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Review

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Evolution

Stonefly systematics: past, present, and future

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Stoneflies (Insecta: Plecoptera) are a widespread group of freshwater insects known for their ecological significance and sensitivity to environmental change. This diverse order encompasses over 4,000 species across 17 families, with the number of described species predicted to increase substantially over the coming years. This review surveys the past and present landscape of stonefly systematics, emphasizing recent advancements in

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our understanding of the phylogenetic relationships within this group to the ordinal, subordinal, and family level. We highlight the need for expanded biodiversity surveys, particularly in underexplored regions such as high-elevation ecosystems, the Southern Hemisphere, and the Arctic, and identify the key challenges impeding the advancement of systematic research, in particular the decline in taxonomic expertise. Looking forward, we outline a vision for the future of stonefly systematic research, advocating for increased inclusivity, collaborative research efforts, and the integration of advanced molecular methodologies.

Keywords: Plecoptera, taxonomy, diversity, evolution.

Scope of the Review and Definition of Plecoptera

Stoneflies belong to the neopteran clade within the superorder Polyneoptera. A key evolutionary innovation in Neoptera is the presence of basal sclerites that allow the wings to fold over the body (Grimaldi and Engel 2005, Beutel et al. 2013). Recent molecular analyses, as well as morphological and embryological evidence, have supported the monophyletic origin of this lineage (Yoshizawa 2011, Mashimo et al. 2014, Misof et al. 2014, Song et al. 2016, Wipfler et al. 2019), suggesting that Plecoptera occupies a phylogenetic position as a sister group to the "core Polyneoptera," except for Zoraptera + Dermaptera (Wipfler et al. 2019). For detailed information on the synapomorphies that unite all Plecoptera, refer to *Clear Definitions of Major Clades* section.

Stoneflies currently comprise over 4,000 extant species in 17 families (Fig. 1), distributed across all continents except Antarctica and remote islands (Stark et al. 2009, DeWalt et al. 2024). The probable origin of the order dates to the Upper Carboniferous period approximately 300 million years ago (Mya) (Béthoux et al. 2011), but significant diversification into 2 major clades—Arctoperlaria and Antarctoperlaria—occurred only in the Lower Jurassic period around 180 Mya. This divergence has been supported by both morphological and molecular data (Zwick 2000, McCulloch et al. 2016, Ding et al. 2019) and is consistent with the fragmentation of Pangea into the large continental masses of Laurasia and Gondwana, from which Arctoperlaria and Antarctoperlaria evolved, respectively (McIntyre et al. 2017). Only 2 families of Arctoperlaria—Perlidae and Notonemouridae—have successfully established in the southern hemisphere, most likely through 2 independent invasions (Illies 1965, Zwick 2000, McCulloch et al. 2016).

The Antarctoperlaria includes 412 species and is divided into 2 superfamilies: the Eustheniodea (containing families Diamphipnoidae and Eustheniidae) and the Gripopterygoidea (containing families Austroperlidae and Gripopterygidae) (Table 3). By contrast, the suborder Arctoperlaria is far more diverse, accounting for 4,090 species (DeWalt et al. 2024). These numbers include both extant and fossil species. Arctoperlarians are divided into 2 infraorders: the Euholognatha and the Systellognatha (Zwick 2000). The Euholognatha includes families Capniidae, Notonemouridae, Taeniopterygidae, Nemouridae, Scopuridae, and Leuctridae, while the Systellognatha includes Chloroperlidae, Peltoperlidae, Perlodidae, Styloperlidae, Pteronarcyidae, Perlidae, and Kathroperlidae (Table 3). Kathroperlidae was established in 2021, after its component species, which were originally placed in Chloroperlidae, were discovered to be morphologically and genetically distinct (South et al. 2021a).

Plecoptera systematics is still in an active phase of description and taxonomic revision (see Table 1 for a list of notable stonefly taxonomists). Species are being described continuously across continents (DeWalt and Ower 2019), including numerous microendemic species (McCulloch et al. 2022, Murányi and Kovács 2024). The number of described species has strikingly increased in the last 5 decades, from ~2,000 established species in 1976 (Fochetti and Tierno de Figueroa 2008) to over 4,000 known today, doubling species numbers in roughly 50 years. It is expected that by the year 2100, there will be an additional 2,130 ± 330 new species if the average global rate of 43.6 species descriptions/year continues (DeWalt and Ower 2019).

Research on stonefly systematics is crucial for cataloging and understanding this biodiversity and for providing advances for guiding conservation efforts and ecological studies as many species remain undiscovered or poorly understood. Thus, this is an exciting time to be working in Plecoptera systematics. In this review, we provide an overview of the order Plecoptera and summarize our current understanding of the phylogenetic relationships within this group, with a particular focus on the ordinal, subordinal, and family levels. We highlight key researchers who have shaped our understanding of stonefly systematics and trace how this knowledge has evolved over time. Additionally, we identify regions where further biodiversity research is needed and discuss the future directions of Plecoptera systematics.

Review of Biology and Natural History

Stonefly nymphs typically inhabit clean, fast-flowing, well-oxygenated rivers or springs. However, the nymphs of some species exist in lentic systems, such as lakes or ponds. In addition, some Antarctoperlarian nymphs are completely terrestrial, living in cool, humid, microhabitats under rocks (McLellan 1977) or deep within alpine vegetation (McLellan 1993). Stonefly adults are usually terrestrial, feeding, and mating near the stream from which they emerged. There are, however, a few exceptions, such as the aquatic adults of *Capnia lacustra* (Jewett 1963) that inhabit Tahoe Lake (USA) or *Zapada cinctipes*, whose females remain underwater for oviposition for prolonged periods (Caires et al. 2016).

Nymphs fill a variety of niches, with some species recorded as predators (eg Eustheniidae and most Perloidea), shredders (eg many Austroperlidae, Pteronarcyoidea, Nemouridae, Notonemouridae, Scopuridae, Gripopterygidae), collector-gatherers (eg many Leuctridae), and scrapers (eg some Taeniopterygidae) (Tierno de Figueroa and López-Rodríguez 2019). However, ontogenetic changes in diet have been reported for many species, with most exhibiting generalist feeding behaviors, and some even displaying omnivorous tendencies (Tierno de Figueroa and López-Rodríguez 2019).

Nymphal development varies across and within species but is usually conditioned by environmental factors (eg temperature, flow regimen; Brittain 1990, Stewart and Stark 2002). Nymphal diapause has been described for some species as a mechanism to avoid adverse conditions (eg periods of drought or frost; Hynes 1976, Zwick

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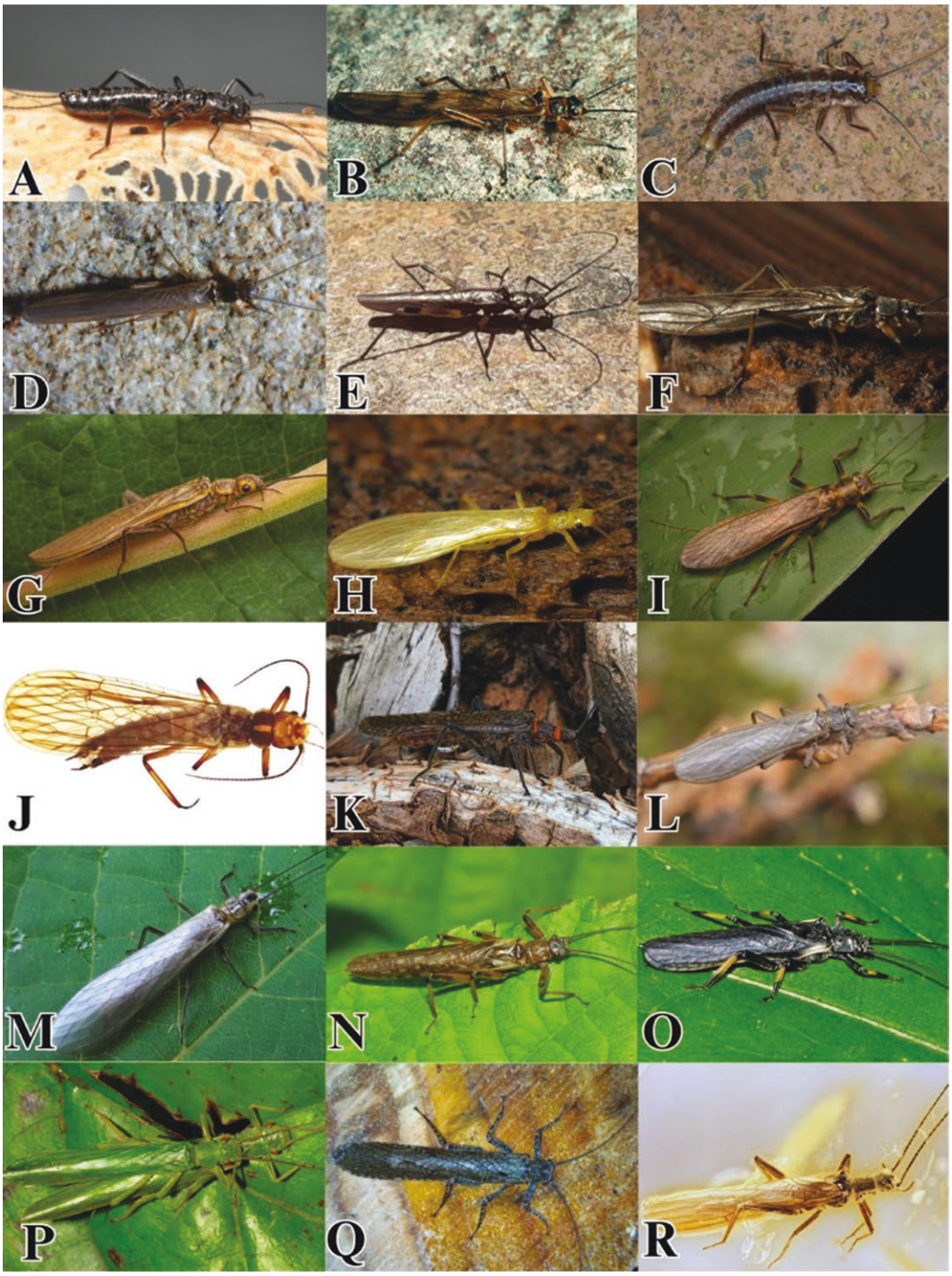

