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Literature review of the fossil record of Systellognatha (Insecta: Plecoptera) and its implications for the biogeography of the Order

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Abstract

The unusual anti-tropical distribution of the Plecopteran (Insecta, stoneflies) suborders Antarctoperlaria and Arctoperlaria, and the biogeographical processes that caused it have fascinated researchers for decades. In particular, debate surrounds what led to the initial diversification of each sub-order, and the dispersal of two Arctoperlarian families, Notonemouridae and Perlidae, into the Southern Hemisphere. The fossil record of Plecoptera is vital for exploring these questions, as it provides the only direct evidence of ancient Plecopteran diversity and occurrence, and can be used to constrain phylogenetic studies. However, many authors question the stonefly fossil record, citing uncertain and contradictory taxonomy caused by an overreliance on phenetic similarity instead of syn- and autapomorphies. Here, we review the published descriptions and figures of all fossilised Systellognatha and fossilised austral species to assess the presence of apomorphic characters, and critically examine their placement in the Plecopteran phylogeny. As the monophyly and diagnoses of extinct families and genera are not assessed, formal systematic reclassifications are not proposed, and this work is explicitly disclaimed as a nomenclatural revision in terms of Article 8.2 of the International Code of Zoological Nomenclature. We found insufficient evidence to support the current classification of 56% of the 113 fossil species reviewed. From the remaining species, specimens with apomorphies of Gripopterygidae, Notonemouridae, Peltoperlidae, Pteronarcyidae, Perlidae and Perlodidae were identified. These allowed for the recommendation of 12 fossil species for the calibration of dated phylogenetic analyses and palaeobiogeographical interpretations. These fossils point to Antarctoperlaria and Arctoperlaria diverging due to vicariance, either on Pangea or shortly following its separation in the Jurassic. Notonemouridae probably dispersed into the Southern Hemisphere during the Early Jurassic, with two independent dispersals of Perlidae occurring in the Cenozoic.

Key words: Systematics, Evolution, Stoneflies, Palaeoentomology, Morphology

Introduction

The Plecoptera (stoneflies) are divided into two suborders, Antarctoperlaria and Arctoperlaria (Zwick 2000). These suborders have a generally disjunct distribution, with each limited to the Southern and Northern Hemisphere, respectively (DeWalt & Ower 2019; Fochetti & Tierno de Figueroa 2008; Zwick 2000). However, there are some exceptions to this pattern. The Arctoperlarian family Notonemouridae Ricker is not present in the Northern Hemisphere, and members are instead distributed in the southern reaches of Australasia, South America, South Africa and Madagascar (DeWalt & Ower 2019, Fochetti & Tierno de Figueroa 2008; McLellan 1991; Stevens *et al.* 2018; Zwick 2000). Similarly, the Arctoperlarian family Perlidae Latreille dispersed into the Southern Hemisphere in two independent events, with ten Acroneuriinae genera occurring in South America (DeWalt *et al.* 2025; Zwick 2000), and at least 84 species of the otherwise Asian and North American genus *Neoperla* Needham found in Africa (DeWalt *et al.* 2025; Zwick 2023; Zwick & Zwick 2023).

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The biogeographical processes that shaped these current distribution patterns have been the subject of much debate (Ding *et al.* 2019; Fochetti & Tierno de Figueroa 2008; García-Girón *et al.* 2024; Hynes 1988; Illies 1965; Letsch *et al.* 2021; McCulloch *et al.* 2016; Zwick 2000). Three questions dominate: 1. What led to the divergence of Antarcoperlaria and Arctoperlaria and their isolation in the Southern and Northern Hemispheres, respectively? 2. How and when did Notonemouridae and Perlidae migrate into the Southern Hemisphere, and what led to their modern distributions? 3. What processes led to the distributions of the extant families and species within each hemisphere?

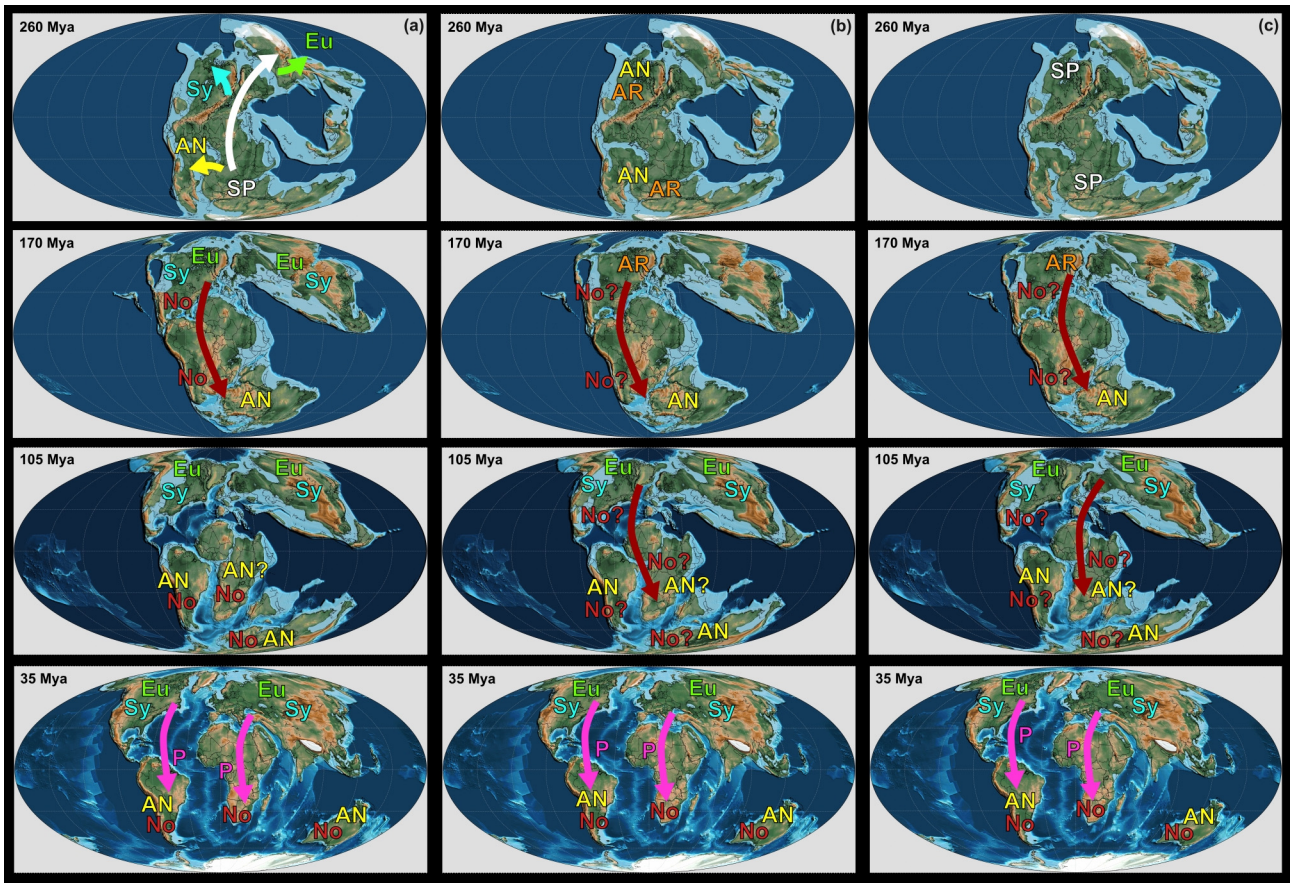

FIGURE 1. Three hypotheses of the palaeobiogeography of Plecoptera, from the Permian (270 Ma) to the Palaeogene (35 Ma), based on interpretations of extant and fossil distributions. (a) Origination and migration from the Southern Hemisphere (Illies 1965). (b) Both suborders were present across Pangea, but reciprocal extinctions limited each to a single hemisphere (Zwick 2000). (c) Vicariance caused by the rifting of Pangea (Zwick 2000). Abbreviations: SP: Stem-Plecoptera, AN: Antarctoperlaria, AR: Arctoperlaria, Eu: Euholognatha, Sy: Systellognatha, No: Notonemouridae, P: Perlidae. Palaeomaps from Scotese *et al.* (2025) are used under the Creative Commons Attribution 4.0 International License, available from https://doi.org/10.5281/zenodo.10659112 (Accessed 24 February 2025).

Illies (1965) proposed the first relatively complete hypothesis of Plecoptera biogeographical history (Fig. 1a), with Plecoptera originating in the austral region of Pangea during the Permian. They crossed the equator by at least the late Permian, and subsequently gave rise to the "Setipalpia" (= Pteronarcyidae Newman + Perloidea) and "Filipalpia" (= Euholognatha + (Gripopterygoidea + Scopuridae Uéno + Peltoperlidae Claassen)) in the Northern Hemisphere. Those that remained in the Southern Hemisphere founded the Eusthenioidea. Later, the initially boreal Notonemouridae migrated over the equator prior to the rifting of Madagascar and became extinct in the north. During the Cenozoic, the Perlidae followed into post-Gondwanan South America and Africa in two independent migrations.

Alternative explanations or variations have since been presented (Banarescu 1990; Hynes 1988). Zwick (2000) summarized these in two possible scenarios: either the Antarctoperlaria and Arctoperlaria had pan-Pangean distributions and countervailing extinctions then restricted each to a single hemisphere (Fig. 1b); or stem stoneflies were present across Pangea, and the suborders diverged because of vicariance after the rifting of Pangea (Fig. 1c).

Zwick (2000) considered the latter explanation more likely. The disjunct distribution of Antarctoperlaria within the Southern Hemisphere was explained by the suborder evolving on a continuous landmass that subsequently split. Zwick was equivocal about whether this occurred on Gondwana (in which case Antarctoperlaria later became extinct in Africa) or after Africa and South America split from the rest of Gondwana (circa 166 Ma: Boger 2011; Roche & Ringenbach 2022; Scotese *et al.* 2025). Relationships in the Northern Hemisphere are more complex, and the modern distributions appear to reflect a combination of vicariance, faunal exchange, extinction and displacement throughout the Jurassic—Pleistocene (Hynes 1988; Zwick 2000). Estimates for the dispersal times of Perlidae and Notonemouridae were left uncertain, but *Neoperla* was postulated to have migrated into Africa during the Miocene or Pliocene, 23–2.6 Ma (Zwick 2000).

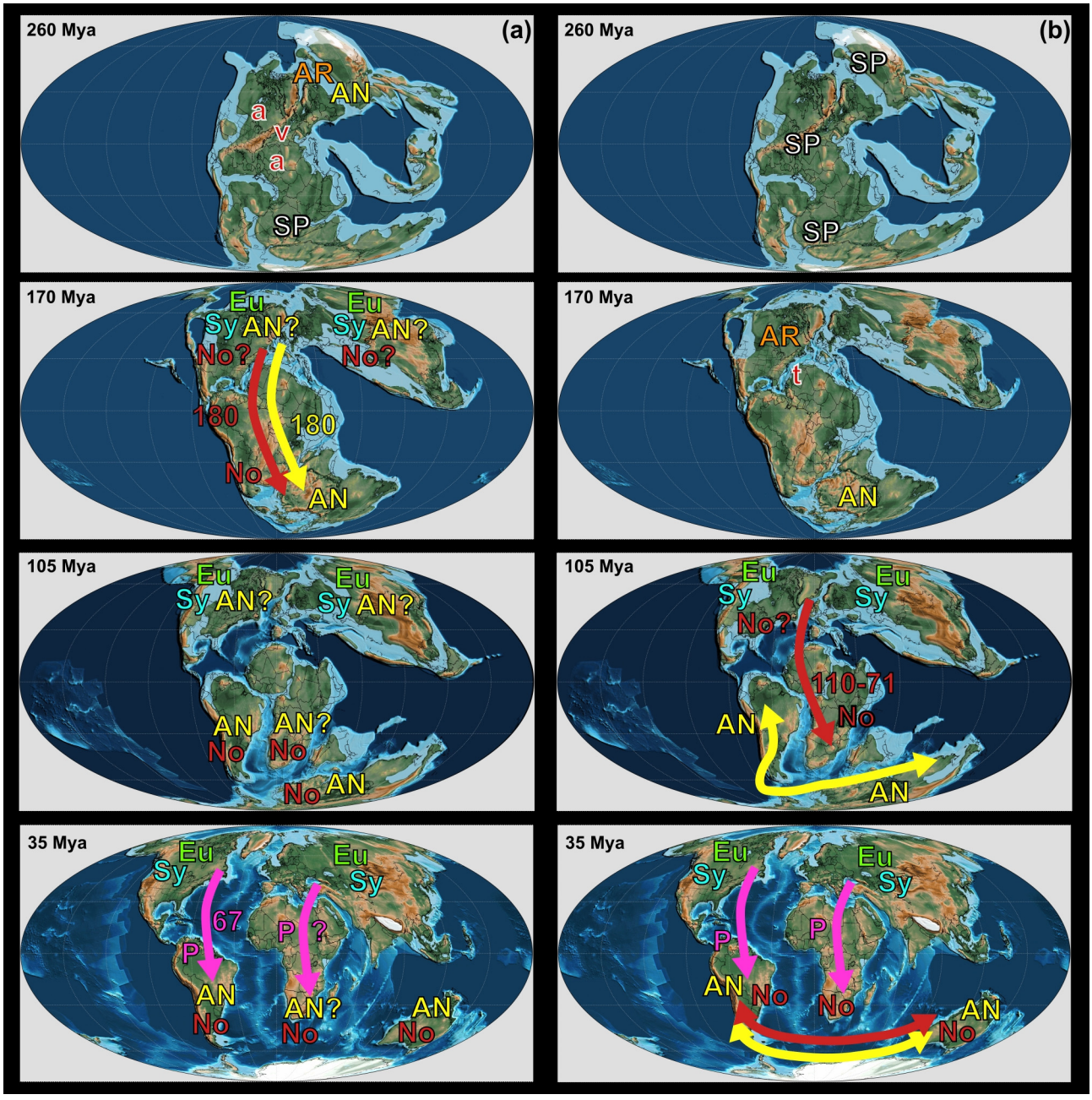

FIGURE 2. Two hypotheses of the palaeobiogeography of Plecoptera, from the Permian (270 Ma) to the Palaeogene (35 Ma), based on time calibrated phylogenies. (a) Origination and migration from the Northern Hemisphere, followed by extinction of Antarctoperlaria in the Northern Hemisphere (Letsch *et al.* 2021). (b) Vicariance, followed by long-distance dispersal (Ding *et al.* 2019; Garcia-Giron *et al.* 2024; McCulloch *et al.* 2016). Abbreviations: SP: Stem-Plecoptera, AN: Antarctoperlaria, AR: Arctoperlaria, Eu: Euholognatha, Sy: Systellognatha, No: Notonemouridae, P: Perlidae, a: Arid region, t: Tethys seaway. Palaeomaps from Scotese *et al.* (2025) are used under the Creative Commons Attribution 4.0 International License, available from https://doi.org/10.5281/zenodo.10659112 (Accessed 24 February 2025).

