longer than wide (Fig. 2C). Antennae probably nearly completely preserved, visible portions up to  $0.7 \times$  body length (Fig. 2A, B). Compound eyes rounded, positioned laterally. Ocelli not visible. Clypeus trapezoidal, approximately twice wider than long (Fig. 2C). Labrum rounded anteriorly. Other mouthparts not recognizable. — **Thorax:** Prothorax rectangular, ca  $1.5 \times$  wider than long, lateral margins rounded (Fig. 2A, B). Meso- and metathorax equal in length, each ca  $1.4 \times$  longer than prothorax. Two pairs of fully developed wings. Forewing incomplete, probably slightly longer than body. Forewing venation only partially preserved (Fig. 1A, B,

F–H), ScP adhered to RA and again diverges from it more distally, RA simple, crossvein between RA and RP close to the point of connection of ScP with RA. Further two crossveins between RA and PR more basally. RP bifurcated just distally from the crossvein between RA and RP. Two crossveins between RP and M in proximal portion of wing, further oblique slightly sigmoidal crossvein between RP and M more distally, close to RP bifurcation. Hind wings preserved only fragmentary in anterior part, course of discernible veins (C, ScP, RA and RP) identical to forewing (Fig. 1A, B, F–H). Legs slender, length increases from forelegs to hind legs. Femora and tibiae elongated, femora ca 4–6 × longer than wide, tibiae ca 10–14 × longer than wide. Tarsi incomplete, with only second and third tarsomeres preserved; length of second tarsomere subequal to two thirds of third tarsomere length (Fig. 1C). Claws approximately as long as third tarsomere width. — **Abdomen:** Elongate, narrow, ca 5 × longer than wide. In female, pronounced, well sclerotized and corrugated subgenital plate on sternite VIII (Figs 1D, E, 2D, E). Sternite IX produced posteromedially into narrow corrugated subanal plates. Male genitalia unknown. Cerci short, one-segmented (Fig. 1D, E).

**Additional Plecoptera specimens.** Apart from the holotype and paratype of *Talbragarina australis* **gen. et sp. nov.**, two further specimens of Plecoptera from the same locality were identified in the collection of the Australian Museum, Sydney, Australia under accession numbers F.136 851 (part and counterpart, Fig. 2F,G) and F.137 324 (Fig. 2H). Due to their state of preservation and lack of diagnostic characters, it is not possible to attribute them unambiguously to *T. australis* **gen. et sp. nov.**, although due to their similarity in size they might be conspecific.

## 4. Discussion

### 4.1. Phylogenetic placement

Although the wing venation is not completely preserved in the specimens of *Talbragarina australis* **gen. et sp. nov.**, the anterior part of the wings is unambiguously discernible (Fig. 1A, B, F–H). It features the so-called nemourid X, consisting of ScP that fuses with RA and again diverges from it more distally (Cui et al. 2018), the basal part of RP bifurcation and a crossvein between RP and M. According to Zwick (2000), this pattern of veins is generally present in the families Nemouridae and Notonemouridae (Arctoperlaria, Euholognatha). Although the nemourid X indicates a close relationship between *T. australis* **sp. nov.** and the Nemouridae + Notonemouridae clade, a similar pattern of veins can also be observed in the likewise euholognathan families Taeniopterygidae and Capniidae (Zwick 2000). However, the possible attribution of *T. australis* **sp. nov.** to these families can be excluded using other characters. Capniidae are characterised by an apomorphic reduction of m-cua crossveins (at most two)

and cua-cup crossveins (at most one) (Zwick 2000). In our fossils, the number of respective crossveins is obviously higher, despite the fragmentary preservation, but there are no crossveins in the apical portion of the wings (Fig. 1F). Taeniopterygidae exhibit an elongated second tarsomere, which is at least 4/5 of the length of the third tarsomere and represents an apomorphy of this family (Nelson 2009). The second tarsomere in *T. australis* **sp. nov.** is shorter, subequal to 2/3 of the length of the third tarsomere (Fig. 1C). Since the first tarsomere is missing in available specimens of *T. australis* **sp. nov.**, there is a possibility that the second tarsomere is broken basally and incomplete. However, since the first tarsomere is not preserved on the counterpart, we assume that the second and third tarsomeres are the only ones present in the fossil and the fragmentation of the tarsus happened not during the splitting of the matrix, but early in the fossilization process. Thus, a disarticulation between tarsomeres is more probable than a crack within a basal part of tarsomere. Consequently, we consider the second tarsomere to be likely complete. Therefore, all available morphological evidence testifies for the placement of *T. australis* **sp. nov.** into either Notonemouridae or Nemouridae. Zwick (2000) questioned the monophyly of notonemourids based on the presence of an ovipositor in some genera only. Based on morphology, he considered Notonemouridae as possibly representing a paraphyletic assembly (grade) of early nemourid lines surviving on fragmented Gondwanaland. However, the families Notonemouridae and Nemouridae were recovered as sister groups in the molecular phylogeny of Ding et al. (2019) and the monophyly of Notonemouridae is strongly supported by McCulloch et al. (2016). One more purely fossil family with a close relationship to the Nemouridae + Notonemouridae clade is represented by Pronemouridae, hypothesised by Liu et al. (2011) to represent the stem group of this clade.