Fig. 1. Adult representatives of families within Plecoptera. A) Capniidae *Capnia nana* (Claassen 1924), B) Taeniopterygidae *Taeniopteryx shoenemundi* (Mertens 1923), C) Scopuridae *Scopura montana* (Uchida and Maruyama 1987), D) Leuctridae *Leuctra* sp., E) Notonemouridae *Afronemoura amatolae* (Balinsky 1956), F) Nemouridae *Protonemoura* sp., G) Perlodidae, H) Chloroperlidae *Chloroperla* sp., I) Perlidae *Anacroneuria* sp., J) Kathroperlidae, K) Pteronarcyidae *Pteronarcys californica* (Newport 1848), L) Peltoperlidae *Microperla brevicauda* (Kawai 1958), M) Styloperlidae, *Styloperla starki* (Zhao et al. 2019), N) Gripopterygidae *Zelandoperla fenestrata* (Tillyard 1923), O) Austroperlidae *Austroperla cyrene* (Newman 1845), P) Eustheniidae *Stenoperla prasina* (Newman 1845), Q) Diamphipnoidae *Diamphipnoa annulata* (Brauer 1869). R) Leuctridae in Baltic amber. Photo credits: A) C. Riley Nelson, B) Romolo Fochetti, C) Shodo Mtow, D) Romolo Fochetti, E) Abigail Kirkaldy, F) Romolo Fochetti, G) Frederico Salles, H) Romolo Fochetti, I) Frederico Salles, J) Qing-Bo Huo, K) Anna Eichert, L) Shodo Mtow, M) Qing-Bo Huo, N) Steve Kerr, O) Steve Kerr, P) Steve Kerr, Q) Israel Parra, R) Michele Baldi.

1980). Nevertheless, nymphs of some species can develop even at 0 °C (Brittain 1990). The number of nymphal instars varies among species and can even differ among sexes (Brittain 1990). In temperate environments, most stonefly species have a univoltine life cycle, but some have a semivoltine or merovoltine pattern (Hynes 1976, DeWalt et al. 2015). Cases of bivoltinism have also been cited, but more rarely (Hynes 1976, Wolf and Zwick 1989). When the emergence period arrives, mature nymphs climb to stones or plants

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to complete the imaginal molt, usually following temperature and/or photoperiod clues (Hynes 1976).

The adult emergence period varies significantly across species (McCulloch and Waters 2018), with males typically emerging before females (Hynes 1976, Tierno de Figueroa et al. 2019). Emergence periods are often seasonal and synchronized in cold and temperate areas (McCulloch and Waters 2018) but can be almost continuous in tropical areas (eg Zwick 1976, Sheldon and Theischinger 2009). Some tropical species engage in diapause to avoid severe temperatures and have a peak emergence period during the warm-rainy season (Bispo et al. 2002). The adult life span is relatively short, from a few days to a few weeks (Stewart 2009). Adult stoneflies are typically winged; however, wing-reduced species are common in some alpine regions (McLellan 1977, McCulloch et al. 2019a), and all species from the family Scopuridae are wingless (Uéno 1938). Wing reduction most often occurs in both males and females, but in some species only males have reduced wings (Roff 1994). Males and females of many species feed during their imaginal stage, ingesting mainly pollen, lichens, fungi, cyanobacteria, or, more occasionally, animal matter (Tierno de Figueroa and López-Rodríguez 2019). Nevertheless, feeding seems to be less important in larger species (Tierno de Figueroa and López-Rodríguez 2019).

Mate-finding is often facilitated by direct searching and encounter, but vibrational communication (see Supplementary File 1) is also involved in Arctoperlarians (Rupprecht 1968, Stewart 2001, Tierno de Figueroa et al. 2019). Duets are established between males and females, in which the male emits a vibrational signal, and the female answers, announcing its position (Tierno de Figueroa et al. 2019). This mechanism also allows females to discriminate among males of different fitness. In many species, a 3-way signal (male-female-male) is produced (Tierno de Figueroa et al. 2019). These signals can be produced by drumming, rubbing, or tremulation, or by a combination of these types (Stewart 2001, Sandberg and Stewart 2006, Tierno de Figueroa et al. 2019). In those species that do not use vibrational communication (principally Antarctoperlaria) or that occur in habitats where it is not effective, other mate-encountering mechanisms are likely to be important. For instance, certain substrates could act as encounter sites (Stewart 1994). Stonefly copulation usually happens on stones or vegetation, and male displacement attempts can occur frequently (Tierno de Figueroa et al. 2019, Kroos et al. 2021). Erroneous mating attempts have been occasionally noted between males of the same species, between adults of different species (males with males and males with females), and even between adult males and both mature nymphs and dead adult females (Tierno de Figueroa et al. 2019, Huo et al. 2022).

Oviposition typically takes place on the water surface (though some females dive for a short period; Hynes 1974). Females typically lay down their eggs in clutches (Hynes 1974, 1976). Separate eggs are fixed to substrates with specialized structures such as attachment discs, filament-like projections with hooked tips, or gelatinous membranes (Hynes 1974, 1976). Alternatively, eggs may be burrowed partially into the substrate (Hynes 1976, DeWalt et al. 2015). Cases of parthenogenesis have been reported in several Capniidae species, but this phenomenon is apparently rare (Hynes 1976). Likewise, ovoviviparity has been suggested to occur in some species (eg *Tyrrhenoleuctra* cf. *minuta*, *Nesoperla fulvescens*; López-Rodríguez et al. 2009, Smith and Storey 2018) but is uncommon. Eggs can experience a resting state, either quiescence or diapause, usually to avoid unfavorable environmental conditions (Hynes 1976, Lillehammer 1987). The duration of the incubation period and hatching success are dependent on temperature (Brittain 1990).

Plecoptera are one of the most threatened freshwater insect groups due to their sensitivity to environmental changes (DeWalt et al. 2005, Sánchez-Bayo and Wyckhuys 2019). In the current scenario of global change, their habitats are particularly threatened, and many populations are decreasing or disappearing (Sánchez-Bayo and Wyckhuys 2019). Furthermore, their low dispersal capacity, which favors the existence of many microendemic taxa (McCulloch et al. 2022, Murányi and Kovács 2024), makes this situation even worse. Thus, conservation measures are essential to guarantee their survival in the future (Fochetti 2022).

Contribution from Taxonomists of the Past and Present

In ancient times, Plecoptera were unknown. Rare depictions and summary descriptions of Perlidae were found from 1500 BC, though the preimaginal stages were often confused with the Trichoptera or with the Odonata (Pictet 1841, Zwick 1980). In the Systema Naturae, Linnaeus (1758) includes a couple of species of Plecoptera and the Trichoptera in the genus *Phryganea*. Poda (1761) and Scopoli (1763) reported that the genus *Phryganea* included insects that differed in the position and conformation of the wings and cerci, attributable to the current Plecoptera and Trichoptera, but these contributions were ignored for many decades. Concurrently, Geoffroy (1762) established the new genus *Perla*, distinguishing it from the genus *Phryganea*, which contained the Trichoptera.

At the end of the 18th century, Latreille (1796) raised the Plecoptera to the rank of a separate family to which he attributed the name Perlariae, and also described the new genus *Nemoura* (Table 2). In the first half of the 19th century, various authors (Gray. 1832, Newman 1833, 1839, Stephens 1836) discovered and described clearly and exhaustively some new plecopteran species and created new genera. The name Plecoptera, which currently identifies this order, was originally coined by Burmeister (1839).

The Genevan naturalist François Jules Pictet made a fundamental contribution to the study of Plecoptera and can be considered the first modern scholar of these insects. He published a monograph on the "Family of Perlids" (Pictet 1841), accompanied by a large number of illustrations and drawings. Half of the species Pictet covered were new to science. Notable contributions to plecopteran taxonomy were subsequently made by Morton (1894, 1896), Klapalek (1896), Kempny (1898, 1899), and Ris (1902), who introduced the study of the external genital organs. Studies were later extended to the internal genital armor of the Perloidea by Despax (1936) and Wu (1938).

From the end of the 19th century, the study of Plecoptera became increasingly widespread, also extending to non-European countries. The vast number of new specific and supraspecific taxa required a more adequate systematic organization of the order than the now obsolete one of Latreille, which dated back to the end of the 1700s. The subsequent proposals of Klapálek (1905, 1909), Enderlein (1909), Tillyard (1921), Frison (1935), Ricker (1950, 1952), and Illies (1960, 1965), although bringing useful and important modifications, were not entirely satisfactory (Table 2). Finally, Zwick (1969, 1973, 2000), applying principles of phylogenetic systematics, proposed a classificatory system that is now broadly accepted. Still in occasional use for fossil stoneflies is a variation of this classification with similar infraorders, but a different topology (see, for example, Sinitshenkova 1987, 2002, 2018, Aristov 2013).