Interest has persisted into the molecular era, and four time-calibrated phylogenies have been used to investigate these scenarios (Ding *et al.* 2019; García-Girón *et al.* 2024; Letsch *et al.* 2021; McCulloch *et al.* 2016). While some consistent patterns have emerged from these studies, most dates have varied significantly. In particular, explanations for the origin of each suborder have differed, with Letsch *et al.* (2021) recovering a much older divergence in the Permian (265 Ma) than the remaining studies (< 181 Ma). In this scenario (Fig. 2a), the suborders were interpreted as evolving in the high latitudes of Pangea, separated from the globally-distributed stem-Plecoptera by arid bands across the midlatitudes of the supercontinent (Chaboureau *et al.* 2014) and the equatorial Variscan mountain range (Kroner & Romer 2013). Antarctoperlaria and Notonemouridae each had a Northern Hemisphere origin and dispersed into the south approximately 180 Ma as the Variscan mountain range subsided with the rifting of Pangea to form Gondwana and Laurasia (Hasterok *et al.* 2022; Letsch *et al.* 2021).

In this interpretation, Antarctoperlaria and Notonemouridae were present across Gondwana prior to its rifting, and their modern distributions may be the result of vicariance, followed by extinction of the former in Africa. Faunal exchanges between South America, Australia, and New Zealand persisted over Antarctica until those continents separated, starting with the separation of West Gondwana (Africa and South America, circa 166 Ma; Boger 2011; Roche & Ringenbach 2022; Scotese *et al.* 2025), followed by New Zealand, approximately 84 Ma (Mayes *et al.* 1990; McLoughlin 2001; Storey 1996), and Australia approximately 41 Ma (McLoughlin 2001; Scher & Martin 2006). Euholognatha and Systellognatha were present in the Northern Hemisphere by the Jurassic, and their modern distributions follow the model presented by Zwick (2000). Acroneuriinae dispersed from North to South America by "island-hopping" via a chain of meso-American islands some 67 Ma. *Neoperla* first appeared in Asia approximately 92 Ma, suggesting a possible earlier expansion into the Afrotropics, but the lack of Afrotropical taxa in the analysis (at the time only a single African species was regarded as valid and was not included) prevented a test of this hypothesis.

McCulloch *et al.* (2016), Ding *et al.* (2019), and García-Girón *et al.* (2024) placed the divergence of the two suborders after the splitting of Pangea (121, 181, or 170 Ma respectively), supporting Zwick's hypothesis of vicariance. In this interpretation, most families and genera are younger, first appearing in the Cretaceous (Fig. 2b). Antarctoperlaria arose on Gondwana, after the isolation of Africa and South America, and its extant distribution is explained, in part, by the same vicariance patterns between New Zealand, Australia, South America and Antarctica discussed above. At the time, South America was thought to have remained connected to the rest of Gondwana via Antarctica throughout the Early Cretaceous (McLoughlin 2001; McCulloch *et al*. 2016), possibly allowing for faunal exchanges. However, more recent models instead suggest that South America had already separated from West Gondwana by the Late Jurassic (Boger 2011; Roche & Ringenbach 2022; Scotese *et al.* 2025). As New Zealand shares more recent taxa with other continents, including South America, long-distance dispersal between continents must have occurred. This dispersal was attributed to winds, with stoneflies carried as aerial plankton by the Antarctic Circumpolar Current, or West Wind Drift, circulating Antarctica (García-Girón *et al.* 2024; McCulloch *et al.* 2016).

Stoneflies seem to remain close to their natal rivers, with more than 90% of adults from species where this has been tested (belonging to five families: Notonemouridae, Leuctridae, Chloroperlidae, Peltoperlidae and Perlodidae) remaining within 100 m of their source rivers (Briers *et al.* 2002; Griffith *et al.* 1998; Petersen *et al.* 1999; Rahman *et al.* 2021; Winterbourn 2005). Longitudinal flights upstream may compensate for downstream drift and allow stoneflies to move between tributaries and headwaters of the same river system, but this seems to occur only in some species (Rahman *et al.* 2021; Wagner 2003) that also remain close to the river's edge (Rahman *et al.* 2021). Lateral dispersal between rivers and the colonization of novel systems is therefore probably rare (Briers *et al.* 2002; Griffith *et al.* 1998). Additionally, while increases in wing length have been positively correlated with range size and dispersal ability in stoneflies (Malmqvist 2000; McCulloch *et al.* 2017), this same trait may hamper the ability of stoneflies to cross ecological barriers. DeWalt & South (2015) found that larger stoneflies (>14 mm) were unable to cross 22–70 km of Lake Superior to Isle Royale National Park, perhaps due to increased drag preventing dispersal by wind. Furthermore, most stoneflies fly in short bursts (Hynes 1977) and often remain at ground level or in flight corridors over the river, rather than migrating vertically into the canopy (Bowman & Smith 2021; Wagner 2003). This limits the potential for them to be accidentally caught by winds, and strong winds above the treeline have been correlated with the loss of wings in Plecoptera (McCulloch *et al.* 2019). Considering these limitations, dispersal as aerial plankton across continents is unlikely.

Long-distance dispersal between continents may instead have been facilitated by rafting, with stoneflies

carried across the ocean by wind-driven currents and surface winds. This route seems more likely than flight for the Plecoptera, and has been proposed for the 800 km marine dispersal of flightless insects from New Zealand to the Chatham Islands (Trewick 2000). A third possibility is that stonefly eggs are passively dispersed by migrating birds, either on their feathers and feet (epizoochory; Green *et al.* 2023) or in their intestines (endozoochory; cf. Green & Sánchez 2006; Sánchez *et al.* 2007; Hawse 2009; Suetsugu *et al.* 2018, 2023). Either way, Notonemouridae were estimated to have arisen recently (110, 76, or 71 Ma), suggesting that their distribution across the Southern Hemisphere is attributed to some form of long-distance dispersal. The dates recovered for the Northern Hemisphere taxa are largely congruent with those of Letsch *et al.* (2021) and the summary presented by Zwick (2000). The dispersals of Perlidae into South America and Africa were not investigated.

The pronounced differences in these interpretations indicate that the biogeographic history of the Plecoptera remains unclear. While patterns in the Northern Hemisphere after the rifting of Pangea are generally congruent between studies, the processes that led to the divergence of the suborders, the modern distribution patterns of Antarctoperlaria, and the dispersal of Notonemouridae and Perlidae into the Southern Hemisphere remain unresolved.

The fossil record of Plecoptera represents the best source of evidence to resolve these contradictions and improve the dating estimates of some of these processes. Fossils provide the only primary source of evidence of ancient distributions, evolutionary times and evolutionary changes in phenotypes including transitionary forms and extinct groups (Mongiardino Koch *et al.* 2021; Prevec *et al.* 2022; Raff 2007). Fossil data significantly improve phylogenetic and biogeographical analyses, even when they are marred by large gaps or incomplete sampling (Crisp *et al.* 2011; Louca & Pennell 2020; Mongiardino Koch *et al.* 2021; Puttick 2016; Raff 2007; Silvestro *et al.* 2016; Slater *et al.* 2012). Within time-calibrated phylogenies, fossil data can constrain divergence times (Cai *et al.* 2022; Mongiardino Koch *et al.* 2021; Raff 2007), ground-truth widely different biogeographical interpretations (Louca & Pennell 2020; Prevec *et al.* 2022; Raff 2007), and significantly improve the resolution and biogeographical understanding of ancient and diverse groups (Cai *et al.* 2022). Despite these advantages, fossil data must be carefully selected and constrained, as inaccurate taxonomy, age estimates or expected prior probabilities of calibration points can all alter results, leading to inaccurate or inconsistent dating estimates (Heads 2005; Klopfstein 2021; Parham *et al.* 2012; Wolfe *et al.* 2016). Crucially, fossils provide only a minimum age for divergence events, and may represent clades that are much older (Klopfstein 2021; Mongiardino Koch *et al.* 2021).

At first glance, applying the fossil record of the Plecoptera to these biogeographical questions should be straightforward. The fossil record is rich, with 322 species and 1742 specimens (Jouault *et al.* 2022b) described from the Carboniferous (Béthoux *et al.* 2011; Schubnel *et al.* 2019) to Holocene (Sinitshenkova 1987). Additionally, at least one fossil species is attributed to 13 of the 17 extant families (DeWalt *et al.* 2025; Uhen *et al.* 2023). Unfortunately, the assignment of many plecopteran fossils, and their relationships to extant taxa, are unreliable (Cui *et al.* 2019; Jouault *et al.* 2021; Zwick 2000). Many established apomorphic characters of extant stonefly clades and families involve internal anatomy, occur in only a single life stage, or are seldom visible in fossils (Jouault *et al.* 2021; Zwick 2000). Fossil stoneflies are therefore often classified based on wing venation, which can vary significantly, often even in a single species or individual specimen (Béthoux 2005; Cui *et al.* 2015; Jouault *et al.* 2021). Furthermore, many Plecopteran fossils are assigned to a different phylogenetic system than the extant representatives (Sinitshenkova 1987, 2002). While Sinitshenkova's proposed phylogeny broadly matches the extant groupings of Zwick (2000), which have been corroborated by molecular studies with only a few disparities (Ding *et al.* 2019; García-Girón *et al.* 2024; Letsch *et al.* 2021; McCulloch *et al.* 2016; South *et al.* 2021; Terry 2004), it differs significantly in topology (Fig. 3).

This uncertainty confounds any biogeographic interpretations of the fossil record and prevents the selection of reliable or consistent fossil calibration points for phylogenetic analyses. Indeed, calibration points have varied significantly between molecular studies. For example, the root of Plecoptera was constrained to 319.9 Ma by Letsch *et al.* (2021) and 167.41 Ma by García-Girón *et al.* (2024), an almost twofold difference. Differences in these calibration points can probably explain much of the variation recovered in the results and interpretations of these analyses. A review of the fossil record of Plecoptera is, therefore, urgently required, and calibration points for genetic analyses must be chosen conservatively from fossils with genuine (syn/aut)apomorphic characters. While a complete review of the Plecopteran fossil record is currently underway (Kirkaldy *et al. in prep*), all Systellognatha and austral fossils are reviewed here to provide reliable calibration points for a time-calibrated phylogeny of *Neoperla* in the Afrotropical region, which is currently in preparation (Kirkaldy 2025; Kirkaldy *et al. in prep*).