The only one of these families known from the Southern Hemisphere is Notonemouridae (Zwick 2000); therefore its presence in the Upper Jurassic of Australia is more probable than in the case of Nemouridae or Pronemouridae. Cui et al. (2018) introduced a new apomorphic wing venation character to define Notonemouridae, namely CuP in the forewing closely approaching the posterior wing margin (just distal of the end of AA1), then diverging from it, until it reaches it more distally. This character is only partially observable in our fossils, since the posterior portion of wings is not completely preserved. In the specimen F.136 857, a short visible portion of CuP is distally converging with CuA (Fig. 1G, H). It indicates the course of CuP as characteristic for Notonemouridae. Nevertheless, other evidence for the attribution of *T. australis* **sp. nov.** to Notonemouridae is represented by the structure of the female genitalia that very closely resembles some Recent notonemourids. It exhibits a pronounced corrugated subgenital plate posteriorly on sternite VIII enabling interlocking with the male epiproct or other copulatory structures, and posteriorly narrowed subanal plates on sternite IX (compare Figs 1D, E, 2D, E and fig. 3.5 in Stevens 2008). Furthermore, *T. austra-*

*lis* **sp. nov.** differs from the families Pronemouridae and Nemouridae in the structure of the tarsi. The second tarsomere in both above-mentioned families is distinctly short, reaching to approximately one-half of the third tarsomere (Nelson 2009; Liu et al. 2011). The length of the second tarsomere in *T. australis* **sp. nov.** is slightly longer, subequal to two thirds of the length of the third tarsomere, which represents a value reported for several representatives of Recent Notonemouridae (Nelson 2009). Pronemouridae are further characterised by two plesiomorphic characters, CuA ending with two branches and multisegmented cerci (Liu et al. 2011). Cerci in *T. australis* **sp. nov.** are one-segmented (Fig. 1D, E), an apomorphic character shared with Notonemouridae and Nemouridae (Cui et al. 2018). The course of CuA in *T. australis* **sp. nov.** is not observable distally of the M-CuA crossvein, however, no bifurcation is visible in the preserved portion of CuA (Fig. 1F). Also taking into account the biogeographic pattern of the discussed individual stonefly taxa, we consider the attribution of *T. australis* **sp. nov.** to Notonemouridae as the most probable.

Within Notonemouridae, Cui et al. (2018) established a subfamily Paranotonemourinae to accommodate two fossil species of the genus *Paranotonemoura* Cui and Béthoux, 2018. The species *Talbragaria australis* **sp. nov.** is not attributable to Paranotonemourinae since the mp-cua crossvein is not more than twice as long as the longest crossvein in the area between CuA and CuP (Fig. 1F), which does not comply with the diagnosis of Paranotonemourinae (Cui et al. 2018). Therefore, we attribute *T. australis* **sp. nov.** to the subfamily Notonemourinae within Notonemouridae.

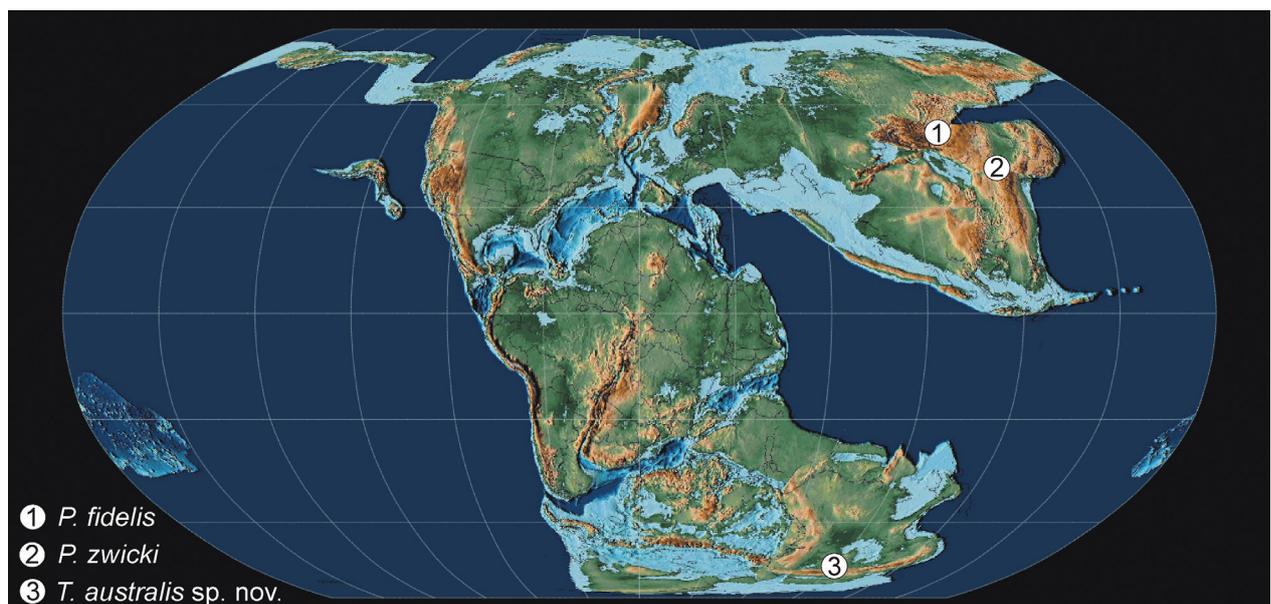
There are 23 extant genera of Notonemouridae (DeWalt et al. 2023). It is difficult and in some cases impossible to compare *T. australis* **sp. nov.** with these genera, since some are defined based on characters not visible in