Over the last 60 years, this line of research has solidly established itself, as attested by the countless published contributions. Among

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Table 1. Taxonomists who have significantly contributed to our understanding of Plecoptera systematics. Taxonomists with 10 or more valid species descriptions are included, along with several pioneering taxonomists who have made significant contributions to the field (indicated with a *). **Alt text:** A table that lists the names of important stonefly taxonomists that have described at least 10 valid species during their career. This table provides information about the era the taxonomist was active, the number of species they described, their active publication dates, and what region of the world they described stonefly species from.

Era	Taxonomists	Valid species described	Active publication dates	Regional interest
18C	Linnaeus C.*	3	1758–1771	World
18C	Geoffroy E.L.*	1 (genus)	1762	Europe
18C	Latreille P.A.*	1 (genus)	1796–1802	World
19C	Pictet J.F.	57	1832–1841	World
19C	Newman E.	22	1833–1845	World
19C	Burmeister C.H.*	9	1839	World
19/20C	Morton K.J.	16	1894–1930	World
19/20C	Banks N.	163	1895–1948	World
19/20C	Klapálek F.	225	1896–1923	World
20C	Enderlein G.	24	1905–1909	World
20C	Needham J.G.	58	1905–1927	World
20C	Claassen P.W.	92	1922–1937	North America
20C	Frison H.T.	59	1929–1944	North America
20C	Tillyard R.J.	28	1921–1935	World
20C	Wu C.F.	134	1923–1973	World
20C	Chu Y.T.*	8	1928–1986	Asia
20C	Barnard K.H.	13	1934–1964	Africa
20C	Ricker W.E.	109	1935–1975	North America
20C	Hanson J.F.	20	1941–1969	North America
20C	Aubert J.	147	1943–1995	World
20C	Illies J.	77	1952–1975	World
20C	Kawai T.	48	1954–1975	East Asia
20C	Consiglio C.	19	1955–1975	Europe/Africa
20C	Jewett S.G.	82	1954–1975	North America
20C	Gaufin A.R.	31	1964–1976	North America
20C	Nebeker A.V.	10	1965–1967	North America
20C	Hynes H.B.N.	17	1974–1982	World
20/21C	Zhiltzova L.	141	1956–2012	Russia-Asia
20/21C	Froehlich C.G.	82	1960–2024	South America
20/21C	Nelson C.H.	12	1968–2001	North America
20/21C	McLellan I.D.	101	1966–2008	South Hemisphere
20/21C	Harper P.P.	42	1971–2008	World
20/21C	Stewart K.W.	33	1973–2013	North America
20/21C	Szczytko S.W.	38	1974–2015	North America
20C/21C	Kirchner R.F.	29	1978–2009	North America
20/21C	Kondratieff B.	118	1979–2022	World
20/21C	Surdick, R.F.	16	1980–2004	North America
20/21C	Yang C.K.	34	1989–2005	Asia
20/21C	Zwick P.	188	1967–present	World
20/21C	Baumann R.	123	1969–present	World
20/21C	Brittain J.*	–	1973–present	Europe
20/21C	Theischinger G.	17	1974–present	World
20/21C	Ravizza C.	22	1975–present	Europe
20/21C	Sivec I.	273	1980–present	World

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Table 1. Continued

Era	Taxonomists	Valid species described	Active publication dates	Regional interest
20/21C	Fochetti R.	13	1991–present	World
20/21C	Stark B.	210	1973–present	World
20/21C	Picker M.D.	10	1980–present	Africa
20/21C	Uchida S.	16	1983–present	World
20/21C	Sinitshenkova N.D.	204	1983–present	World (fossils)
20/21C	Nelson R.C.	25	1987–present	World
20/21C	Pardo I.	18	1989–present	Europe
20/21C	Teslenko V.	22	1989–present	Europe-Asia
20/21C	DeWalt E.*	7	1998–present	North America
20/21C	Vinçon G.	73	1989–present	Europe-North Africa
20/21C	Yang D.	187	1989–present	Asia
20/21C	Stevens D.M.	10	1995–present	Africa
20/21C	Grubbs S.	24	1996–present	North America
20/21C	Shimizu T.	48	1997–present	Asia
20/21C	Du Y.Z.	158	1998–present	Asia
20/21C	Zúñiga M. d C.	32	1999–present	South America
21C	Tierno de Figueroa J.M.	10	2001–present	World
21C	Bispo P.C.	35	2004–present	South America
21C	Li W.H.	261	2005–present	Asia
21C	Wang Z.	18	2006–present	Asia
21C	Wang Z.	16	2006–present	Asia
21C	Murányi D.	73	2007–present	World
21C	Liu Y.S.	17	2007–present	Asia (fossils)
21C	Lecci L.S.	16	2010–present	South America
21C	Wang G.Q.	63	2012–present	Asia
21C	Novaes M.C.	20	2013–present	South America
21C	Duarte T.	13	2014–present	South America
21C	Verdone C.	10	2015–present	North America
21C	Wang Y.	10	2016–present	Asia
21C	Mo R.R.	61	2016–present	Asia
21C	Chen Z.T.	75	2016–present	World (also fossils)
21C	Huo Q.B.	20	2017–present	Asia
21C	Almeida L.H.	11	2017–present	South America

The different colors are to highlight the different time periods of active publication dates per taxonomist listed.

the most significant are those of Hynes (1970, 1976) and Zwick (1980). More recently, important contributions to Plecoptera research have been published by Zhiltzova and Sinitshenkova (Russia), Stewart, Kondratieff, and Baumann (USA), McLellan (New Zealand), Froehlich (Brasil), Sivec (Europe), Du, Li, and Chen (China), and Zwick, Picker, and Stevens (Africa), among others. Since 1974, an update of this bibliography has been published in the "Perla" files, the newsletter and bibliography of the International Society of Plecopterologists, recently on an annual basis. Plecopterologists meet at regular intervals (every 3 years) in international working groups, congresses, and symposiums. See Table 1 for a curated list of past and present stonefly taxonomists that have greatly contributed to the field.

The History of the Systematics of Plecoptera

Systematic Studies of Plecoptera

The placement of Plecoptera in Neoptera has been problematic, with 3 interpretations based on morphological similarities proposed. Hamilton (1972) placed the order as a sister group of the "higher Neoptera," ie Eumetabola (= Paraneoptera + Holometabola) based on a modified mesotrochantin (Hamilton 1972). However, this hypothesis has no real morphological support, as the mesotrochantin varies within Holometabola and is present in some so-called "lower Neoptera," Zoraptera and Embioidea (Grimaldi and Engel 2005). The remaining 2 hypotheses instead placed Plecoptera as either sister to all Neoptera (Hennig 1969, Zwick 1973, Beutel and Gorb 2006), or somewhere within Polyneoptera, although the exact placement

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Table 2. Comparison of the higher categories in Plecoptera (by Du (1999)).

Latreille (1802)	Newman (1853)	**Klapálek (1905, Klapálek 1909)**	Enderlein (1909)	**Tillyard (1921, 1926)**	Claassen (1940)	**Illies (1965, 1966)**	**Zwick (1973, Zwick 1980)**
Perlariae	Nemouridae	1. Filipalpia	1. Holognatha	(1) Eustheniodea	1. Holognatha	1. Archiperlaria	1. Antarctoperlaria
=Perlidae	Perlidae	Capniidae	Gripopterygidae	Eustheniidae	=Filipalpia	(1) Eustheniodea	(1) Eustheniodea
		Taeniopterygidae	Capniidae	(2) Leptoperloidea	Eustheniidae	Eustheniidae	Eustheniidae
		Nemouridae	Nemouridae	Leptoperlidae	Austroperlidae	Diamphipnoidae	Diamphipnoidae
		Leuctridae	Pteronarcyidae	Austroperlidae	Pteronarycidae	2. Filipalpia	(2) Gripopterygoidea
		2. Subulipalpia	2. Systellognatha	(3) Nemouroidea	Peltoperlidae	(2) Leptoperloidea	Austroperlidae
		=Setipalpia	Perlidae	Capniidae	Leptoperlidae	Austroperlidae	Gripopterygidae
		Perlodidae		Nemouridae	Scopuridae	Scopuridae	2. Arctoperlaria
		Perlidae		(4) Subulipalpia	Taeniopterygidae	Peltoperlidae	1) Euholognatha
				Pteronarcyidae	Nemouridae	Gripopterygidae	(3) Scopuroidea
				Perlidae	Leuctridae	(3) Nemouroidea	Scopuridae
					Capniidae	Capniidae	(4) Nemouroidea
					2. Systellognatha	Leuctridae	Capniidae
					=Subulipalpia	Nemouridae	Leuctridae
					=Setipalpia	Taeniopterygidae	Nemouridae
					Perlodidae	3. Setipalpia	Notonemouridae
					Perlidae	(4) Pteronarcyoidea	Taeniopterygidae
						Pteronarcyidae	2) Systellognatha
						(5) Subulipalpia	Pteronarcyidae
						Perlidae	Peltoperlidae
						Perlodidae	(5) Subulipalpia
						Chloroperlidae	=Perloidea
							Perlodidae
							Perlidae
							Chloroperlidae

Note: 1.—suborder; 1)—infraorder; (1)—superfamily.