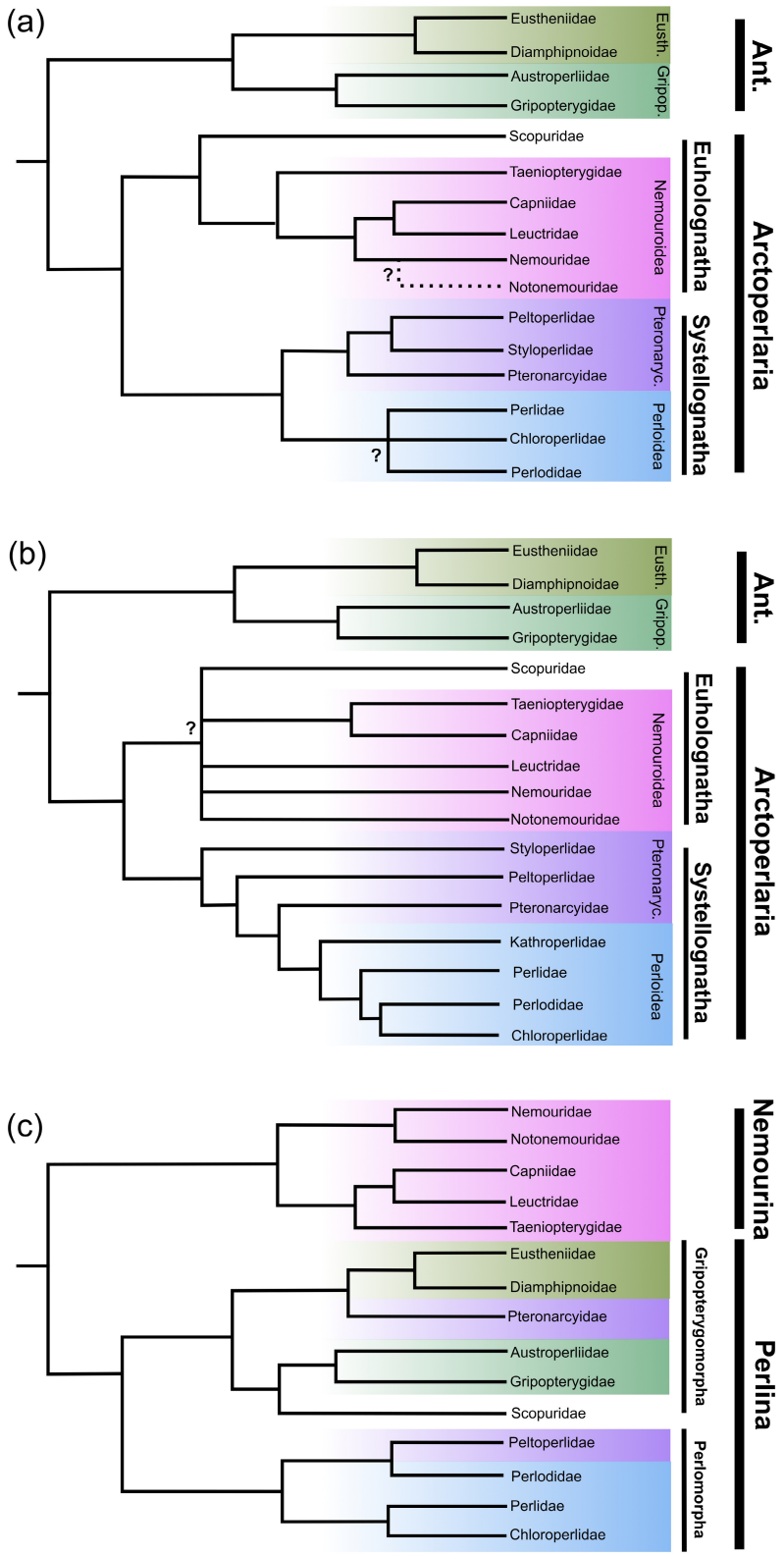

FIGURE 3. Cladograms showing hypothesized phylogenetic relationships in Plecoptera. (a) Based on the morphological review of Plecoptera by Zwick (2000) and supported by a phylogeny constructed by Ding *et al.* (2019) using Mitochondrial genomes. (b) Consensus cladogram based on phylogenies from Letsch *et al.* (2021), South *et al.* (2021) and Garcia-Giron *et al.* (2024). (c) Phylogeny of Plecoptera proposed by Sinitshenkova (1987, 2002), to which most fossil species are assigned. Sub-orders and infra-orders are represented by bars on the right of each phylogeny. Each coloured block represents the currently accepted superfamily assignment of each family. Eusth.: green, Eusthenioidea; Gripop.: sea green, Gripopterygoidea; Nemouroidea: pink, Nemouroidea; Pteronarcy.: purple, Pteronarcyoidea; Perloidea: blue, Perloidea.

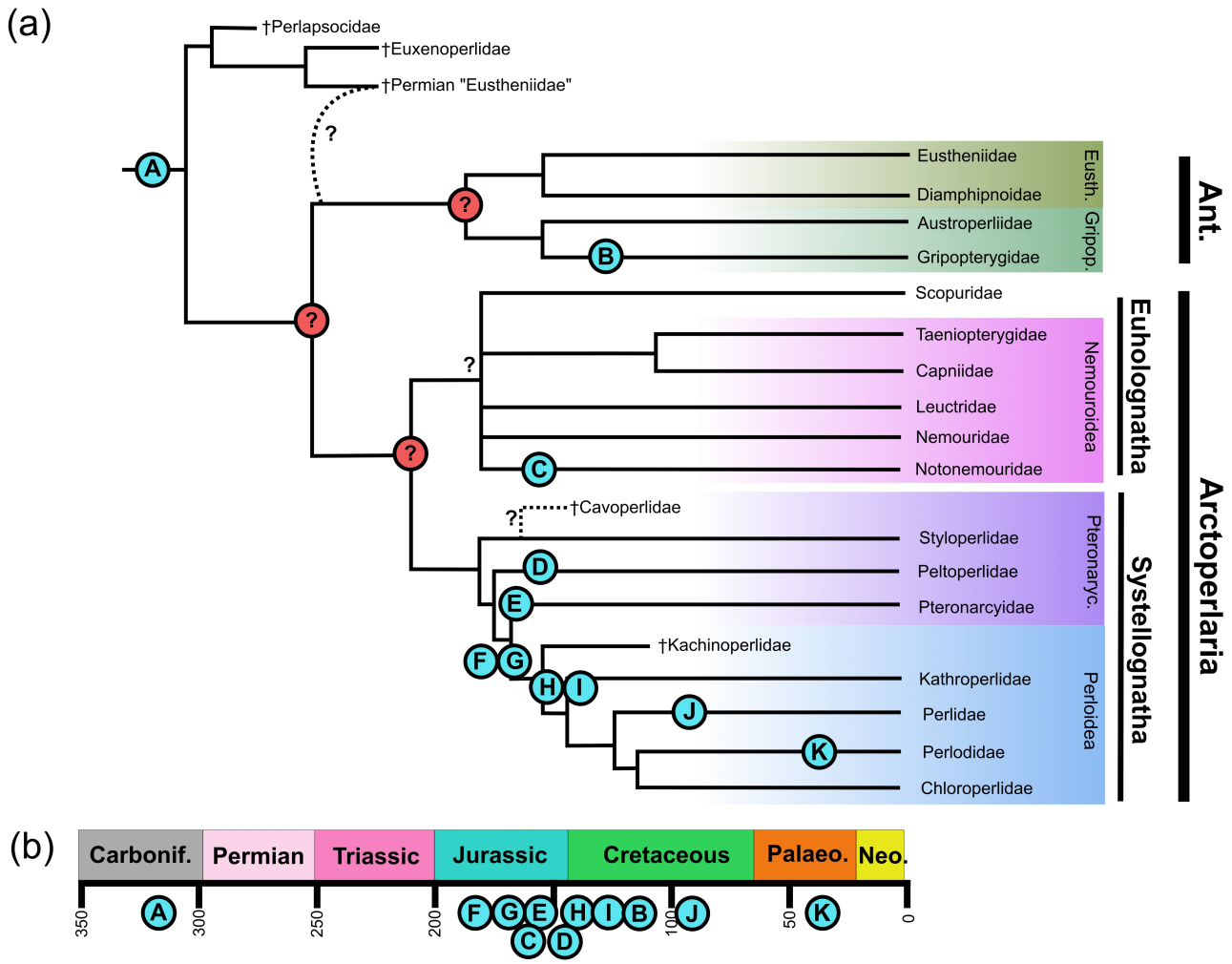

FIGURE 4. (a) Cladogram showing likely phylogenetic relationships of the fossil families reviewed here, mapped to the consensus phylogeny based on Letsch *et al.* (2021), South *et al.* (2021) and Garcia-Giron *et al*. (2024). Dotted lines represent the uncertain affinities of Southern Hemisphere Permian "Eustheniidae" to Antarctoperlaria, and †Cavoperlidae to Pternonarcyioidea, respectively. Fossil species that are recommended as calibration points for future phylogenetic studies are represented by letters in blue circles. (b) Time scale showing relative ages of key calibration points for the phylogeny of Systellognatha. Calibration points: A: First stem-Plecoptera: †*Gulou carpenteri* Béthoux *et al*. (314.6–311.45 Ma) & †*Gulou oudardi* Schubnel *et al.* (314.6–306.95 Ma). ?: Lack of clear fossil representatives of the earliest Antarctoperlaria and Arctoperlaria. B: First Gripopterygidae: †*Eodinotoperla duncanae* Jell & Duncan (122.46–112.6 Ma). C: First stem Notonemouridae: †*Talbragaria australis* Sroka & Prokop (157.3–145.0 Ma). D: First Peltoperlidae: †*Ecdyoperla fairlightensis* Sinitshenkova (145.5–140.2 Ma). E: First Pteronarcyidae: †*Pteroliriope sinitshenkovae* Cui *et al.* (164.7–155.7 Ma). F–I: First stem-Perloidea: F: †*Platyperla platypoda* Brauer *et al.* (183.0–155.7 Ma), G: †*Platyperla conferta* Sinitshenkova (171.6–164.7 Ma), H: †*Bestioperlisca inulta* Sinitshenkova (150.8–145.5 Ma), I: †*Trianguliperla quassa* Sinitshenkova (140.2–125.45 Ma). J: First Perlidae: Several species from Myanmar, e.g. †*Lagusoperla acus* Chen *et al.* & †*Electroneuria ronwoodi* Sroka *et al.* (99.7–94.3 Ma) K: First Perlodidae (& *Isoperla*): *Isoperla* †*baltica* Jouault *et al.* (37.2–33.9 Ma).

Methods

We examined possible relationships and affinities of individual Systellognathan and austral fossil species and critically assessed their relationships to extant Plecoptera. A separate review of the remaining Plecopteran fossil species is under way (Kirkaldy *et al. in prep*). Likely polyphylies in families and genera are discussed only when species are preserved with incongruent (syn/aut)apomorphic characters. Our results provide a set of reliable calibration points for future molecular and fossil phylogenetic analyses (Bell & Lloyd 2015; Parham *et al.* 2012; Wang *et al.* 2016) and highlight fossil families and genera whose systematic placement should be reassessed.

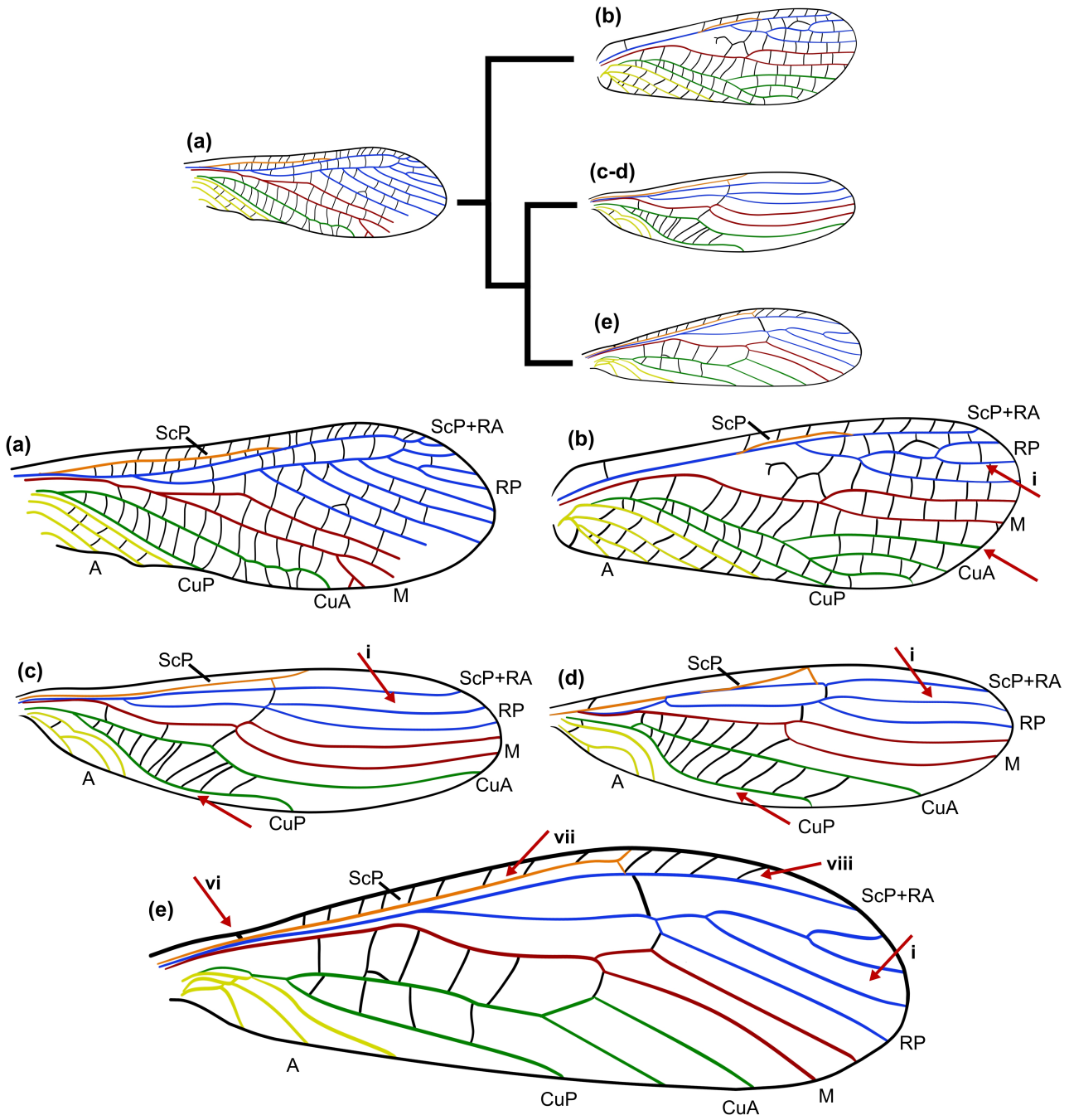

FIGURE 5. Differences in the forewing venation pattern of Plecoptera. Wing veins are as follows: Posterior Subcosta (ScP): orange, Anterior (RA) and Posterior (RP) Radius: blue, Media (M): red, Anterior (CuA) and Posterior (CuP) Cubitus: green, Analis (A): yellow. (a): Stem-Plecoptera: Gulouidae, *Gulou carpenteri* Béthoux *et al.* Diagram of wing modified from Figure 2H in Béthoux *et al.* (2011). (b) Antarctoperlaria: Eustheniidae, *Eusthenia costalis* Banks, showing the presence of crossveins in the (ScP +) RA–RP field (lost in Arctoperlaria, character i in Supplementary Table 3), and a distally terminating CuA (arrowed). (c) Arctoperlaria, Euholognatha: Notonemouridae, *Afronemoura amatolae* Balinsky, showing the loss of crossveins in the (ScP +) RA–RP field (arrowed, character i in Supplementary Table 3), and the CuP approaching the hind margin of the wing, before turning away and rejoining distally (arrowed). (d) Arctoperlaria, Euholognatha: Leuctidae, *Leuctra despaxi* Mosely, showing the same venation characters as Notonemouridae. (e) Arctoperlaria, Systellognatha: Perlidae, *Neoperla burgeoni* Navás, showing the short, obliquely opposed first crossvein between ScP and anterior margin (arrowed, character vi in Supplementary Table 3), the narrow area between ScP and the anterior margin (arrowed, character vii in Supplementary Table 3), numerous crossveins in the costal field (arrowed, character viii in Supplementary Table 3), and the absence of crossveins in the (ScP +) Ra–RP field (character i in Supplementary Table 3).