*T. australis* **sp. nov.** (notably all characteristics of male genitalia). In any case, given the estimated ages of Plecoptera clades (Cui et al. 2016, 2018), it is not reasonable to expect a Recent genus being already present in the Jurassic. We would like to refrain from implying closer relationship to any particular Recent genus, which is not really grounded because of the lack of reliable characters.

## 4.2. Biogeography

Our finding from the Southern Hemisphere complements the journey of Notonemouridae by confirming their presence in the territory of Gondwana already in the Late Jurassic, since Talbragar Fish Beds are dated as Oxfordian–Tithonian (ca 157.3–145.0 Ma) and Notonemouridae must have already been established in the area of current Australia at that time. Their dispersal to the Southern Hemisphere thus predates the rifting of Pangaea, exactly as presumed by Liu et al. (2011) and Cui et al. (2018). Therefore, the hypothesis of McCulloch et al. (2016) and Ding et al. (2019) about the more recent colonisation of Gondwana by Notonemouridae by long-distance dispersal postdating the Gondwana break-up can be rejected. Recent representatives of this family occur only in the fragments of Gondwana, suggesting that the southward dispersal was followed by the extinction of Notonemouridae in the Northern Hemisphere. This extinction possibly occurred in the mid-Cretaceous, when a massive increase of the extinction rate was reported for Plecoptera (Jouault et al. 2022).

The fact that Notonemouridae were present in Australia in the Late Jurassic and at about the same time also occurred in China and Mongolia (Cui et al. 2018) further indicates that the lineage must have been very widespread, considering that the dispersal route by land between these



**Figure 3.** Palaeogeographical map of the Late Jurassic with marked positions of known Notonemouridae fossils of *Perlariopsis fidelis*, *Paranotonemoura zwicki*, and *Talbragaria australis* **gen. et sp. nov.** The map generated using GPlates (Müller et al. 2018) and raster images from Scotese (2016).

sites spanned several of today's continents (Fig. 3). Importantly, it also provides evidence that the lineages within stonefly suborders up to the level of some families were already diversified in the Late Jurassic. Given the fact that Notonemouridae is not a basal lineage in the Plecoptera phylogeny (Zwick 2000; Ding et al. 2019), this indicates that the split between the suborders Antarctoperlaria and Arctoperlaria occurred much earlier than the Late Jurassic. Thus, some published age assessments for this split are certainly underestimated. McCulloch et al. (2016) dated the split between suborders as Early Cretaceous (121 Ma, with a confidence interval 143–109 Ma) and Ding et al. (2019) estimated the split of Antarctoperlaria vs Arctoperlaria as Early Jurassic (181.45 Ma, although with a wide confidence interval spanning most of Mesozoic, 106–250 Ma). Probably a more realistic estimate for the major divergences within Plecoptera were given by Cui et al. (2016, 2018) based only on the study of the fossil species. They suggested that the Antarctoperlaria vs Arctoperlaria split occurred in the early Mesozoic or the late Palaeozoic (approximately 260–230 Ma). Interestingly, this timing would rule out the possibility that the split between stonefly suborders was a vicariant event resulting from the continental break-up between Gondwana and Laurasia 215 to 175 Ma, as traditionally hypothesised (Zwick 2000; Ding et al. 2019). Since some Recent families were already diversified in the Late Jurassic, the split must have occurred much earlier, predating the break-up.

## 5. Conclusions

The newly described fossil stonefly species, *Talbragararia australis* **gen. et sp. nov.** from the Upper Jurassic of Australia, is placed in the family Notonemouridae on the basis of several morphological characters, in particular the wing venation pattern. This family is phylogenetically nested within a suborder Arctoperlaria, which is almost exclusively Laurasian. Our results provide evidence for the presence of Notonemouridae in the Southern Hemisphere prior to the main continental break-up, confirming the earlier hypothesis of north-to-south dispersal of notonemourids across Pangea.

## 6. Acknowledgements

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