differed between authors (Martynov 1925, Matsuda 1970, Kristensen 1975, Grimaldi and Engel 2005, Zwick 2009). Plecoptera, as sister to Neoptera, was supported by a suite of plesiomorphic characters (Hennig 1969, Zwick 1973, 2009), including a complex pluricellular organ used in osmoregulation that is shared with Ephemeroptera (Wichard 1997, Zwick 2009). Zwick (2009) argued that the loss of this structure from all other Neoptera may suggest a basal Plecoptera. Plecoptera within Polyneoptera is supported by the presence of a large anal region in the hind wing (Martynov 1925, Kristensen 1975, Grimaldi and Engel 2005, Zwick 2009). Both hypotheses were reviewed by Zwick (2009), who found insufficient evidence to fully support either interpretation. Indeed, morphological data alone has proved insufficient to resolve relationships within the Polyneoptera as a whole, as most orders lack clear homologies to support relationships (Kristensen 1975, Grimaldi and Engel 2005). However, recent molecular and embryological evidence has since supported the position of Plecoptera within a monophyletic Polyneoptera (discussed above in *Scope of the Review and Definition of Plecoptera* section). The first phylogenetic studies using morphological characters to infer the phylogeny of Plecoptera started in the 1950s to 1980s with the works by Ricker (1952), Illies (1965), Zwick (1973, 1980), and Brodskiy (1982). Their work was reassessed in a numerical cladistic analysis by Nelson (1984) that generally confirmed the hypotheses by Zwick (1973), who proposed the Plecoptera being subdivided into the southern hemisphere Antarctoperlaria (Gripo pterygoidea + Eusthenioidea) and the mainly northern hemisphere Arctoperlaria (Systellognatha (Pteronarcyoidea + Perloidea) + Euhol ognatha) (Table 2). These relationships were further corroborated in Zwick's seminal work in 2000 on the phylogenetic relationships and biogeographical history of stoneflies. However, Arctoperlaria was so far united only by the single putative synapomorphy of drumming behavior (Supplementary File 1, Fig. 3G and H, Zwick 2000).

As morphological evidence began to clarify the higher-level relationships within Plecoptera in the late 1900s, it also became vital for unraveling infra-familial relationships at the generic and species level. Morphology-based studies enabled the identification of key diagnostic characters, clarified generic boundaries, and provided a foundation for phylogenetic hypotheses. Concurrent with the reviews of higher-level relationships discussed above, several comprehensive generic reviews of families were completed between the

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Table 3. Classification of Plecoptera and their distribution by regions (modified from Stark et al. 2009). The use of colors highlights the different clades within Plecoptera. *Abbreviations*: Australia (A), Afrotropical (Af), Andean (An), Holarctic (H), Eastern Palaearctic (EP), Nearctic (Na), Neotropical (Nt), New Zealand (NZ), Oriental (Or). Classification of Plecoptera and their distribution by regions (modified from Stark et al. 2009). *Abbreviations*: Australia (A), Afrotropical (Af), Andean (An), Holarctic (H), Eastern Palaearctic (EP), Nearctic (Na), Neotropical (Nt), New Zealand (NZ), Oriental (Or). **Alt text:** The current taxonomic classifications for stoneflies, and the regions that each group is distributed in.

Suborders	Infraorders	Superfamilies	Families	Distribution
Antarctoperlaria		**Eusthenioidea**	Diamphipnoidae Ricker 1950	An
			Eustheniidae Banks 1913	A, An, Nt, NZ
		Gripopterygoidea	Austroperlidae Tillyard 1921	A, An, Nt, NZ
			Gripopterygidae Enderlein 1909	A, An, Nt, NZ
Arctoperlaria	**Euholognatha**	**Nemouroidea**	Capniidae Banks 1900	H, Or
			Leuctridae Klapálek 1905	H, Or
			Nemouridae Billberg 1820	H, Or
			Notonemouridae Ricker 1950	A, An, Af, Nt, NZ
			Taeniopterygidae Klapálek 1905	H, Or
		–	Scopuridae Uéno 1935[a]	EP
	Systellognatha	**Perloidea**	Chloroperlidae Okamoto 1912	H, Or
			Kathroperlidae Banks 1947	Na
			Perlidae Latreille 1802	An, Af, H, Nt
			Perlodidae Klapálek 1909	H, Or
		Pteronarcyoidea	Peltoperlidae Claassen 1931	EP, Na, Or
			Pteronarcyidae Newman 1853	EP, Na
			Styloperlidae Wu 1935	EP, Or

[a]Family is not associated with superfamily.
The use of colors highlights the different clades within Plecoptera.

1900s and early 2000s, including Nemouridae (Baumann, 1975), Notonemouridae (McLellan 1972, 1991, 2000, Zwick 2000), Leuctridae (Nelson and Hanson 1973, Shepard and Baumann 1995), Perlidae (Stark and Gaufin 1976, Sivec et al. 1988, Stark 2001), Pteronarcyidae (Nelson and Hanson 1971), Styloperlidae (Uchida and Isobe 1989), and Gripopterygidae (Illies 1963, McLellan 1977, McLellan and Zwick 2007). These works have refined subfamily structures, revised subfamilies, and genera with the proposal of new taxa, and developed more inclusive phylogenies. They have also explored monophyly, key phylogenetic characters, and the impact of continental breakup on the evolutionary history of Plecoptera.

Many of these phylogenies have been refined through regional reviews (eg McLellan 2001, Stewart and Stark 2002, Stark et al. 2009, Froehlich 2010, Stevens et al. 2018, Pessacq et al. 2019), and taxonomic revisions to genera (eg Uchida and Isobe 1989, Duarte et al. 2022, Zwick 2023). As evolutionary relationships within and among families were refined, the use of morphological characters such as egg morphology (Stark and Szczytko 1982, 1988, Ubero-Pascal et al. 2001) and drumming behavior (Supplementary File 1, Fig. 3G and H, Stewart and Zeigler 1984, Stewart et al. 1988, Sandberg and Stewart 2006) were expanded to further evaluate relationships within families, genera, and species.

Hand-in-hand with these morphological reviews, the advent of molecular techniques (discussed below) has led to an increase in integrative systematic reviews of taxa. This has proven particularly powerful for unraveling species complexes in morphologically similar species that can often only be differentiated by adult genitalia and egg morphology, eg *Neoperla* (Perlidae) (Zwick 2023, Zwick and Zwick 2023) and *Siphonoperla* (Weiss et al. 2012), and clarifying relationships of genera within families where affinities are unclear, such as Notonemouridae (McCulloch et al. 2016, Stevens et al. 2018) and Perlidae (Zwick 2023).

The first phylogenetic study on Plecoptera using molecular data was conducted by Thomas et al. in 2000, who used ribosomal *18S* sequences to reconstruct the evolution of locomotion behavior in stoneflies. Their analyses contradicted the subdivision of Plecoptera into Antarctoperlaria and Arctoperlaria, as has been suggested by Zwick (1973, 2000); they recovered monophyletic Antarctoperlaria and Systellognatha nested within paraphyletic Euholognatha, with Nemouridae as the sister group to all remaining Plecoptera. The advent of DNA barcoding using the mitochondrial cytochrome *c* oxidase I (*COI*) gene began soon after (Hebert et al. 2003), which has continually expanded the knowledge of intra- and interspecific genetic variability within stonefly taxa and allowed for taxonomically curated databases to exist, such as the Barcode of Life Data (BOLD) System, MIDORI2, and GenBank (Ratnasingham and Hebert 2007, Benson et al. 2009, Laini et al. 2024). DNA barcoding continues to be one of the most popular and influential molecular techniques for biodiversity assessment and the conservation of stoneflies (DeWalt and Ower 2019, Hlebec et al. 2022).

An important contribution to the molecular phylogenetics of stonefly relationships was the creation of a 6-gene dataset by Terry (2003) that comprised mitochondrial *COII*, ribosomal subunits *12S rRNA*, *16S rRNA*, nuclear ribosomal subunits *18S rRNA*, *28S rRNA*, and protein-coding histone 3 (*H3*) gene portions. The combination of these molecular data with morphological characters in a total-evidence approach corroborated the principal subdivision of Plecoptera, according to Zwick (1973, 2000). Within Antarctoperlaria, Austroperlidae + Eusthenioidea were nested within paraphyletic Gripopterygidae. In Systellognatha, Perloidea

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were nested within paraphyletic Pteronarcyoidea, and the originally chloroperlid genus *Kathroperla* was sister to all perloid families. Within Euholognatha, Scopuridae appeared as a sister group to Taeniopterygidae and Leuctridae as sister to all other families.

Sanger sequence datasets for Plecoptera were further enhanced by a study of McCulloch et al. (2016), who used *COI, 18S rRNA*, and *H3* genes to infer the relationships of Antarctoperlaria and its dispersal in the southern hemisphere, further corroborating the subdivision into Gripopterygoidea (Gripopterygidae + Austroperlidae) and Eustheniodea (Eustheniidae + Diamphipnoidae). The study included a significant number of South American representatives, thus adequately representing the sparsely diverse Patagonian families, with well-resolved relationships supported by other studies (eg Zwick 2000, Ding et al. 2019). Neotropical representatives of Perlidae were not included in this study, while Gripopterygidae, due to its greater diversity, remained proportionally underrepresented. Pessacq et al. (2020) conducted a phylogenetic analysis using a morphological matrix, focusing on most Patagonian representatives of Gripopterygidae. Their results supported the monophyletic nature of the subfamily Antarctoperlinae sensu McLellan (1977); however, the inclusion of additional genera and species from this family is necessary to obtain more conclusive results regarding internal relationships and subfamily validity.

In 2019, Ding et al. were the first to use complete mitogenomes to investigate plecopteran relationships. Their dataset comprised 47 taxa, representing all families except Scopuridae. Their analyses confirmed the relationships as proposed by Zwick, including a monophyletic (but only weakly supported) Pteronarcyoidea in Systellognatha. They also recovered Leuctridae as the sister group to all other families in Euholognatha, but generally, the support among Euholognatha was low. Another subsequent study, based on mitogenomes, also found insufficient support to resolve family relationships in Euholognatha (Cao et al. 2024).