A complete species list of fossil Plecoptera was synthesised from the Palaeobiology Database (Uhen *et al.* 2023), EDNA fossil insect database (Mitchell 2013) and the Plecoptera Species File (DeWalt *et al.* 2025). Original descriptions and published figures were examined to assess the presence and absence (and availability) of diagnostic (syn/aut)apomorphic characters. Nineteen austral fossil species and 87 Systellognatha, or "Perlomorpha", from the Northern Hemisphere were reviewed. Some related fossil taxa from Euholognatha and "Gripopterygomorpha" were considered when affinities were relevant. Assignments to suborder, superfamily, and extant families proposed here are based on previously published phylogenetic reviews (Cui *et al.* 2015; Sivec *et al.* 1988; Uchida & Isobe 1989; Zwick 2000). All date ranges for species were obtained from the Palaeobiology Database (Uhen *et al.* 2023), which follow the 2023 estimates provided by the International Commission on Stratigraphy (www.stratigraphy.org).

Recommended calibration points were selected only from specimens that clearly had multiple, reliable, derived character states supporting their assignment. Taxonomic terminology follows Klopfstein (2021), and wing vein definitions and abbreviations (explained in Fig. 5) follow Béthoux (2005).

A comprehensive taxonomic review of fossilised Plecoptera is beyond the scope of this study. Many extinct families and genera are supported by purely morphometric conditions such as body proportions (Sinitshenkova 1987; Zwick 2000) and may be para- or polyphyletic. With few exceptions, we did not assess the monophyly of extinct families and genera, nor are the diagnoses of these families and genera reviewed here. For this reason, no formal systematic changes are proposed, and this work is explicitly disclaimed as a nomenclatural revision in terms of Article 8.2 of the International Code of Zoological Nomenclature (ICZN 2000).

Results

In total, 117 fossilized species (including some Euholognatha and "Gripopterygomorpha") were identified. The descriptions of 113 of these species were reviewed, and we recommend the reclassification of 63 species (Supplementary Tables 1–3; Fig. 4).

3.1. Austral fossils

Although only 19 species of fossil Plecoptera are reported from the Southern Hemisphere, they are currently assigned to at least eight families and 11 genera (Supplementary Table 1). Four of these families are extinct: †Euxenoperlidae Sinitshenkova, †Perlapsocidae Pinto and Piñeiro, †Palaeonemouridae Sinitshenkova and †Platyperlidae Sinitshenkova. Four more are extant: Eustheniidae Banks, Notonemouridae, Gripopterygidae Enderlein and Austroperlidae Tillyard. A single genus, †*Afroperla* van Dijk & Geertsema, is unplaced.

3.1.1. *Incertae sedis*

†*Afroperla* is known from only a single Permian species, †*A. permiana* van Dijk & Geertseema. This genus was not assigned to a family, although similarities to †Palaeonemouridae, a widespread family from Russia, Kazakhstan and Antarctica (Sinitshenkova 1987) were noted (Van Dijk & Geertsema 2004). Possible affiliations of †Palaeonemouridae are discussed below. This species is known from only a single forewing that has no preserved apomorphies to support its assignment anywhere within crown-Plecoptera. Assignment to stem-Plecoptera is supported by an anterior Cubitus (CuA) with three distal branches, an anterior Radius (RA)—posterior Radius (RP) crossvein, and a Media (M) with two branches (Béthoux 2005; Béthoux *et al.* 2011, Van Dijk & Geertsema 2004).

Several specimens of likely Plecoptera have been collected from the Middle Permian, dated 272–265 Ma (Prevec *et al.* 2022). These species are currently undescribed, but an assignment to stem-Plecoptera was proposed (Prevec *et al.* 2022).

3.1.2. †Euxenoperlidae

†Euxenoperlidae is represented in South Africa by five species from two genera, †*Euxenoperla* Riek and †*Euxenoperlella* Riek, described from the Upper Permian-Upper Triassic (Riek 1973, 1976a; b). Some additional †*Euxenoperla* are not assigned to any species owing to poor preservation of the main veins (Riek 1976b). Two additional genera, †*Argentinoperlidium* Martins Neto & Gallego (1 sp.) and †*Gondwanoperlidium* Pinto & Purper (4 spp.), are known from Argentina and Australia during the same period (Martins-Neto *et al.* 2003; Pinto & Purper 1978; Riek 1956). †Euxenoperlidae was originally placed, with some uncertainty, as a subfamily of the extant Antarctoperlarian Gripopterygidae based on similarities in wing venation (Riek 1973) but later shifted to its own family within Gripopterygoidea in "Gripopterygomorpha" (a polyphyletic assemblage roughly equivalent to Antarctoperlaria, but including Pteronarcyidae and Scopuridae) by Sinitshenkova (1987). This shift was made as the wing venation characters used by Riek (1976b) to diagnose the subfamily, such as a distinctly upturned R, a reduction in crossveins and widely separated posterior (CuP) and anterior (CuA) Cubitus, were not shared with any other "Gripopterygomorpha" families or genera (Sinitshenkova 1987).

Monophyly of Antarctoperlaria is supported by a modified sternal depressor muscle in the fore-trochanter, while Gripopterygoidea is supported by internal genital characters, namely a large accessory gland in males and the loss of the seminal vesicle in females (Zwick 2000). †Euxenoperlidae has been described from wings only (Martins-Neto *et al.* 2003; Pinto & Purper 1978; Riek 1973, 1976a; b), so none of these characters can be assessed in any Euxenoperlid specimens.

The wing venation characters that Riek (1973) used to place the family, namely widely separated CuP and CuA veins, and a reduction in crossveins, are unconvincing. While the CuP and CuA veins are widely spread, it is not to the degree commonly seen in extant Antarctoperlaria, and the distance between the two is comparable to that of the stem-Plecopteran †*Gulou carpenteri* Bethoux *et al.* Similarly, a reduction in crossvenation is common to many Plecoptera (Béthoux 2005; Béthoux *et al.* 2011), and may be a homoplasy correlated with body size and wing loading (Combes & Daniel 2003; Wootton 1981, 1990). Carpenter (1992) suggested there was insufficient evidence to support the familial placement of any of the included species, and Grimaldi & Engel (2005) placed the family in stem-Plecoptera as sister to Antarctoperlaria.

Considering the lack of substantive evidence to resolve the relationships of †Euxenoperlidae, the family should be considered stem-Plecoptera (Fig. 4).

3.1.3. †Perlapsocidae

The placement of the †Perlapsocidae even within Plecoptera is uncertain (Pinto *et al.* 2000). Wing venation (M with two branches, CuA with more than three branches) provides evidence for its placement in the stem-Plecoptera.

3.1.4. †Palaeonemouridae

†Palaeonemouridae, a large Permian family, is represented in the Southern Hemisphere by a single nymph from Antarctica, †*Ohionympha schopfi* Carpenter. Nymphs are placed in this family based on morphometric characters such as proportions of the wing pads, legs, abdominal segments and pronotum (Sinitshenkova 1987).

Sinitshenkova places this family within "Nemourina" (equivalent to Nemouroidea Billberg), based on the lack of crossveins in the distal region of the wing (Fig. 5) and long first and third tarsomeres, compared to subequal, moderately long or shortened first two tarsomeres in Antarctoperlaria and Systellognatha (Nelson 2009; Sinitshenkova 1987). Both characters are derived, as they differ from the stem-group species †*G. carpenteri* (Béthoux *et al.* 2011), and are regularly used in keys (see for example: Zwick 2004, DeWalt & Resh 2015, Fenoglio *et al.* 2021). A long first tarsomere is a synapomorphy of most Nemouroidea (Nelson 2009), but can be inconsistent for identification; Gripopterygidae also regularly have long first tarsomeres (McLellan & Zwick 2007; Nelson 2009; Sinitshenkova 1987), and all three are the same length in Taeniopterygidae Klapalek (Fenoglio *et al.* 2021).

The combination of wing venation and tarsomere length provides at least circumstantial evidence that †Palaeonemouridae are stem-Euholognatha. However, the assignment of †*O. schopfi* to this family, or even stem

Euholognatha, is unsupported as the fossilised nymph lacks wing venation and preserved tarsi, or association with an adult.

3.1.5. †Platyperlidae (part)

Sinitshenkova (1987, 2002) and Grimali & Engel (2005) both consider †Platyperlidae, a predominantly Jurassic family (ages between 201.6–130.0 Ma), as a stem representative of Systellognatha. This family is known only from nymphs that inhabited montane lakes (Gallego *et al.* 2011; Sinitshenkova 1985, 1987, 2002). Their placement is well supported; some species have a short first tarsomere (Brauer *et al.* 1889; Gallego *et al.* 2011; Sinitshenkova 1985, 1987), and at least the nymphs of †*Platyperla platypoda* Brauer *et al.* and †*Platyperla conferta* Sinitshenkova show adaptations to carnivory (Sinitshenkova 1982, 1985, 2002). As mentioned above, proportions of tarsomeres can be unreliable, but a short basal tarsomere may be a homoplasious apomorphy of Systellognatha and some Antarctoperlaria, and was present in some of the earliest representatives of the infraorder (Nelson 2009; Sroka *et al.* 2018). A short-to-moderately-long basal tarsomere was independently derived in Antarctoperlaria (Avelino-Capistrano *et al.* 2018; McLellan & Zwick 2007; Nelson 2009). However, as Antarctoperlaria (or at least its stem relatives) is speculated to have become limited to the Southern Hemisphere by the early–mid Jurassic (Ding *et al.* 2019; García-Girón *et al.* 2024; Illies 1965; Letsch *et al.* 2021; McCulloch *et al.* 2016; Zwick 2000), boreal †Platyperlidae are almost certainly Systellognathan.

Carnivory is an autapomorphy of the Perloidea (Perlodidae + Perlidae + Chloroperlidae + Kathroperlidae; Zwick 2000). The apparently omnivorous or carnivorous diet of some †Platyperlid species, inferred from their narrow, sharply-toothed mandibles and maxillae (Sinitshenkova 1982, 1985), therefore provides strong support for their placement within Perloidea. A possible omnivorous diet does not preclude this, as some species of extant Perloidea, in particular Perlodidae, show ontogenetic diet shifts from detritivory to omnivory or carnivory (Céréghino 2006; Feminella & Stewart 1986; Miyasaka & Genkai-Kato 2009; Tierno De Figueroa & López-Rodríguez 2019), or are omnivorous throughout their nymphal stages (Feminella & Stewart 1986). Amongst extant Perloidea, carnivorous †Platyperlids are most similar to Perlodidae, as they have long, clearly separated wing pads that may be secondarily derived in the family (Zwick 2000), and the thickened, lancet-like mandibles and maxillae are similar to some extant omnivorous Perlodidae such as *Isoperla namata* Frison (Feminella & Stewart 1986) and *Megarcys signata* Hagen (Stewart & Stark 1984). However, these features could represent transitional forms in the gradual development of carnivory in Perloidea. Some evidence for this transition is provided by the incomplete development of autapomorphies in †Platyperlidae, such as narrowed distal palpomeres while the basal palpomeres remain thick, and the molar region of the mandible reduced but remaining thickened basally (Sinitshenkova 1982). Therefore, while similarities to Perlodidae are certainly present, in the absence of further autapomorphies we recommend the more conservative assignment to stem-Perloidea, rather than to the crown group.

The placement of the only representative in the Southern Hemisphere, †*Platyperla marquati* Gallego *et al.* (235–221.5 Ma) within this lineage is doubtful because it is assigned to †Platyperlidae on the basis of expanded, flat femora, and its discovery in a fluvial-to-lacustrine deposit (Gallego *et al.* 2011). The tarsomeres were not preserved, and while a carnivorous lifestyle is suggested by chitin in the gut contents and short, transverse labrum, the head differs from the Perloidea, as the frons and clypeus are clearly divided by a suture in †*P. marquati*, instead of being fused (Zwick 2004). Carnivory is not limited to Systellognatha and occurs in some Antarctoperlaria such as Eustheniidae (Zwick 2000). In addition, †*P. marquati* shows a significant reduction in the size of its wing pads, a state shared with †*Platypoda caudiculata* Sinitshenkova. However, wing reductions are common across Plecoptera, including Antarctoperlaria, and have evolved independently multiple times (McCulloch *et al.* 2019, 2022). This suggests a greater affinity of this species with the stem group of Antarctoperlaria than with Systellognatha, but a firm conclusion is not possible without any autapomorphies of this suborder or its component superfamilies. It is also possible that †*P. marquati* belongs to †Euxenoperlidae, which was present across the Southern Hemisphere concurrently, but the nymphal stage of that family has not yet been described.