In 2021, 2 phylogenomic studies investigated the relationships of Plecoptera. South et al. (2021b) used transcriptomic data (1,400 orthologous genes) from 94 species of North American stoneflies. Their analyses showed high support for the monophyly of North American families of Euholognatha, and Nemouridae + Capniidae being sisters to one another, whereas the other relationships in Euholognatha remain unresolved. Within Systellognatha, they retrieved high support for the earliest diverging family of Perloidea being Perlidae, and Peltoperlidae as sister to the rest of Systellognatha. As in Terry (2003), *Kathroperla* was discovered to be morphologically and molecularly distinct from Chloroperlidae. Banks (1947) had previously placed this genus in the monogeneric subfamily Kathroperlinae, but South et al. (2021a) suggested that the phylogenetic placement of this genus (sister to the remaining Perloidea) warranted its elevation to family status. Letsch et al. (2021) combined transcriptomic data (2,997 orthologous genes) from 30 species and Sanger sequences from 7 gene fragments (as in Terry (2003) and McCulloch (2016)) for 498 species in a supertree analysis that recovered well-supported Antarctoperlaria, Systellognatha, and Euholognatha clades (Fig. 2). The relationships among the families within Systellognatha appeared consistent, with a monophyletic Perloidea (comprising Perlidae, Perlodidae, Chloroperlidae, and the monogeneric family Kathroperlidae) nested within a paraphyletic Pteronarcyoidea (Pteronarcyidae, Peltoperlidae, and Styloperlidae). Styloperlidae was the sister group to all remaining families. Despite the consistency of the relationships within Systellognatha, the relationships within Euholognatha remained unclear, with only 2 sister groups that consistently received support: *Megaleuctra* + Capniidae and Scopuridae + Taeniopterygidae. The position of Nemouridae, Notonemouridae, Leuctridae, and these sister groups varied throughout the analyses.

Recently, García-Girón et al. (2024) presented a time-calibrated phylogeny of stoneflies based on a combined analysis of *COI, 12S, 16S, 18S, 28S rRNA*, and *H3* gene fragments. This study indicated that Arctoperlaria, Antarctoperlaria, Eustheniodea, Gripopterygoidea, Systhellognatha, Euholognatha, and Perloidea are monophyletic, but found that Pteronarcyoidea was paraphyletic (with Styloperlidae the sister group of the remaining Systhellognatha). All the stonefly families were likewise monophyletic (except Kathroperlidae, which was not included in the analysis). Their results also indicated that Perlidae is sister to Chloroperlidae + Perlodidae, and Scopuridae is sister to Taeniopterygidae, supporting the findings of Letsch et al. (2021).

Nevertheless, contradictory phylogenetic placements of different Euholognatha families among different studies (eg Ding et al. 2019, Letsch et al. 2021, García-Girón et al. 2024) make this topic currently unresolved. For instance, Notonemouridae, an Arctoperlarian family distributed across the Southern Hemisphere, has been recovered as a monophyletic family by most analyses, although their position varies (Terry 2003, McCulloch et al. 2016, Letsch et al. 2021, García-Girón et al. 2024). Previously, this family was suspected to be a paraphyletic gradotaxon, consisting of multiple lineages of stem-Nemouridae that independently dispersed into the Southern Hemisphere (McLellan 1991, Zwick 2000).

The biogeographical processes that led to the unusual antitropical distribution of Plecoptera have fascinated authors for decades (Illies 1965, Hynes 1988, Banarescu 1990, Zwick 2000, Fochetti and Tierno de Figueroa 2008). In particular, what gave rise to the Antactoperlaria and Arctoperlaria, and what led to their modern distributions? How and when did 2 Arctoperlarian families, Notonemouridae and Perlidae, disperse into the Southern Hemisphere? Four studies have produced time-calibrated phylogenies (calibrated by node) to directly investigate these questions (McCulloch et al. 2016, Ding et al. 2019, Letsch et al. 2021, García-Girón et al. 2024). The estimated dates recovered by these analyses, and by extension their interpretations, have varied, with Letsch et al. (2021) recovering significantly older estimates for the divergence of many groups.

McCulloch et al. (2016), Ding et al. (2019), and García-Girón et al. (2024) all placed the origin of Antarctoperlaria and Arctoperlaria during or after the split of Pangea at 121, 181, and 170 Mya, respectively. This timing is congruent with previous biogeographical interpretations, which attributed the divergence of the 2 suborders to vicariance, caused either by the rifting of Pangea or complementary extinctions in each hemisphere (Zwick 2000). Within the Southern Hemisphere, divergences between Eustheniodea and Gripopterygoidea were found to have occurred relatively recently (McCulloch et al.: 69 Mya, Ding et al.: 114 Mya, García-Girón et al.: 115 Mya), well after the breakup of Gondwana, which began in the late Jurassic, some 180 Mya (McLoughlin 2001). Very few of the clades within these families are geographically restricted, with close relatives shared between Australia, New Zealand, and South America (McCulloch et al. 2016, García-Girón et al. 2024). This has been attributed to the families being widespread across Gondwana before the splitting of the supercontinent (Illies 1965, Zwick 2000, Fochetti and Tierno de Figueroa 2008), but these estimates instead point to a combination of long-distance dispersal events and vicariance caused by Australia and South America becoming isolated after the opening of the Drake passage 41 Mya (McLoughlin 2001, Scher and Martin 2006), prior to which they were connected via Antarctica (McCulloch et al. 2016, García-Girón et al. 2024). Similarly, a recent origin (110 to 71 Mya) for Notonemouridae was

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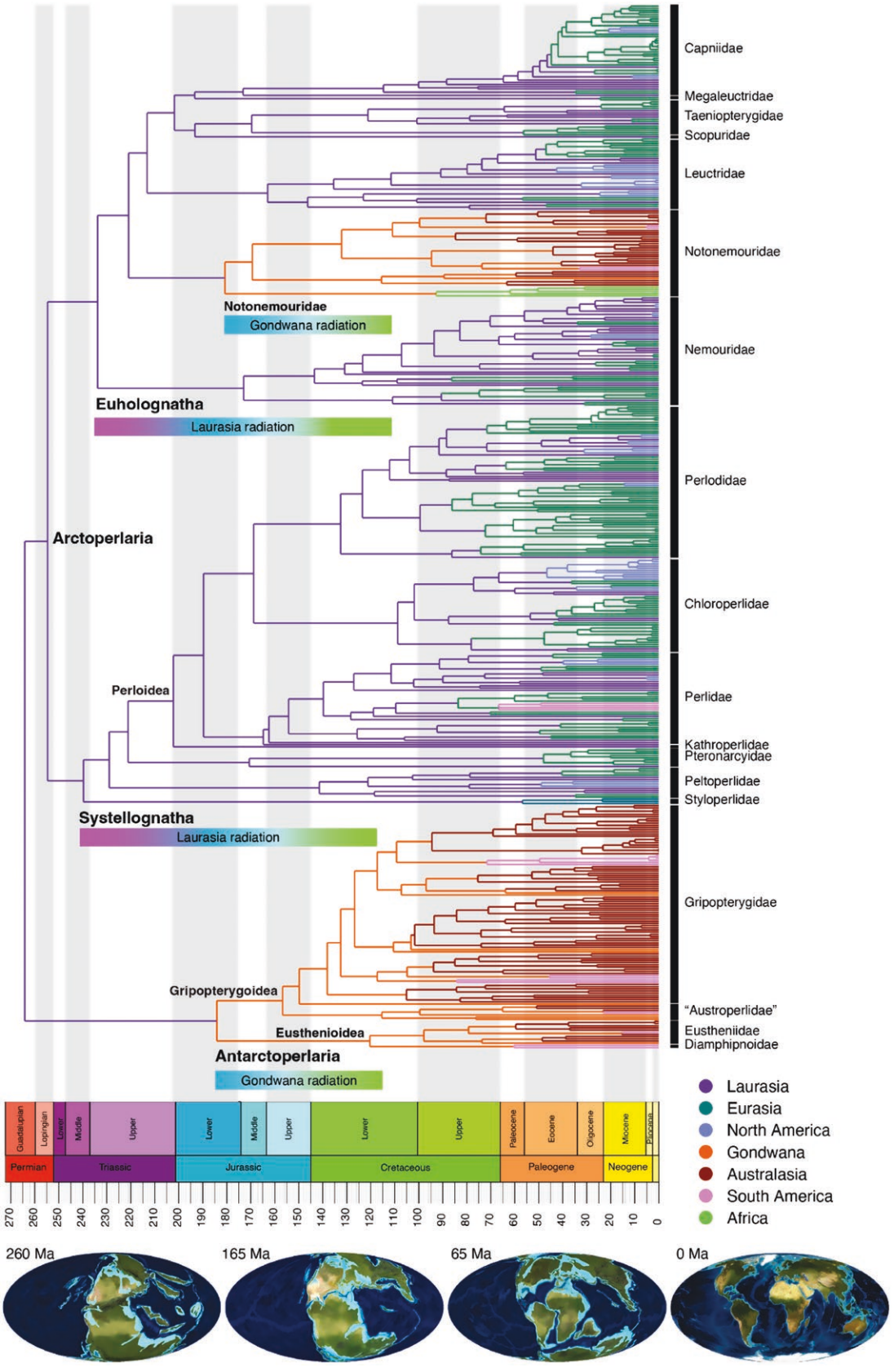

Fig. 2. Chronogram showing the relationships and divergence times of plecopteran families as derived from the Bayesian inference analyses in Letsch et al. (2021). Colored branches indicate the ancestral distribution as derived from the biogeographic analysis. Area color codes: Laurasia, violet; Eurasia, ocean green; North America, blue; Australasia, red; South America, pink; and Africa, light green.