3.1.6. Eustheniidae

Eustheniidae fossils are known from the Southern Hemisphere by two genera, †*Stenoperlidium* Tillyard and †*Mesontoperla* Riek. These placements were supported by similarities in the wing and nymph of †*Stenoperlidium* to the extant *Stenoperla* McLachlan (Tillyard 1935), and the presence of many crossveins throughout the wing in †*Mesontoperla* (Riek 1954). The assignment of both ancient genera (Permian and Triassic, respectively) to an extant family was considered uncertain by the authors, and is still questioned (Aristov *et al.* 2013; Carpenter 1992; Grimaldi & Engel 2005; Riek 1954; Tillyard 1935). Interestingly, Eustheniidae is one of the few families with an autapomorphy in the wing: the posterior margin of the hind wing is smoothly rounded, without a notch separating the anal fan from the remigium (Zwick 1979, 2000). Unfortunately, the hind wing is not preserved, or this character is not visible, in all fossil representatives of this family including the Northern Hemisphere †*Boreoperlidium* Sinitshenkova (Aristov *et al.* 2013; Riek 1954; Sinitshenkova 2018; Tillyard 1935). Extensive crossvenation is plesiomorphic (Fig. 5) to the order (Béthoux *et al.* 2011) and the character state "CuA reaching wing margin in three branches", suggested by Aristov *et al.* (2013), cannot be accepted as synapomorphic because it differs in many extant representatives of the family (Tillyard 1935). Furthermore, all †*Boreoperlidium* fossils have very few or no crossveins in the (ScP+) RA–RP field (Aristov *et al.* 2013; Sinitshenkova 2018). The loss of crossveins in this field is an autapomorphy of Arctoperlaria (Cui *et al.* 2015), making the assignment to Eustheniidae highly unlikely. Instead, a narrow space between the ScP and anterior margin of the wing, and many crossveins in the basal region of the costal field both support an assignment to stem-Systellognatha (Cui *et al.* 2015). As such, there is no evidence to support the placement of any of these genera in Eustheniidae.

Nevertheless, the wings of †*Stenoperlidium* and †*Mesontoperla* are similar to those of extant Eustheniidae. The distal half of the wing has extensive crossvenation, including in the RP field. In †*Mesontoperla*, the poorly preserved CuA appears to join the wing margin distally. These are both potentially homoplasious characters, but nevertheless provide some evidence for the placement of these genera among stem-Antarctoperlaria. The same cannot be said for †*Boreoperlidium*, in which neither is present. Tillyard (1935) described the nymph of †*Stenoperlidium* with simple abdominal gills. These gills are not clear in the published photograph, and the validity of this character cannot be assessed. If these gills are indeed present, they are an autapomorphy of Eusthenioidea (Avelino-Capistrano *et al.* 2018; Zwick 2000).

3.1.7. Notonemouridae

The first fossil of a putative Notonemouridae in the Southern Hemisphere is †*Talbragaria australis* Sroka & Prokop. This family lacks accepted apomorphies, and until recently, its monophyly was considered uncertain (Cui *et al.* 2019; McLellan 1972, 1991; Sroka & Prokop 2023; Zwick 2000, 2006). Cui *et al.* (2019) erected the Northern Hemisphere family †Paranotonemouridae Cui & Béthoux as a stem sister to Notonemouridae based on wing venation. The characteristic "Nemourid X" wing vein pattern, which is present in some Notonemouridae and in its putative sister, Nemouridae, is also shared with this family. This is plesiomorphic; it is the remains of an ancient crossvein condition (Zwick 2000), and is present in other Euholognatha. Cui *et al.* (2019) separated the Notonemouridae lineage from Nemouridae by the shape of the CuP vein, which approaches the wing margin, diverges, and rejoins distally in Notonemouridae. While this shape does differ between the families, a similar pattern is present in at least some Leuctridae (e.g., Fig. 5, A. Kirkaldy pers. obs., Fig. 7 *in* Béthoux 2005). As the sister relationship of Notonemouridae and Nemouridae is uncertain (García-Girón *et al.* 2024; Letsch *et al.* 2021; McCulloch *et al.* 2016), this vein pattern may be the remnants of a plesiomorphic condition, an independently derived homoplasy, or a synapomorphy of these two families. Therefore, the assignment of †Paranotonemouridae to stem-Notonemouridae must remain uncertain. Sroka & Prokop (2023) used the same characters to assign †*T. australis* to Notonemouridae. In this case, the above characters are synapomorphies of members within Euholognatha. As Notonemouridae is the only Euholognathan family in the Southern Hemisphere, it is most likely that this fossil represents at least a stem relative of the Notonemouridae.

3.1.8. Gripopterygidae and Austroperlidae

†*Eodinotoperla duncanae* Jell & Duncan clearly belongs to Gripopterygidae (Jell 2004; Jell & Duncan 1986), as evidenced by the autapomorphic anal rosette of fine gills (Zwick 2000).

A possible Austroperlid fossil species from the Early Miocene was discovered, but remains undescribed (Kaulfuss *et al.* 2015; Lee *et al.* 2016).

3.2. Stem-Systellognatha

Systellognatha, or "Perlomorpha", fossils are relatively common, with 93 species from 49 genera and 11 families found predominantly in the Northern Hemisphere (Supplementary Tables 2 & 3). Currently, fossilised species are assigned to five of the seven extant families in Systellognatha, with only Styloperlidae and Kathroperlidae Banks not yet represented.

3.2.1. *Incertae sedis*

†*Sinosharaperla zhaoi* Liu *et al.* was originally placed within "Gripopterygomorpha", but was since moved to Systellognatha due to the lack of crossveins in the distal half of the posterior Subcosta (ScP) + R–RP area (autapomorphy: Arctoperlaria), an opposed, strong first vein between the anterior margin of the wing and ScP (autapomorphy: Systellognatha), and extensive branching of the CuA (autapomorphy: Systellognatha; Fig. 5; Cui *et al.* 2015). Further affinities within Systellognatha are uncertain (Cui *et al.* 2015; Sroka *et al.* 2018). "†A*rchaeoperla rarissimus"* Liu *et al.*, which was synonymized with †*S. zhaoi* (Cui *et al.* 2015; Sroka *et al.* 2018), was originally assigned to the tribe Neoperlini Enderlein as it had hemitergal lobes and a process on tergite 7 (Liu *et al.* 2008). This evidence is insufficient. Neoperlini is diagnosed by a sclerotized aedeagus base (Sivec *et al.* 1988; Zwick 2023; Zwick & Zwick 2023), which cannot be assessed in the fossil. While a process on T7 is an autapomorphy of *Neoperla*, this structure is unclear in †*S. zhaoi*. No other apomorphy of *Neoperla*, or its sister genera, is present. Modified hemitergal lobes with anteriorly upturned hooks are an autapomorphy of the subfamily Perlinae (Sivec *et al.* 1988; Zwick 2000, 2023). The hemitergal lobes in †*S. zhaoi* are not noticeably modified into upwardly turned hooks, precluding its inclusion in crown group Perlidae (Cui *et al.* 2015; Sroka *et al.* 2018).

A large number of fossil families and genera are currently placed in Sinitshenkova's "Perlomorpha" (Sinitshenkova 1987, 2002; Zwick 2000). While this roughly corresponds to Systellognatha, it is paraphyletic; Pteronarcyidae is excluded, and the inclusion of Peltoperlidae makes the Perloidea polyphyletic (Ding *et al.* 2019; García-Girón *et al.* 2024; Letsch *et al.* 2021; Zwick 2000). Sinitshenkova (1987) diagnosed this group using variable or plesiomorphic wing venation characters: rich wing venation in large forms, reduced wing venation in small forms, and a multibranched CuA. Wing venation is strongly linked to insect flight patterns and wing loading, as changes to the structure of main veins and the complexity of crossveins affect the support and flexibility of wings during flight (Wootton 1981, 1990). Larger insects tend to have stiffer wings, regardless of their phylogenetic position (Combes & Daniel 2003). This stiffness is often provided by increased crossvenation (Wootton 1990), suggesting that the richness of veins in "Perlomorpha" is a homoplasy related to body size, rather than an independently derived autapomorphy.

With few exceptions, recognized apomorphies of the Perloidea, Pteronarcyoidea and extant families are not preserved in "Perlomorpha" species, but most species do have a short basal tarsomere. As such, most of these fossils should be placed within stem-Systellognatha, as their relationships with the crown group are unresolved. This applies to †*Chloroperloides* Sinitshenkova, †*Perlisca* Sinitshenkova, †*Perlitodes* Sinitshenkova, and †*Savina* Sinitshenkova.

†*Bestioperlisca* shows clear adaptations to carnivory or omnivory, such as narrow, sharp-toothed mandibles, and sharpened, lancet-like galea and lacinia, possibly supporting its assignment to the Perloidea (Sinitshenkova 1990). As discussed above, carnivory and the presence of long, clearly divided wingpads supports assignment to either stem-Perloidea or Perlodidae. In the absence of further synapomorphies, †*Bestioperlisca* should be assigned to the stem-Perloidea.

Sufficient evidence remains lacking to place these genera within Systellognatha: †*Berekia* Sinitshenkova, †*Perlomimus* Sinitshenkova, †*Pectinoperla* Sinitshenkova, †*Trianguliperla* Sinitshenkova (in part; exception below), and †*Tungussonympha* Sinitshenkova. Unfortunately, we were unable to obtain the original descriptions of †*Trianguliperla optanda* Sinitshenkova, †*Trianguliperla limosa* Sinitshenkova, †*Trianguliperla volucris* Sinitshenkova and †*Triassoperla yongrenensis* Lin for this review. As the character states could not be assessed, they are treated as Plecoptera *incertae sedis* here.

3.2.2. †Tshekardoperlidae and †Palaeoperlidae

The placements of †Tshekardoperlidae Sinitshenkova and †Palaeoperlidae Sharov are uncertain. While many of the component species are figured with a short basal tarsomere (Aristov *et al.* 2013; Sinitshenkova 1987, 2018), this is the only apomorphy present in both families. Wing venation in †Palaeoperlidae retained the plesiomorphic condition. As these families are much older than the other stem-Systellognatha discussed here (limited to the Permian vs. Jurassic and Cretaceous), it is safer to not assign these families to the crown group, although it is possible that they represent a very early stem-ancestor of Systellognatha.

3.2.3. †Platyperlidae (part)

The position of †Platyperlidae as stem-Systellognatha is discussed above. As several characteristics, such as tarsal proportions, vary between species, this family is likely polyphyletic.

†*Platyperla kingi* Ping is unlikely to be a member of Plecoptera. It is drawn with at least four tarsomeres instead of three and has tracheated, oval gills on the first eight abdominal segments (Ping 1935). This gill structure does not occur in any Plecoptera, and instead may suggest placement in Ephemeroptera (eight abdominal gills do not occur in Ephemeroptera either, but this may be an error in the description, as only seven are figured).

Only †*P. platypoda* and †*P. conferta* Sinitshenkova can be assigned with confidence to stem-Perloidea due to their sharply-toothed mandibles providing evidence of carnivory and a short basal tarsomere (Sinitshenkova 1982, 1985).

3.2.4. †Crossoperlidae

†Crossoperlidae Chen is known from a single species, †*Crossoperla teslenkoae* Chen (Chen 2025). Its placement within stem-Systellognatha is supported by a short first tarsomere, the presence of euplantulae, and a multibranched CuA (Chen 2025; Cui *et al.* 2016; Nelson 2009). A strongly shortened head, lacking an anterior ocellus and retracted into the pronotum, is either an autapomorphy of Peltoperlinae (Zwick 2000), or a synapomorphy shared with some †Petroperlinae (Chen *et al.* 2025). While the presence of some additional wing veins differs from extant Systellognatha (Chen *et al.* 2025), this may be a homoplasious adaptation to size-related wing loading and does not preclude placement within Peltoperlidae. Additionally, elongated basal cercomeres are an autapomorphy of male Peltoperlidae (Zwick 2000), and their absence in the female †*C. teslenkoae* does not prevent assignment to the family. Therefore, we propose that the monotypic †Crossoperlidae should be synonymized with Peltoperlidae.

3.3. Pteronarcyoidea

3.3.1. †Cavoperlidae

†*Cavoperla excavata* Chen forms the monotypic family †Cavoperlidae Chen and is considered sister to Styloperlidae due to similarities in wing venation, the loss of giant tibial spurs, and elongated basal cercomeres in the males (Chen 2023b). However, no autapomorphies of Styloperlidae are preserved, such as a dense setal brush on sternite nine in males, an X-shaped sclerotization of sternite ten, or modified tibial setae (Chen 2023b, Uchida & Isobe 1989, Zwick

2000). Contrarily, the laterally expanded arolium is an autapomorphy of Pteronarcyidae (Uchida & Isobe 1989; Zwick 2000), and elongated basal cercomeres is an autapomorphy of Peltoperlinae (Chen *et al.* 2025; Zwick 2000). However, as other apomorphies of all families within Pteronarcyoidea are not present in this species, its relationship to any of the extant families cannot be confidently resolved (Chen 2023b).