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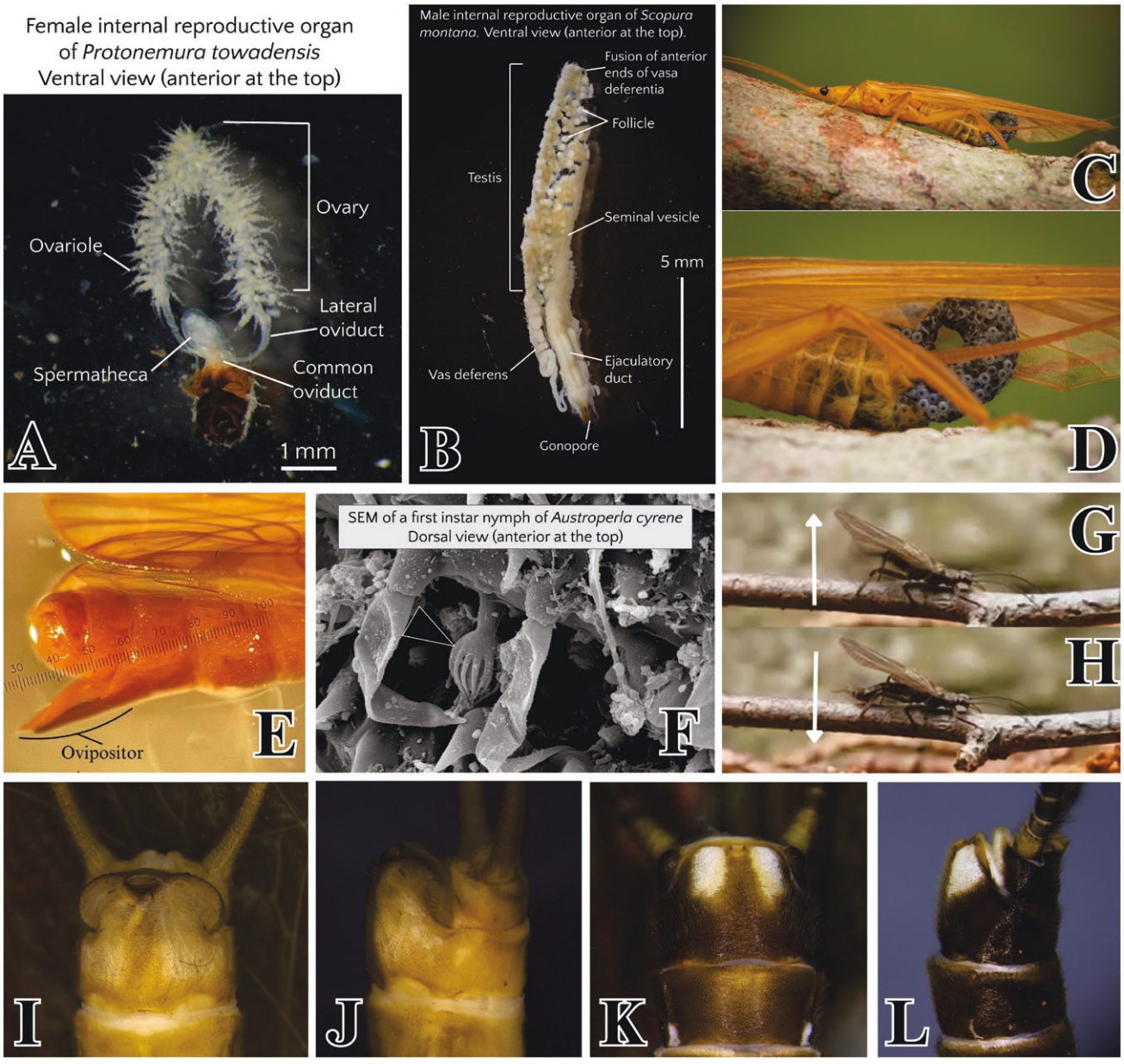

Fig. 3. Identifying features of the Plecoptera, Antarctoperlaria, and Arctoperlaria: A) Ovary of *Protonemura towadensis* (Kawai 1954), with fused ovaries forming a loop, B) Testes of *Scopura montana*, with fusion of the vasa differentia, and stacked seminal vesicles, C and D) Female Kempnyia sp. depositing eggs without an ovipositor, E) Secondarily derived ovipositor in *Megaleuctra* sp., F) *Antarctoperlaria floriform* chloride cell (arrowhead) on the sixth abdominal tergum of *Austroperla cyrene* (Newman 1845), G and H) Arctoperlarian drumming behavior in *Microperla brevicauda* (Kawai 1958), video of drumming behavior can be viewed as Supplementary File 1 (online only), I–L) Arctoperlarian Perlidae examples of the male drumming apparatus, I) Ventral hammer of *Kempnyia* sp., J) Lateral view of ventral hammer of *Kempnyia* sp., K) Ventral hammer of *Enderleina* sp., L) Lateral view of ventral hammer of *Enderleina* sp. Photo credits: A) Shodo Mtow, B) Shodo Mtow, C) Frederico Salles, D) Frederico Salles, E) Anna Eichert, F) Shodo Mtow, G) Shodo Mtow, H) Shodo Mtow, I) Lucas Almeida, J) Lucas Almeida, K) Lucas Almeida, L) Lucas Almeida.

recovered (McCulloch et al. 2016, Ding et al. 2019, García-Girón et al. 2024). The disjunct distribution of this family was therefore explained by long-distance dispersal, likely via the west wind drift, which circulates Antarctica (McCulloch et al. 2016, García-Girón et al. 2024). Within the Northern Hemisphere, divergences between the Systellognatha and Euholognatha, along with their respective families, were all dated to the latest Jurassic and into the Cretaceous (<165 Mya). This aligns with the modern distribution of the families being the result of a complex pattern of vicariance, dispersal, and extinctions throughout the Paleogene and Neogene, summarized by Zwick (2000).

By contrast, Letsch et al. (2021) estimated the divergence between Antarctoperlaria and Arctoperlaria to be during the Permian, 265 Mya. This early split refutes the role of vicariance or reciprocal extinctions in the formation of the suborders. Instead, they suggest that the initial diversification of crown-group Plecoptera occurred in high latitudes on Pangea, while isolated from the globally distributed stem-group Plecoptera by an arid band across mid-latitudes (Chaboureau et al. 2014), and the Variscan mountain range (Kroner and Romer 2013, Letsch et al. 2021). Under this scenario, the Antactoperlaria originated in the Northern Hemisphere and later distributed into the South, along with Notonemouridae, around 180 Mya, and were

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widespread by 165 Mya (Letsch et al. 2021). This provides support for the modern distribution of these groups being caused by vicariance, as discussed above, and a later extinction of Eusthenoidea and Gripopterygoidea from Africa. Some evidence of this journey is found in the fossil record of Notonemouridae (Yushuang et al. 2011, Cui et al. 2019), which were present in Australia by the late Jurassic (Sroka and Prokop 2023). The estimated divergence of the Antarctoperlarian superfamilies (Gripopterygoidea: 158 Mya, Eusthenioidea: 121 Mya) postdates the splitting of Gondwana, which suggests land dispersal via Antarctica played an important role in their distribution. The Northern Hemisphere infraorders Euholognatha and Systellognatha were found to first appear in the Triassic (earlier than in other studies); however, the divergences of the extant families were similar to those found by Ding et al. (2019) and García-Girón et al. (2024) (<172 Mya), pointing to the same patterns of vicariance during the Paleogene (Letsch et al. 2021). Dispersals of Perlidae into the Southern Hemisphere, Acroneuriinae into South America, and *Neoperla* into Africa occurred independently, likely during the early Paleogene and Neogene, respectively (Zwick 2000, Letsch et al. 2021).

While some patterns have consistently emerged in these analyses, some of the recovered dates vary widely, with differences of >100 million years among estimates. This variation is likely caused, at least in part, by different calibration points used between studies. García-Girón et al. (2024) constrained the root of Plecoptera to 167 Mya, based on estimates recovered by Misof et al. (2014). All other studies made use of fossil calibration points, but these differed between analyses. Ding et al. (2019) relied on stem representatives of Polyneoptera, while McCulloch et al. (2016) and Letsch et al. (2021) made use of internal fossils within Plecoptera. These internal fossils differed, with McCulloch et al. relying on definitive fossils within extant genera and families (38 to 5 Mya), while Letsch et al. used stem representatives of several families, stretching back to the Jurassic, as recommended by Cui et al. (2019).

Unfortunately, reliably and consistently choosing fossil calibration points remains difficult. Generally, genitalia provide the most reliable characters for assigning species to families (Jouault et al. 2021), but these are seldom preserved, leading to wing venation being used to identify fossils. The wing venation is highly variable in Plecoptera (Béthoux 2005), and main veins can vary within a single species (Cui et al. 2016, Jouault et al. 2021). Complicating this further, many fossils are assigned to a different phylogenetic system, proposed by Sinitshenkova (1987, 2002), which broadly matches the groupings of Zwick (2000) but differs in topology. This system generally relies on characters such as wing venation, body size, and proportion, rather than established apomorphies of each group, which are seldom preserved (Sinitshenkova 1987, 2002, Zwick 2000). Reviewing the fossil record of the Plecoptera, Cui et al. (2019) noted that the taxonomic placement of many fossils is poorly established and needs to be reevaluated. It is likely that an increased understanding of the Plecoptera fossil record will help better resolve the biogeographic and evolutionary history of Plecoptera.

Paleontological Studies of Plecoptera

According to Jouault et al. (2022a), the fossil record of stoneflies comprises 322 species (130 genera), with 1,742 fossil specimens in total. The oldest fossils attributable to stoneflies date back to the Carboniferous period. Béthoux et al. (2011) described a 300 Mya Pennsylvanian stem-stonefly, *Gulou carpenteri* Béthoux et al., and assigned it to the newly established family Guloidae. Its classification within Plecoptera was later challenged by Aristov (2014). However, Shubnel et al. (2019) restored the Guloidae as a stem-group within Plecoptera, while also describing another Guloidae species from the Carboniferous of France. Additionally, Shubnel et al. (2019) introduced the family Fatjanopteridae—containing 2 species from the Carboniferous of France and early Permian of Russia—within the stem-group Plecoptera.

The Permian period (299 to 252 Mya) boasts a rich fossil record of Plecoptera, including both adult specimens and nymphs (Sinitshenkova 1987, 2004, Carpenter 1992). Interestingly, the wing venation of many Permian taxa closely resembles that of modern stoneflies, with some Permian fossils initially classified within extant families such as Eustheniidae (Tillyard 1935) and Gripopterygidae (Riek 1973, 1976). However, these attributions were later partially reevaluated; Sinitshenkova (1987) separated Permian taxa previously treated within Gripopterygidae into a distinct family, Euxenoperlidae. Nonetheless, some Permian fossils are still categorized within Eustheniidae, such as several species of the genus *Boreoperlidium* from Russia (Sinitshenkova 2013, 2018). Conversely, some Permian taxa lack clear family attribution, such as the genus *Afroperla* from South Africa (van Dijk and Geertsema 2004). The majority of Permian stoneflies belong to extinct families, including Palaeonemouridae, Palaeoperlidae, Perlopseidae, Tshekardoperlidae, Euxenoperlidae, and Perlapsocidae (Carpenter 1992, Pinto and Piñeiro 2000, Sinitshenkova 2002). However, the phylogenetic relationships of these Permian families to modern clades remain largely uncertain. The wing venation is often the only reliable set of characters due to preservation limitations, although its variability in extant and extinct stoneflies has been documented (Béthoux 2005, Jouault et al. 2021). Grimaldi and Engel (2005) proposed a cladogram positioning Permian families as either stem-Plecoptera or stem-Antarctoperlaria. According to Letsch et al. (2021), stem stoneflies were globally distributed during the Permian, while the crown-group originated in the Northern Hemisphere and later dispersed to Gondwana during the Jurassic, ca. 180 Mya. Consequently, Permian fossils, especially those from the Southern Hemisphere, are considered members of the stem-group by Letsch et al. (2021).

Since the Mesozoic era (252 to 66 Mya), some extant families have been reliably documented, as summarized by Cui et al. (2018). The Middle Jurassic Daohugou Formation (China) has yielded the oldest occurrences of several extant families, including Pteronarcyidae (Cui et al. 2016), Capniidae (Liu et al. 2009), Notonemouridae (Cui et al. 2018) and Taeniopterygidae (Liu and Ren 2008). The oldest record of Leuctridae was discovered in the Early Cretaceous locality of Khasurty in Russia (Sinitshenkova 2011; phylogenetic placement reassessed by Cui et al. 2018), while the oldest Nemouridae date back to the Early Cretaceous of Liaoning (Yixian Formation) in China (Liu et al. 2008).

In the Mesozoic era, the earliest records of Gripopterygidae, belonging to antarctoperlarian families, were documented in the Early Cretaceous (145 to 101 Mya) of Russia (Sinitshenkova 1992, 1998) and Australia (Jell and Duncan 1986), while Eustheniidae were found in the Middle Triassic (247 to 237 Mya) of Australia (Riek 1954). However, the familial attribution in the original descriptions was often marked as uncertain and may require revision. Additionally, a species named *Sinisharaperla zhaoi* Liu et al. 2007, initially considered part of the Antarctoperlaria lineage in the Late Jurassic/Early Cretaceous (164 to 100 Mya) was later reclassified under Systellognatha (Cui et al. 2015).

Except for families found in modern fauna, several lineages that existed solely during the Mesozoic era have been identified. The precise phylogenetic placement of some of these extinct Mesozoic families remains uncertain, although they are typically assigned

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to higher clades within the Plecoptera phylogeny. Euxenoperlidae and Siberioperlidae were considered stem-Antarctoperlaria by Grimaldi and Engel (2005). Sinitshenkova (2002) places these families within "Gripopterygomorpha," a clade that is likely not monophyletic and is mainly supported by homoplasic characters (Zwick 2000, Cui et al. 2015). Nonetheless, it mostly comprises families of Antarctoperlaria, leading Sinitshenkova (2002) to suggest affinities with the latter infraorder. Perlariopseidae and Baleyopterygidae are placed within Euholognatha by Grimaldi and Engel (2005), a classification that aligns with Sinitshenkova (2002), who placed these families (together with Mesoleuctridae) in the "Nemourina" clade, roughly corresponding to Euholognatha. Pronemouridae, another extinct Mezosoic family possibly related to Euholognatha, forms a sister lineage to the Nemouridae + Notonemouridae clade (Liu et al. 2011). Finally, the Oecanthoperlidae was initially described in Grylloblattida (a polyphyletic grade encompassing extant Grylloblattidae and diverse putative extinct relatives; Strozhenko 1988) and later transferred to stoneflies (Sinitshenkova and Aristov 2012). Platyperlidae, a Mesozoic family, is thought to belong to the stem Systellognatha by Grimaldi and Engel (2005), a placement consistent with the hypothesis of Sinitshenkova (2002), who uses the clade "Perlomorpha" to unite the same taxa.

The fossil record of stoneflies is relatively rich in amber deposits. Mesozoic ambers, particularly the mid-Cretaceous Kachin amber (ca. 98 Mya, Cenomanian; Northern Myanmar), have yielded a significant number of stonefly inclusions, including representatives of both extant families (ie Perlidae, Peltoperlidae) and extinct families (eg Petroperlidae). Numerous new taxa have been described recently, including several new genera and subfamilies (eg Sroka et al. 2018, Chen and Wang 2019, Jouault et al. 2022b, Chen 2023). Considering the large amount of available material and the rapid pace of publications, it is likely that more descriptions will emerge in the near future along with taxonomic revisions of existing higher taxa. A nymph of Plecoptera was recently discovered in the Ypresian Oise amber (ca. 55 to 53 Mya, Ypresian) but is not yet formally described (C. Jouault, pers. obs.). The late Eocene Baltic amber (ca. 38 to 34 Mya, Priabonian) stands out as the most extensively studied amber deposit, with stonefly descriptions dating back to the mid-19th century (Pictet and Hagen 1856). All the taxa found in Baltic amber belong to extant families (ie Taeniopterygidae, Leuctridae (Fig. 1R), Nemouridae, Perlidae, and Perlodidae), with 10 extant stonefly genera already recorded along with 5 extinct genera (Caruso and Wichard 2010, 2011, Chen 2018a, b, c, Jouault et al. 2021, Chen 2022). Other amber deposits have yielded a comparatively smaller number of stonefly inclusions. For instance, late Eocene Rovno amber only yielded inclusions of 2 extinct genera (*Rovnocapnia* from Capniidae and *Palaeoleuctra* from Leuctridae) (Sinitshenkova 2009). The Miocene Dominican amber (dated 19 to 16 Mya, Burdigalian) biota encompasses a single monotypic extinct genus, *Dominiperla* (Perlidae; Stark and Lentz 1992). Similarly, the recently discovered Miocene Zhangpu amber (between 14.8 ± 0.6 Mya and 14.7 ± 0.4 Mya, Langhian) from China has yielded a single Plecoptera fossil (*Amphinemura himberii* Xu et al. 2023), which was identified as belonging to the Nemouridae family (Xu et al. 2023).

The Mesozoic fossil record of stoneflies, documented mainly from imprints or compressions, starkly contrasts with the amber fossil record. While amber deposits have yielded numerous species, only a few have been documented from nonamber deposits, with entire periods lacking fossil stonefly species altogether (Jouault et al. 2022a). Among the rare species described from rock fossils is *Megaleuctra jewetti* (Lewis 1969), a fossil species belonging to the rare North American genus *Megaleuctra*. However, the disparities observed between the 2 modes of fossilization (amber vs. rocks) do not stem from a scarcity of specimens, but rather from a bias in description practices. Rock fossils pose challenges for study due to the poor preservation of diagnostic characters, such as genitalia, leading to uncertainties or difficulties in classification. In contrast, specimens trapped in amber preserve the 3D morphology of organisms and sometimes internal characters, facilitating more accurate classifications. Consequently, paleoentomologists have favored amber specimens, somewhat neglecting rock fossils. For instance, undescribed rock specimens are known from various worldwide localities, such as adults from the Miocene of the Montagne d'Andance (France), although they have yet to be formally described.

In summary, the fossil record of stoneflies can be categorized into 3 distinct family assemblages: (i) the Paleozoic era, which comprises extinct lineages categorized as either stem-Plecoptera or taxa with uncertain affinities when considered within extant families; (ii) the Mesozoic era, which includes extinct lineages alongside the earliest representatives of modern families, albeit belonging to their stem groups, and is marked by the decline of Paleozoic lineages; and (iii) the Cenozoic era, characterized by the emergence of modern families and the extinction of certain Mesozoic lineages. These 3 assemblages are subject to refinement as the systematics of Plecoptera advances. Importantly, they also align with significant paleoenvironmental changes, raising questions about the timing, causes, and implications of the waxing and waning of these various clades (Jouault et al. 2022a).