3.3.2. Pteronarcyidae

The monophyly of the superfamily Pteronarcyoidea has recently been contradicted by molecular data that place Pteronarcyidae as sister to Perloidea (Fig. 3c; García-Girón *et al.* 2024; Letsch *et al.* 2021). Pteronarcyidae is represented by a single fossil species, †*Pteroliriope sinitshenkovae* Cui *et al.* This species clearly belongs to Systellognatha as it shares most of the wing venation characters of †*S. zhaoi*, but differs in having extensive crossvenation throughout all wings (Cui *et al.* 2016). As discussed above, extensive crossvenation is present in the ground-plan of Plecoptera and Antarctoperlaria (Béthoux *et al.* 2011; Cui *et al.* 2015, 2016) and seems to have reappeared independently in several lines within Systellognatha, including Pteronarcyidae and Perlidae (Cui *et al.* 2016), possibly because it is correlated with greater body size and wing loading (Wootton 1981, 1990). †*Pteroliriope sinitshenkovae* is a large species (forewing length >30 mm), and it is possible that the increased wing venation is associated with large body size rather than phylogenetic affinities. Although no clear autapomorphies of Pteronarcyidae are preserved, close morphometric similarities with extant *Pteronarcys* Newman, and the presence of wing venation characters [M occasionally with more than two branches, numerous crossveins between M and CuA, crossveins between branches of Anterior Analis 2 (AA2)] seen only in Pteronarcyidae amongst Systellognatha provide convincing evidence for this placement (Cui *et al.* 2016).

3.3.3. Peltoperlidae

The fossilized Peltoperlidae are represented by ten species in nine genera (Chen 2023a; Chen *et al.* 2025; Chen & Wang 2020; Chen & Xu 2020, 2022; Sroka *et al.* 2018; Sroka & Staniczek 2020). The taxonomy of the adults was recently reviewed (Chen *et al.* 2025), and †Petroperlinae Sroka *et al.* was placed as a basal subfamily of Peltoperlidae, having previously been treated as a family with uncertain affinities in Systellognatha (Sroka *et al.* 2018; Sroka & Staniczek 2020). This placement was supported by a shortened basal tarsomere, the lack of a frontoclypeal suture, radial area of the wings with few cross veins, the head shortened and retracted into the prothorax (in some species), and the basal cercomeres partially fused or forming a long shaft (Chen *et al.* 2025). The first three of these characters are not diagnostic of Peltoperlidae, as they are all either plesiomorphic or synapomorphies shared with Perloidea and the remaining Systellognatha (Cui *et al.* 2015; Nelson 2009; Sroka *et al.* 2018; Zwick 2000). However, a shortened head and long basal cercomere (possibly due to fusion of the basal cercomeres; Chen *et al.* 2025) are both autapomorphies of Peltoperlinae (Uchida & Isobe 1989; Zwick 2000), providing evidence for the placement of most of the nine genera within Peltoperlidae, either as sister to, or in the stem group of Peltoperlinae. Assignment to crown-group Peltoperlinae is prevented by the presence of the anterior ocellus and tibial spurs, both of which are plesiomorphic (Chen *et al.* 2025). The head is not shortened and the basal cercomeres are incompletely fused instead of long or completely fused in *Graciloperla* Chen *et al.*, while the head of *Lapisperla* Sroka *et al.* is not preserved (Chen *et al.* 2025; Sroka *et al.* 2018). The placement of both genera should therefore be treated as uncertain, but is maintained here owing to the distally terminating RA, which is an autapomorphy of †Petroperlinae (Chen *et al.* 2025; Sroka *et al.* 2018; Sroka & Staniczek 2020).

In addition to the adult specimens, †*Siberiopelta bashkuevi* Sinitshenkova & Yan and †*Ecdyoperla fairlightensis* Sinitshenkova clearly belong to this family because of the autapomorphic "cockroach-like" body shape of the nymph (Sinitshenkova 1998; Sinitshenkova & Yan 2024; Uchida & Isobe 1989; Zwick 2000). Uncertainties regarding the number of ocelli and fusion of the basal cercomeres in †*E. fairlightensis* (Sinitshenkova 1998) do not necessarily contradict this assignment, as these are autapomorphies of the subfamily Peltoperlinae rather than the family as a whole (Zwick 2000).

3.4. Perloidea

3.4.1. *Incertae sedis*

†*Trianguliperla* is almost certainly polyphyletic. The genus is described from the Triassic-Late Cretaceous and varies significantly in morphology throughout that time (Sinitshenkova 1985, 1987, 1990). Apomorphies of Systellognatha are not preserved, except in †*Trianguliperla quassa* Sinitshenkova, which possibly belongs to the Perloidea. This species has a small basal tarsomere, sharply toothed lacinias, and long, slender palpi (Sinitshenkova 1987). The latter two states are established autapomorphies of Perloidea (Zwick 2000).

3.4.2. †Kachinoperlidae

Assignment of the monotypic family †Kachinoperlidae Chen to the stem-Perloidea is strongly supported by slender mandibles lacking a mola, long sharply-pointed lacinias, and slender palps (Chen 2022), which all suggest a predatory lifestyle. Subequal glossae and paraglossae prevent the inclusion of †Kachinoperlidae among any extant Perloidea families, but the lack of these synapomorphies does not preclude inclusion of the family amongst stem-Perloidea.

3.4.3. Chloroperlidae

Chloroperlidae fossils are known from nymphs of a single genus, †*Dipsoperla* Sinitshenkova, that was assigned to Chloroperlidae based on short wing pads (Sinitshenkova 1987); no other characteristic features of the family or its subfamilies (e.g., minute terminal palpomere, oval prothorax; Zwick 2000, 2006) were preserved. Mouthparts are not figured or described, and it is unclear whether the nymphs were carnivorous. Some morphometric similarity supports a close affiliation to Chloroperlidae, including cerci shorter than the abdomen and a slender body shape, but without more conclusive evidence, this genus must be placed in Systellognatha *incertae sedis*.

3.4.4. Perlodidae

Perlodidae fossils are known from two extinct Jurassic genera and two extant Palaeogene genera. Unfortunately, this family lacks established apomorphies and is generally supported by variable characters, such as colouration, that are not visible in many fossils (Zwick 2000). The nymph of †*Isoperlodes perstrictus* Sinitshenkova is incomplete, without the head or tip of the abdomen preserved. It was assigned to Perlodidae as the wingpads are elongated near the apex, which is similar to the condition of extant *Isoperla* Banks (Sinitshenkova 1992). This is not an autapomorphy of the family or genus. Nevertheless, †*I. perstrictus* is probably Systellognathan, as it has a short first tarsomere.

†*Derancheperla* Sinitshenkova clearly falls within Perloidea, supported by the presence of slender mandibles without a mola (suggesting a carnivorous lifestyle), and the loss of the frontoclypeal suture (Sinitshenkova 1990). The nymph shows strong similarities to the nymphs of both Perlidae and Perlodidae, but lacks any clear autapomorphies of either. This absence of apomorphies does not preclude a possible assignment to stem-Perlidae instead of stem-Perlodidae, and therefore this species can be placed confidently only within Perloidea. The presence of a notal contour between the wing pads, present in †*Derancheperla*, may be derived in Perlodidae. The wing pads are instead rounded and meet medially in Perlidae and Chloroperlidae (Zwick 2000), a trait that appears to have been secondarily lost in the Perlodidae.

The type specimens of *Isoperla* †*succinica* Hagen and *Perlodes* †*resinatus* Hagen have been lost (Caruso & Wichard 2010; Jouault *et al.* 2021). As the original descriptions are vague, we follow Jouault *et al.* (2021) in treating their placement as uncertain and exclude them from this review.

The assignment of *Isoperla* †*baltica* Jouault *et al.* is relatively well supported. While it is assigned to the Perlodidae predominantly on the absence of any apomorphies of other families, it can be placed within Isoperlinae based on paraprocts modified into simple upcurved hooks, and specifically in *Isoperla* based on wing venation

(e.g., lack of cubital crossveins in the hindwing) (Jouault *et al.* 2021). *Isoperla* †*baltica* also shares the longitudinal thoracic stripe commonly seen in Perlodidae (Zwick 2000).

3.4.5. Perlidae

Perlidae is well represented in the fossil record, with 23 species from 11 genera known. Of these, eight genera and 19 species are preserved in Baltic amber from Myanmar. The placements of †*Pinguisoperla* Chen, †*Burmacroneuria* Chen and †*Starkoperla* Chen & Wang in Perlidae are likely, but somewhat uncertain. Their placements are supported by a short first tarsomere, numerous crossveins in the basal region of the costal field (plesiomorphy: Systellognatha), tarsal euplantulae (plesiomorphy: Systellognatha), occasionally an abdominal hammer (synapomorphy within Arctoperlaria, secondarily lost in some families; homoplasious apomorphy: Acroneuriinae), slender palpi (autapomorphy: Perloidea), and similar wing venation to †*S. zhaoi* (autapomorphy: Perloidea) (Chen 2018d, 2019b; Chen & Wang 2020). As most established apomorphies of Perlidae are internal, or visible only in nymphs (Zwick 2000), assignment to the family must be considered uncertain.

Acroneuriinae has been recovered as either para- or polyphyletic in all recent molecular analyses (García-Girón *et al.* 2024; Letsch *et al.* 2021; South *et al.* 2021; Xiang *et al.* 2021). The monophyly of the subfamily is therefore not established, and it may instead represent a grade of multiple, independent basal clades of Perlidae. Some further evidence of this is seen in the fossil record, as the autapomorphies and synapomorphies of Acroneuriinae are present in the earliest Perlidae fossils (see below), suggesting these may instead represent plesiomorphies of the family that were later lost in Perlinae. Comparatively, Perlinae has generally been recovered nestled within Acroneuriinae, although topology within the subfamily has differed significantly between analyses (García-Girón *et al.* 2024; Letsch *et al.* 2021; South *et al.* 2021; Xiang *et al.* 2021). Considering the uncertainty surrounding relationships within Perlidae, we recommend assignment of the following fossils only to the family.

The remaining Burmese fossil genera [†*Burmaperla* Jouault & Nel (1 sp.), †*Electroneuria* Sroka *et al.* (1 sp.), †*Cretacroneuria* Chen (1 sp), †*Burmesoperla* Chen (1 sp.) and †*Largusoperla* Chen (13 spp.), including adults and a single nymph] can all confidently be assigned to Perlidae. These assignments are supported by the presence in adults of a hammer on the abdomen (Synapomorphy: Arctoperlaria, excludes membership of Perlinae) and paraprocts altered into anteriorly curved hooks (autapomorphy: Acroneuriinae / plesiomorphy: Perlidae), and in nymphs of an occipital row of short spinules (autapomorphy: Perlidae), incomplete laterally (autapomorphy: Acroneuriinae / plesiomorphy: Perlidae) (Chen 2018c, b; a, 2019a, 2020; Chen *et al.* 2018; Chen & Tierno de Figueroa 2025; Chen & Wang 2019; Jouault *et al.* 2022a; Sroka *et al.* 2018).

†*Euperlida parvicercifera* Cifuentes-Ruiz can be assigned to Perlidae due to the tufted thoracic and anal gills visible in the impression fossil (Cifuentes-Ruiz *et al.* 2007).

†*Dominiperla antigua* Stark & Lentz is represented by a female specimen, thus preventing assessment of the male autapomorphies in relation to other species. However, the similarity of the specimen's eggs to extant *Acroneuria* Pictet supports the placement of the species within Perlidae (Stark & Lentz 1992).

Perla †*prisca* Pictet belongs to the Perlinae and can be placed within the (*Perla* + (*Eoperla* + *Dinocras*)) clade due to its interrupted tergum 9 (Carpenter 1992; Pictet & Hagen 1856; Sivec *et al.* 1988). However, affinities with any of these genera cannot be confirmed.

The description of a fossilised representative of the extant *Perla burmeisteriana* Claassen was unavailable for this review and is therefore not evaluated.

Discussion

These findings strongly agree with previous opinions (Cui *et al.* 2015, 2019; Jouault *et al.* 2021; Zwick 2000) that the classifications and assumed phylogenetic relationships of many Plecoptera fossils are ill-supported. We recommend the reclassification of 63 species (56%) of the 113 fossilised species reviewed (including some Euholognatha and "Gripopterygomorpha"). Some of these shifts utterly alter the phylogenetic significance of these species. For example, †*Boreoperlidium* is currently assigned to extant Eustheniidae (Aristov *et al.* 2013; Sinitshenkova 2018) and is reclassified here as a stem-Plecopteran, while †*P. kingi* is moved from stem-Systellognatha to Ephemeroptera.

These significant shifts are not unprecedented, as †*S. zhaoi* was previously moved from "Gripopterygomorpha" to Systellognatha (Cui *et al.* 2015).

We were cautious and assigned species only when several (syn/aut)apomorphies, or multiple lines of character evidence, were present. The sharing of plesiomorphic character states is insufficient to place exemplars in a crown group. Some genuine representatives of extant families and clades may, therefore, have been excluded through lack of preserved evidence. This is particularly true of several Perloidea species *incertae sedis*, where definitive morphological similarities to extant families are present, but equivocal (Chen 2018d; Chen & Wang 2020; Sinitshenkova 1987, 1990, 1992). Because incorrectly interpreted fossils can significantly alter the results of fossil-calibrated phylogenies (Heads 2005; Parham *et al.* 2012), we recommend that only fossil species with uncontested (syn/aut)apomorphies preserved are used for the calibration and interpretation of these analyses (Crisp *et al.* 2011; Heads 2005; Klopfstein 2021; Parham *et al.* 2012; Wang *et al.* 2016; Wolfe *et al.* 2016).

Our results are congruent with the summary of the fossil record presented by Jouault *et al.* (2022b). The Paleozoic Era is dominated by stem-Plecoptera or dubiously-stem representatives of the Arctoperlaria and Antarctoperlaria. Throughout the Mesozoic, the first clear representatives of the crown-group Plecoptera began to appear. This started with stem-Systellognatha and stem-Perloidea in the mid-Jurassic, and was followed by stem representatives of extant families in the mid-Jurassic and early-Cretaceous. Finally, extant genera and families arose during the Cenozoic Era. The Systellognatha fossil record suffers from the same gaps seen across the Plecopteran fossil record in general, with very few species preserved from the Early Cretaceous or the Late Cretaceous-Oligocene (Jouault *et al.* 2022b). Both of these gaps are problematic, as they seem to coincide with the early diversification of the extant stonefly families and genera, respectively (Jouault *et al.* 2022b). In the Southern Hemisphere, only two post-Triassic fossils are known: a stem-Notonemourid from the Jurassic (Sroka & Prokop 2023), and a Gripopterygid from the Cretaceous (Jell 2004; Jell & Duncan 1986).

4.1. Divergence of Antarctoperlaria and Arctoperlaria

None of the fossils reviewed here can be assigned to stem-Antarctoperlaria or stem-Arctoperlaria with confidence (Fig. 4). While some early fossils from the Permian and Triassic do show some morphological affinities to these suborders (e.g., †*Stenoperlidium* and †*Mesonotoperla* to Antarctoperlaria), these relationships are tenuous. This uncertainty prevents drawing any direct conclusions on the origin of these suborders.

As the first definitive Systellognatha, Perloidea and Pteronarcyoidea appeared during the mid-Jurassic (see below), both suborders must have originated prior to this. It is possible that this divergence was caused by the rifting of Pangea, followed by a period of relatively rapid diversification giving rise to the Euholognatha and Systellognatha (Fig. 1c, 5c). This scenario was partially corroborated by a recent analysis of the drivers of diversification in Plecoptera, in which the timing of continental fragmentation was positively correlated with lineage origination (Jouault *et al.* 2022b). However, this analysis also revealed stable origination, extinction and net-diversification rates throughout the Jurassic (Jouault *et al.* 2022b). Zwick (2000) suggested that an ancient origin of extant families so soon after the rifting of Pangea would leave insufficient time for the formation of the suborders via the breakup of Pangea.

These early Systellognatha fossils could also point to an ancient origin of the suborders on Pangea, supporting either reciprocal extinctions in each hemisphere (Fig. 1b; Zwick 2000), or dispersal of one suborder, followed by a localized extinction, from either the Northern (Fig. 2a; Letsch *et al.* 2021) or Southern Hemisphere (Fig. 1a; Illies 1965). Both scenarios have some support from fossils assigned to Northern "Gripopterygomorpha" and Southern "Perlomorpha" and "Nemourina" during the Permian–Jurassic (Aristov *et al.* 2013; Cui *et al.* 2015; Gallego *et al.* 2011; Liu *et al.* 2008; Sinitshenkova 2002, 2018). If these records were correctly interpreted, they provide evidence of both suborders sharing a distribution on Pangea. However, all of the species from these groups that we examined were instead assigned to either stem-Plecoptera or a different suborder. Although not discussed in detail here, none of the remaining "Gripopterygomorpha" in the Northern Hemisphere (Aristov *et al.* 2013; Sinitshenkova 1987, 1990, 1992, 2018) have convincing apomorphies of Antarctoperlaria, let alone the families within it. Jouault *et al.* (2022b) similarly did not find evidence to support either hypothesis.

Beyond the lack of palaeontological evidence, both hypotheses are biologically unlikely. They require the complete extinction of at least one suborder from across an entire hemisphere, with neither remnant lineages in the fossil record nor extant species. In the case of long-distance dispersal of one suborder, a further extinction of all

stem-Plecoptera in the receiving hemisphere is required. No mechanisms have been proposed for these asymmetrical hemisphere-wide extinctions, nor for the ability of the remaining suborder to survive such a widespread event. Competitive exclusion is unlikely, as the Arctoperlarian Notonemouridae coexists with Antarctoperlaria today. While Jouault *et al.* (2022b) found evidence of two major extinction events in Plecoptera during the Permian–Triassic crisis and the end of the Early Cretaceous, apparently correlated with the appearance of angiosperms; these extinctions do not align with either hypothesis. Therefore, divergence of a common stock of stem-Plecoptera after becoming isolated remains the most likely explanation for the origin of the suborders (Fig. 6).

If this divergence occurred on Pangea, the mechanisms proposed by Letsch *et al.* (2021) may have resulted in the isolation of each suborder in its respective hemisphere (Fig. 6). The earliest stoneflies are known from the equator of Pangea at the end of the Carboniferous, some 310 Ma (Béthoux *et al.* 2011, Schubnel *et al.* 2019). The transition to the Permian appears to have resulted in a diversification process for Plecoptera (Jouault *et al.* 2022b). A similar trend has occurred in many plants and animals (Condamine *et al.* 2020a; Montañez *et al.* 2007). This diversification was likely accompanied by significant range expansions, facilitated by several periods of cooling and increased rainfall throughout the transition to the Permian, despite a general warming trend (Jouault *et al.* 2022b; Montañez *et al.* 2007; Roscher & Schneider 2006). Increased orogeny and an abundance of glacial streams would have provided suitable habitats for these early stoneflies (Jouault *et al.* 2022b). This expansion is clear in the fossil record, and stem-Plecopteran species were globally distributed by at least the Middle Permian (Fig. 6a; Illies 1965; Letsch *et al.* 2021; Prevec *et al.* 2022; Sinitshenkova 1987; Zwick 2000).

Most Plecoptera are cold-adapted, occurring in cold, fast-flowing and oxygen-rich waters such as mountain streams (Fochetti & Tierno de Figueroa 2008; Hynes 1976), although diapause and adaptations to maximize oxygen absorption in warm waters (e.g., branched thoracic gills) have facilitated a significant radiation of stoneflies into warmer waters and intermittent streams (DeWalt *et al.* 2015). Nevertheless, aridification, particularly in the middle reaches of Pangea (Chaboureau *et al.* 2014; Péron *et al.* 2005; Roscher & Schneider 2006) and the Variscan orogeny (Kroner & Romer 2013; López-Gómez *et al.* 2021) throughout the Permian may have limited stoneflies to mid-to-high latitudes and prevented exchanges between the hemispheres (Fig. 6b). It is possible the Variscan Mountains instead acted as refuges for stem-Plecoptera at low latitudes, by providing colder habitats at high altitude. However, these mountains were generally hot and humid in the early Permian, becoming more arid into the late Permian and Triassic (López-Gómez *et al.* 2021; Péron *et al.* 2005), potentially limiting Plecopteran diversity. Nevertheless, by at least the late Triassic, Plecopteran species were present in this region, as †*Siberioperla angulata* Sinitshenkova (221.5–205.6 Ma), †*Berekia neglecta* Sinitshenkova (221.5–205.6 Ma) and †*Trianguliperla innoxia* Sinitshenkova (221.5–205.6 Ma) were all recorded from modern-day Ukraine. It is unclear if stoneflies were present prior to this, or if these records represent range expansions and dispersals during the Late Triassic, possibly facilitated by changing climatic conditions (Miller & Baranyi 2019).

Unfortunately, until clear ancient representatives of either suborder can be found, the above hypotheses remain speculation. As stoneflies apparently showed increased diversification immediately following extinction events (Jouault *et al.* 2022b), both the end Permian–Triassic and end Triassic–Jurassic extinction events may have facilitated their divergence into the extant suborders while isolated on either Pangea or Gondwana and Laurasia, respectively. Hoyal Cuthill *et al.* (2020) showed that extinctions and radiations are generally decoupled, suggesting origination does not necessarily follow a mass extinction event. Nevertheless, a period of generally increased radiation was associated with the end of the Permian mass extinction (Hoyal Cuthill *et al.* 2020), correlating with the period of increased diversification detected in the fossil record of Plecoptera at the same time (Jouault *et al.* 2022b).

4.2. Diversification of Antarctoperlaria

Only a single species, †*Eodinotoperla duncanae*, can be assigned with confidence to the Antarctoperlaria (Figs. 4, 6). This species is known from the Early Cretaceous (122.46–112.6 Ma), by which point East and West Gondwana had already separated (Fig. 6c–d; Boger 2011; Roche & Ringenbach 2022; Scotese *et al.* 2025). As fossils provide only a minimum age for their associated clades (Klopfstein 2021), the appearance and dispersal of Antarctoperlaria may have occurred prior to Early Cretaceous. East and West Gondwana were separated by a narrow (approximately 70 km), shallow water gap across the Davie ridge (Roche & Ringenbach 2022; Scotese *et al.* 2025) in the Late Jurassic and Early Cretaceous. Extant Plecoptera have been shown to cross similar distances (DeWalt & South, 2015), and it is possible that stem-Antarctoperlaria dispersed across Gondwana either prior to its separation, or by

crossing this ocean gap. It is unclear if Antarctoperlaria were ever present in Africa, and absences of otherwise pan-Gondwanan groups are common (Gheerbrant & Rage, 2006). However, if the suborder was ever present in Africa, it is likely that hot and dry periods during the Late Cretaceous and Palaeogene (Jacobs 2004; Myers *et al.* 2011; Rees *et al.* 2004; Sellwood & Valdes 2008) led to its localized extinction (Fig. 6d–e). Alternatively, a later dispersal into South America via Antarctica across the Weddellian Isthmus land bridge, which may have connected Antarctica and South America, is possible. However, the Weddellian Isthmus land bridge likely only formed in the Late Cretaceous, and may not have been consistently aerial (Reguero *et al*. 2014).

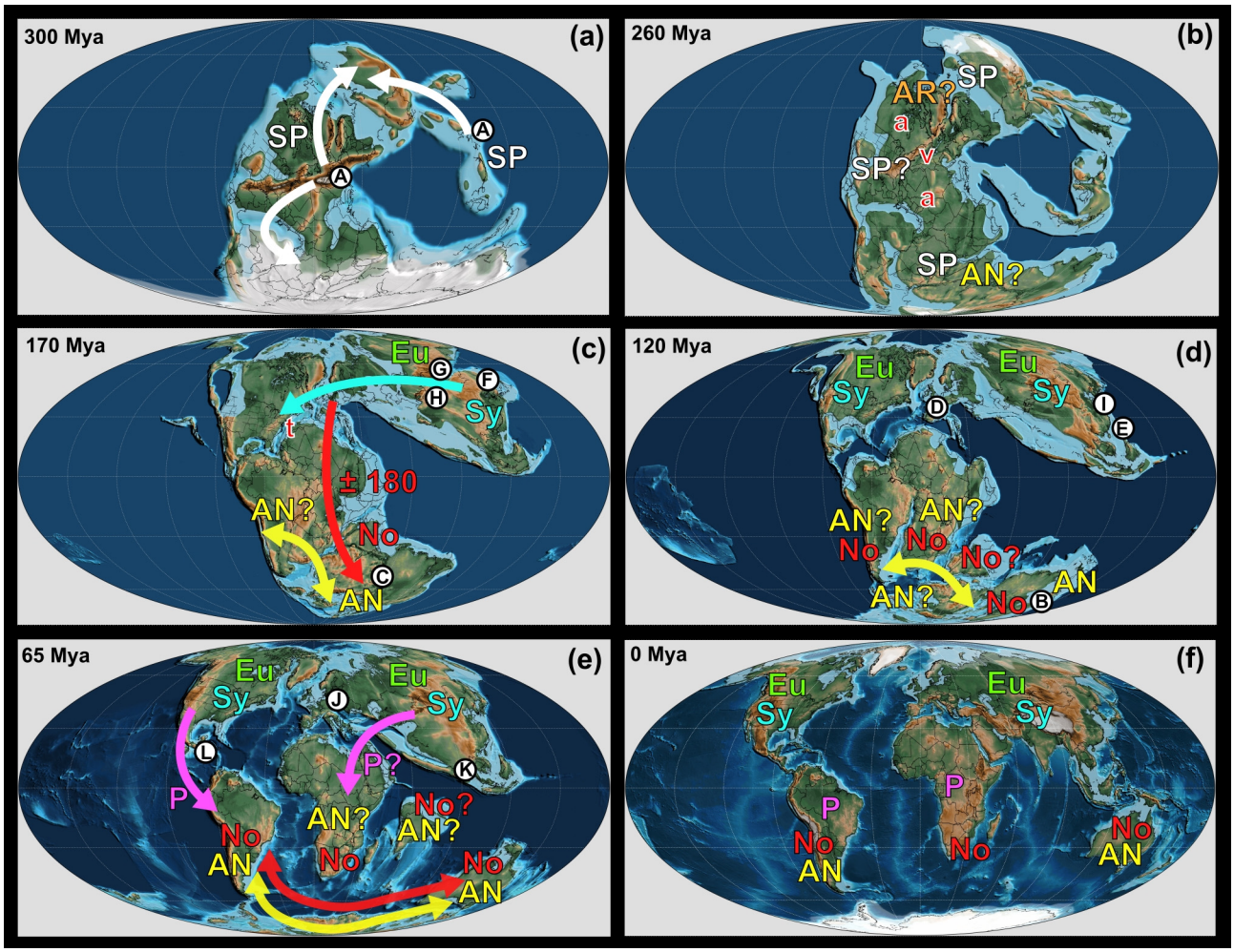

FIGURE 6. Hypothesized palaeobiogeographical history of Plecoptera, from the Carboniferous (300 Ma) to the Present Day, based on the results of our review of the fossil record. Abbreviations: SP: Stem-Plecoptera, a: arid zone, v: Variscan orogeny, t: Tethys Seaway, AN: Antarctoperlaria, AR: Arctoperlaria, Eu: Euholognatha, Sy: Systellognatha, No: Notonemouridae, P: Perlidae. Labels in white circles represent the same fossil species and labels as Figure 4, with the following addition: L: *Dominiperla antigua* Stark & Lentz (20.4–13.7 Ma). (a) Carboniferous: origin of Plecoptera, and oldest fossil stem-Plecoptera. (b) Permian: stem-Plecoptera have distributed worldwide and become isolated in the austral and boreal regions of Pangea by arid bands and the Variscan orogeny. Possible origin of Antarctoperlaria in the Southern Hemisphere, and Arctoperlaria in the Northern Hemisphere. (c) Jurassic: If not formed on Pangea, Antarctoperlaria and Arctoperlaria form due to vicariance with the separation of Laurasia and Gondwana. Systellognatha and Euholognatha arise in the Northern Hemisphere and stem-Notonemouridae disperse into the Southern Hemisphere. West and East Gondwana separate. (d) Cretaceous: the Northern and Southern Hemisphere are isolated by the Tethys sea, preventing faunal exchanges. The first records of extant families begin to appear, possibly correlated with Angiosperm radiation. Extant Antarctoperlaria first appear in the fossil record, and spread across the remnants of Gondwana, either via land bridges or long-distance dispersal (e) Palaeogene: extant genera first appear in the fossil record. Perlidae migrate into the Southern Hemisphere in two independent events. The timing of the migration of *Neoperla* into the Afrotopics remains unclear. (f) Modern day. Palaeomaps from Scotese *et al.* (2025) are used under the Creative Commons Attribution 4.0 International License, available from https://doi.org/10.5281/zenodo.10659112 (Accessed 24 February 2025).

As many Plecopteran taxa and clades are not geographically isolated across the rest of the Southern Hemisphere, at least some movement across the austral region must have continued after these families first appeared (García-Girón *et al.* 2024; Letsch *et al.* 2021; McCulloch *et al.* 2016). Migrations probably occurred predominantly via Antarctica, which was generally cool and covered in temperate rainforests during the Cretaceous (Bowman *et al.* 2014; Francis & Poole 2002). However, migrations may have persisted after the separation of South America, Africa, Australia and New Zealand, possibly via the West Wind Drift, which could have dispersed stoneflies as aerial plankton (postulated by Ding *et al.* 2019; García-Girón *et al.* 2024; McCulloch *et al.* 2016), via rafting on vegetation mats in ocean currents, or through zoochory (Fig. 6e; discussed above).

4.3. Diversification of Systellognatha, and selection of calibration points for node-dating in phylogenetic analyses

The earliest crown-group Systellognatha appeared in the fossil record of the mid-Jurassic, shortly after the separation of Gondwana and Laurasia some 180 Ma (McLoughlin 2001; Schettino & Scotese 2005; Schettino & Turco 2009; Scotese *et al.* 2025). As a short first tarsomere can be unreliable for classification, this estimate is based on †*Platyperla platypoda* (183–155.7 Ma), †*Platyperla conferta* (171.6–164.7 Ma) and †*Bestioperlisca inulta* (150.8–145.5 Ma), as the sharply toothed mandibles support a probable carnivorous feeding strategy, and their assignment to stem-Perloidea (Zwick 2000). While carnivory is an autapomorphy of Perloidea (Zwick 2000), these species were assigned to stem-Perloidea instead of the crown-group as the presence of "lance-like" maxillae associated with herbivory suggests that they may have been detritivores or omnivores (Sinitshenkova 1985, 1987), and may be the remnants of a slow shift to carnivory that eventuated in extant Perloidea. These early fossils are all from Russia and Mongolia, suggesting that the initial diversification of Systellognatha occurred in the eastern high latitudes of the Northern Hemisphere (Fig. 6). Diversification probably resulted from isolation within cold, wet climates associated with the movement of Laurasia (Jouault *et al.* 2022b; Schettino & Turco 2009).

Diversification throughout the Jurassic appears to have been slow (Jouault *et al.* 2022b), and most extant families and superfamilies appeared only in the Early Cretaceous. The exception to this is a Pteronarcyidae, †*P. sinitshenkovae* (164.7–155.7 Ma) (Cui *et al.* 2016). Recent molecular phylogenetic analyses have suggested that Pteronarycyidae is a basal sister group to Perloidea (García-Girón *et al.* 2024; Letsch *et al.* 2021; South *et al.* 2021), which is congruent with this early appearance. As †*P. sinitshenkovae* is from China, these basal Systellognathans must have spread across Laurasia by the Early Cretaceous (Fig. 6c–d).

Crown-group Perloidea and the remaining Pternonarcyoidea arose during the Cretaceous. In Pteronarcyoidea, †*Ecdyoperla fairlightensis* (145.5–140.2 Ma) was the first preserved Peltoperlid recorded (Sinitshenkova 1998), followed by †*Siberiopelta bashkuevi* (121.4–113.2 Ma; Sinitshenkova & Yan 2024). Stem-Perloidea remain in the fossil record, evidenced by †*Trianguliperla quassa* and †*Derancheperla collaris* (Sinitshenkova 1987, 1992). This diversification overlapped with the first appearance of angiosperms (Chaboureau *et al.* 2014; Condamine *et al.* 2020a; b) and a mass extinction of Plecoptera hypothesized to have been caused by a shift from "pre-Angiosperm Plecoptera" to the extant groups (Jouault *et al.* 2022b). Similar extinctions and diversifications during this period have been noted in other insect groups, such as Dictyoptera (Condamine *et al.* 2020a). These shifts were potentially precipitated by both direct and indirect challenges to Plecoptera such as eutrophication, replacement of food sources for herbivores, and shifts in the diets and behaviours of predators (Jouault *et al.* 2022a). This scenario is harmonious with our results, as representatives of Peltoperlidae (†*Borisoperla,* †*Branchioperla*, †*Crossoperla*, †*Dewaltoperla,* †*Graciloperla,* †*Lapisperla*, †*Ovaloperla*, †*Petroperla,* and †*Zwickoperla*: Chen 2023b, 2025; Chen *et al.* 2025; Chen & Wang 2020; Chen & Xu 2020, 2022; Sroka *et al.* 2018; Sroka & Staniczek 2020) and Perlidae (†*Burmaperla,* †*Electroneuria,* †*Cretacroneuria,* †*Burmesoperla* and †*Largusoperla*: Chen 2018b, Chen *et al.* 2018, Sroka *et al.* 2018) were present by the late Cretaceous, some 99.7–94.3 Ma (Fig. 6e).

Peltoperlidae and Perlidae continued to diversify throughout the Cretaceous, and extant genera first appeared by at least the Palaeogene (*Isoperla* †*baltica,* 37.2–33.9 Ma; Jouault *et al.* 2021). Many of these genera probably arose and shifted between continents following the complex network of exchanges and isolations during the Palaeogene and Miocene posited by Zwick (2000).

4.4. Dispersal of Notonemouridae

The discovery of †*Talbragaria australis* in Australia shows that stem-Notonemouridae were present in the Southern Hemisphere by the mid-Jurassic, 157.3–145 Ma (Sroka & Prokop 2023). This scenario matches most biogeographical interpretations, as the current presence of this family in Madagascar suggests that it dispersed prior to the island splitting from Africa (Cui *et al.* 2016; Illies 1965; Letsch *et al.* 2021; Sroka & Prokop 2023; Zwick 2000), some 165 Ma (Kusky *et al.* 2007; McLoughlin 2001). Madagascar remained connected to India until the Late Cretaceous (McLoughlin 2001), suggesting the family likely occurred in Greater India but became locally extinct, possibly with increased temperatures during the landmass's movement north. Alternatively, faunal exchanges between Africa and Madagascar persisted after the separation of the two landmasses (Gheerbrant & Rage 2006), and a latter dispersal across the Mozambique Channel via aerial plankton, rafting in marine currents, or zoochory is possible (Fig. 6d–e).

Notonemouridae probably entered the Southern Hemisphere via Africa (Letsch *et al.* 2021), shown by the Afrotropical taxa forming a basal clade in molecular phylogenies (Fig. 6c; Letsch *et al.* 2021; McCulloch *et al.* 2016; Terry 2004). This route and timing aligns with Jurassic geographical and paleoenvironmental patterns. The opening of the Tethys seaway led to the separation of Gondwana and Eastern Laurasia, with isolation occurring in the Middle to Late Jurassic (Fig. 6). At that point, the seaway would have formed a significant barrier to stonefly migration (Gheerbrant & Rage 2006). By the time of this final split, Africa was concurrently separating from the rest of the East Gondwanan landmasses and Western Laurasia (McLoughlin 2001), and a later date of migration likely would have prevented dispersal across the rest of the austral realm (Fig. 6c–d). This timing coincided with a major cooling event during the Aalenian (174.7–170.9 Ma) that resulted in cold temperate climates across northern Africa and Europe, increased rainfall in northern Africa, and a significant drop in sea level during the middle Jurassic (Haq 2018; Kairouani *et al.* 2024; Korte *et al.* 2015), all providing ideal conditions for Notonemouridae to spread south.

This narrative has been contradicted by some dated molecular phylogenies that place the origin of Notonemouridae later, during the Cretaceous (García-Girón *et al.* 2024; McCulloch *et al.* 2016). A Cretaceous origin and migration for Notonemouridae seem unlikely because, although trans-Tethyan migrations of mammals, reptiles and dinosaurs into Africa occurred repeatedly during the Cretaceous (Gheerbrant & Rage 2006), northern Africa had become hot and arid by the late Jurassic (Myers *et al.* 2011; Rees *et al.* 2004; Sellwood & Valdes 2008). This climate persisted throughout the Early Cretaceous, with increased humidity and rainfall eventually leading to more tropical habitats only in the late Cretaceous (Jacobs 2004). This warm climate would be a significant barrier to the spread of the cold-adapted Notonemouridae, beyond the already significant physical barrier of the Tethys. These conditions persisted into the Paleogene and Miocene, after the Tethys closed (Jacobs 2004; Morley 2000; Steinthorsdottir *et al.* 2021). If Notonemouridae was widespread in Africa, it is plausible that this period of warming led to its extinction in the northern reaches of the continent, resulting in its restricted distribution in South Africa and Madagascar today.

It is generally assumed that stem-Notonemouridae went extinct in the Northern Hemisphere after migrating south (Ding *et al.* 2019; García-Girón *et al.* 2024; Hynes 1988; Illies 1965; Letsch *et al.* 2021; McCulloch *et al.* 2016; Zwick 2000). This extinction was obliged by its assumed derived position within Euholognatha. However, most molecular analyses have not supported the presumed sister relationship between Notonemouridae and Nemouridae, and the position of the family in Euholognatha is poorly resolved by both morphological and molecular analyses (García-Girón *et al.* 2024; Letsch *et al.* 2021; McLellan 1991; Zwick 2000). This journey may, therefore, have been made by a stem-Euhologнathan, which gave rise to the Notonemouridae in the south, while its remnants in the north developed into some, or all, of the extant crown-Euholognatha.

4.5. Dispersal of Perlidae

None of the recovered fossils provide biological context or biogeographical evidence for the migration of *Neoperla* into the Afrotropics.

In the New World, †*Dominiperla antigua* (20.4–13.7 Ma) might be a remnant of Acroneuriinae migrating into South America from North America. No extant Plecopterans are known from the Dominican Republic, where this fossil was collected from rich amber beds (DeWalt *et al.* 2025; Stark & Lentz 1992). It is dated to the early Neogene, suggesting that this migration occurred prior to the Miocene, perhaps during the early Palaeogene (Letsch *et al.*

2021; Zwick 2000). As a land bridge did not exist between the continents at the time, this migration could have occurred by "island hopping" via a chain of meso-American islands (Letsch *et al.* 2021) or by zoochory involving migrating waterfowl or waders.

Conclusions

Our findings showcase the problematic nature of the taxonomy of many Plecoptera fossils (Cui *et al.* 2015, 2019; Jouault *et al.* 2021; Zwick 2000), as we found insufficient evidence to support the current assignment of 56% of the 113 fossilised species reviewed here. This uncertainty surrounding the taxonomy of ancient Plecopterans confounds biogeographical interpretations (Heads 2005; Klopfstein 2021; Parham *et al.* 2012; Wolfe *et al.* 2016), and has contributed to the vastly different results recovered by molecular analyses (Ding *et al.* 2019; García-Girón *et al.* 2024; Letsch *et al.* 2021; McCulloch *et al.* 2016). Despite these issues, many stonefly fossils show apomorphies, enabling their placement in the phylogeny of Plecoptera, and providing valuable insight into the order's evolution and biogeography.

We have presented the first comprehensive morphological re-evaluation of fossil Plecoptera and proposed 12 key fossil species, supported by synapomorphies, that can help to test biogeographical hypotheses and calibrate future molecular analyses. Our results point to novel hypotheses of vicariance and long-distance dispersal shaping the distribution of extant Plecoptera. While gaps in the palaeobiogeographical history of the Plecoptera remain, the fossil record holds a wealth of evidence to illuminate outstanding questions. Furthermore, the scenarios we have proposed can serve as models for mapping the history and diversification of groups with sparse fossil records. Formal systematic changes were not proposed because research is needed to confirm the systematic placement of the affected fossils. Additionally, the rest of the boreal Plecopteran fossil record should be re-assessed to further clarify the palaeontological history of the stoneflies.

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Conflicts of interest

The authors declare that they have no conflicts of interest.

Ethics declaration

Ethical approval was not required for this study, as it used only publicly available data and did not involve any live organisms.

CRediT

Abigail P. Kirkaldy: Conceptualization (Equal), Data Curation (Lead), Funding Acquisition (Equal), Investigation (Lead), Project Administration (Equal), Writing—Original Draft Preparation (Lead), Writing—Review and Editing (Equal), Figures (Lead). **Helen M. Barber-James:** Conceptualization (Equal), Funding Acquisition (Equal), Project Administration (Equal), Supervision (Equal), Writing—Review and Editing (Equal), Figures.

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