Embryological Studies of Plecoptera

Comparative embryological approaches can potentially provide deep phylogenetic information that can help to resolve uncertain relationships (Mashimo et al. 2014, Tomizuka and Machida 2015). Although detailed studies have been conducted on Pteronarcyidae (Miller 1939) and Perlidae (Kishimoto and Ando 1985), embryological information on Plecoptera remains fragmented, and our embryological knowledge of Antarctoperlaria is almost completely lacking. Recently, Mtow and Machida (2018a, b) and Mtow et al. (2021) conducted comprehensive comparative embryological studies on Plecoptera using 9 arctoperlarian families (Scopuridae, Taeniopterygidae, Leuctridae, Capniidae, Nemouridae, Perlidae, Chloroperlidae, Perlodidae, and Peltoperlidae) along with 3 antarctoperlarian families (Eustheniidae, Austroperlidae, and Gripopterygidae), to reconstruct the embryonic groundplan of Plecoptera.

Based on ultrastructural analysis using scanning and transmission electron microscopes, Mtow et al. (2021) suggested the following evolutionary scenario in Plecoptera eggs: (i) contrary to Zwick's suggestion (Zwick 2000), the thin and less-sclerotized chorion in Austroperlidae of Antarctoperlaria and Euholognatha of Arctoperlaria is a potential groundplan of Plecoptera. (ii) The sclerotized and hard chorion was independently acquired by Eustheniidae and Gripopterygidae of Antarctoperlaria and Systellognatha of Arctoperlaria (Fig. 6A). (iii) A significant ultrastructural difference between the eggs of Gripopterygidae and those of Systellognatha indicates that these structures were also independently derived.

In the comparative embryological study of 9 arctoperlarian stoneflies by Mtow and Machida (2018a), they suggested that: (i) the embryo covered with amnioserosal folds in the earliest stage of development forms the "ball-shaped compressed embryo," which represents a potential autapomorphy of Plecoptera. (ii) The embryo then elongates along the egg surface, which supports the affiliation of Plecoptera to Polyneoptera as this feature represents

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one of polyneopteran embryological autapomorphies (Mashimo et al. 2014). (iii) After the elongation, the embryo sinks into the yolk with its cephalic and caudal ends remaining on the egg surface, kept in s-shape posture, and this unique posture may be regarded as an apomorphic feature of Plecoptera. Mtow and Machida (2018a) also discuss the interrelationship within Plecoptera, suggesting the relationship of (Scopuridae + Taeniopterygidae + Leuctridae) and (Ptero narcyidae + Peltoperlidae) based on katatrepsis types. To reconstruct and understand the groundplan and phylogeny of Plecoptera further, additional embryological studies of Plecoptera covering all families and major lineages, especially the Antarctoperlaria, are strongly needed.

Clear Definitions of Major Clades

Illies (1961, 1965) divided Plecoptera into 3 suborders: Archiperlaria, Filipalpia, and Setipalpia, based on a study of their origin, geographic distribution, and phylogeny. Building on the research of Illies, Zwick (1973, 1980), combined with an analysis of the characteristics, geographical distribution, and phylogeny of the internal organs, divided Plecoptera into Antarctoperlaria and Arctoperlaria. Arctoperlaria is further divided into 2 infraorders, Systellognatha and Euholognatha. Much of the diagnostic character content within this section is summarized by Zwick (2000).

Synapomorphies of Plecoptera

Plecoptera do not have an ovipositor (Fig. 3C and D), except in some Leuctridae (Fig. 3E) and Notonemouridae, where it is secondarily derived (Zwick 2000). The anterior ends of internal genital organs (ovaries and testes) are fused and form a loop (Fig. 3A and B). Males have 2 pairs of stacked seminal vesicles that are looped anteriorly (Fig. 3B). All stoneflies have an accessory circulatory organ, sometimes referred to as the cercus heart. There are intersegmental muscles in the thorax and abdomen of nymphs (Zwick 1973, 2000). The fusion of amnioserosal folds completed in the earliest stage of development to form a ball-shaped "embryo-amnion composite" is a potential autapomorphy of Plecoptera (see Mtow and Machida 2018a, 2018b). After the embryo elongation on the egg surface, the embryo sinks into the yolk with its cephalic and caudal ends remaining on the egg periphery, kept in a s-shape posture (this may be regarded as apomorphic to Plecoptera) (Mtow and Machida 2018a).

Characteristics of Antarctoperlaria

Monophyly is supported in Antarctoperlaria by the presence of a unique sternal depressor of the fore trochanter, and the absence of a typical tergal depressor of the fore trochanter. The presence of floriform chloride cells (Fig. 3F) provides additional support of monophyly among antarctoperlarian species. The only suggested synapomorphy for the group is a thickened sclerotized area in the anal region of the forewing (Zwick 2000).

Diamphipnoidae

Diamphipnoidae is currently composed of 6 species distributed in 2 genera (DeWalt et al. 2024), including the largest extant Plecoptera genus (*Diamphipnoa*, Fig. 1Q) which is endemic to the southern *Nothofaghus* (southern beech) forest of southern South America in Argentina and Chile (Table 3). The monophyly of this taxon is sustained by molecular analysis (McCulloch et al. 2016, Ding et al. 2019, Letsch et al. 2021). Several characters are likely synapomorphies of the family (Zwick 2000), which include 4 pairs of complex abdominal gills that are either epaulet- or brush-shaped (Fig. 4A), a condensed abdominal nerve cord (Illies 1962), a slender mediobasal appendage on the male paraprocts, serrate tarsal claws (Nelson 1991), and the secondary absence of atypical nymphal swimming muscles (Zwick 1973, 1980).

Eustheniidae

Eustheniidae has a Southern Hemisphere distribution (Table 3) and contains 27 species across 8 genera (DeWalt et al. 2024). Nymphs are carnivorous, and long-lived with a lifespan of 2 to 3 years (Zwick 1979). Eustheniids have long filamentous gills on their abdominal segments 1 to 6, which are present in the newly hatched nymphs (Zwick 1979). Adults are large, and often brightly colored (Fig. 1P). The smooth and rounded posterior margin of the hind wing without an incision delineating the anal region is a prominent feature among Eustheniidae (Fig. 4D, Zwick 1979, 2000). Synapomorphies that define Eustheniidae include tibia with only a single medially displaced apical spur, the attachment of prosternal trochanter depressor being shifted back across furcal bases to a position next to spina, the last abdominal ganglion being shifted from segment 7 to segment 8, nymphs that are carnivorous with slender mandibles, nymphs have long filamentous gills on their abdominal segments 1 to 6 (Fig. 4B and C) (Zwick 1979).

Gripopterygidae

Gripopterygidae have a circum-Antarctic distribution (Table 3) with 55 extant genera and about 330 described species (McLellan 1977, DeWalt et al. 2024). The replacement of the terminal filament with a retractable rosette of fine gill filaments in nymphs is a proposed synapomorphy for the family (Fig. 4F and G) with apparent examples of loss in genera *Notoperla*, *Vesicaperla*, and *Rakiuraperla* (Zwick 1973, 2000, McLellan 1977). Adults range from 7 to 38 mm in size, with body colors from light brown to blackish, often with patterned wings, with the distal half showing few to many cross-veins (Fig. 1N). They can be wingless or macropterous, with specialized mouthparts for scraping or shredding algae, fungi, and detritus (McLellan 1983, Stark et al. 2009). Male paraprocts are generally larger than those of females, with a simple female subgenital plate.

Nymphs are mostly brown and cylindrical, some flattened (Stark et al. 2009). The subfamily Antarctoperlinae is characterized by primitive abdominal segmental nerves and ventral longitudinal muscles, similar to Austroperlidae, with nerves lying on top of muscles. Antarctoperlinae and the subfamily Zelandoperlinae are both thought to have an independent loss of tibial spurs (Fig. 4E) (Zwick 2000). Gripopteryginae and Zelandoperlinae both have mouthparts for scraping and shredding as nymphs, whereas Antarctoperlinae are primarily shredders. Leptoperlinae have species that exhibit both feeding behaviors (Stark et al. 2009).

Austroperlidae

Austroperlidae has a circum-Antarctic distribution (Table 3) and includes 15 species across 10 genera (DeWalt et al. 2024). Nymphs are shredders and have tube-like gills in the membrane between the posterior margin of tergite 10 and the anus, and another gill on top of the subanal lobe (McLellan 1997). Adults are dark brown to black, with bright yellow or white patches on the wing margins and tibia (Fig. 1O, McLellan 1997, 2001, Foster et al. 2021). This distinctive color pattern is thought to be aposematic, with several Austroperlidae species unpalatable to predators as they contain hydrogen cyanide (Foster et al. 2021, 2023). The presence of beaded gills derived from the paraproct apex and distal cercal segments (Fig. 4H) is a familial synapomorphy (Zwick 2000).

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Characteristics of Arctoperlaria

Monophyly is strongly supported by a complex (structural and behavioral) character syndrome related to mate-finding: drumming (Fig. 3G and H, Supplementary File 1). Drumming, tremulation, or behavior derived from drumming and/or related male structures (Fig. 3I–L, ventral lobe, hammer, vesicle, hairbrush) is known in all families of Arctoperlaria except for Scopuridae. The occurrence of cervical gills, several types of osmoregulatory organs (unicellular caviform chloride cells, and coniform and bulbiform cell complexes), and similar kinds of chloride cells still cannot be proposed as evidence of arctoperlarian monophyly (Zwick 2000).

Characteristics of Euholognatha

An unpaired corpus allatum fused to the aorta is ample evidence of monophyly within Euholognatha. The softened egg chorion (Fig. 5A) and the presence of segmental nerves that cross under longitudinal abdominal muscles (rather than nerves that lie on top of these muscles) also appear to be synapomorphies of the group (Zwick 2000).

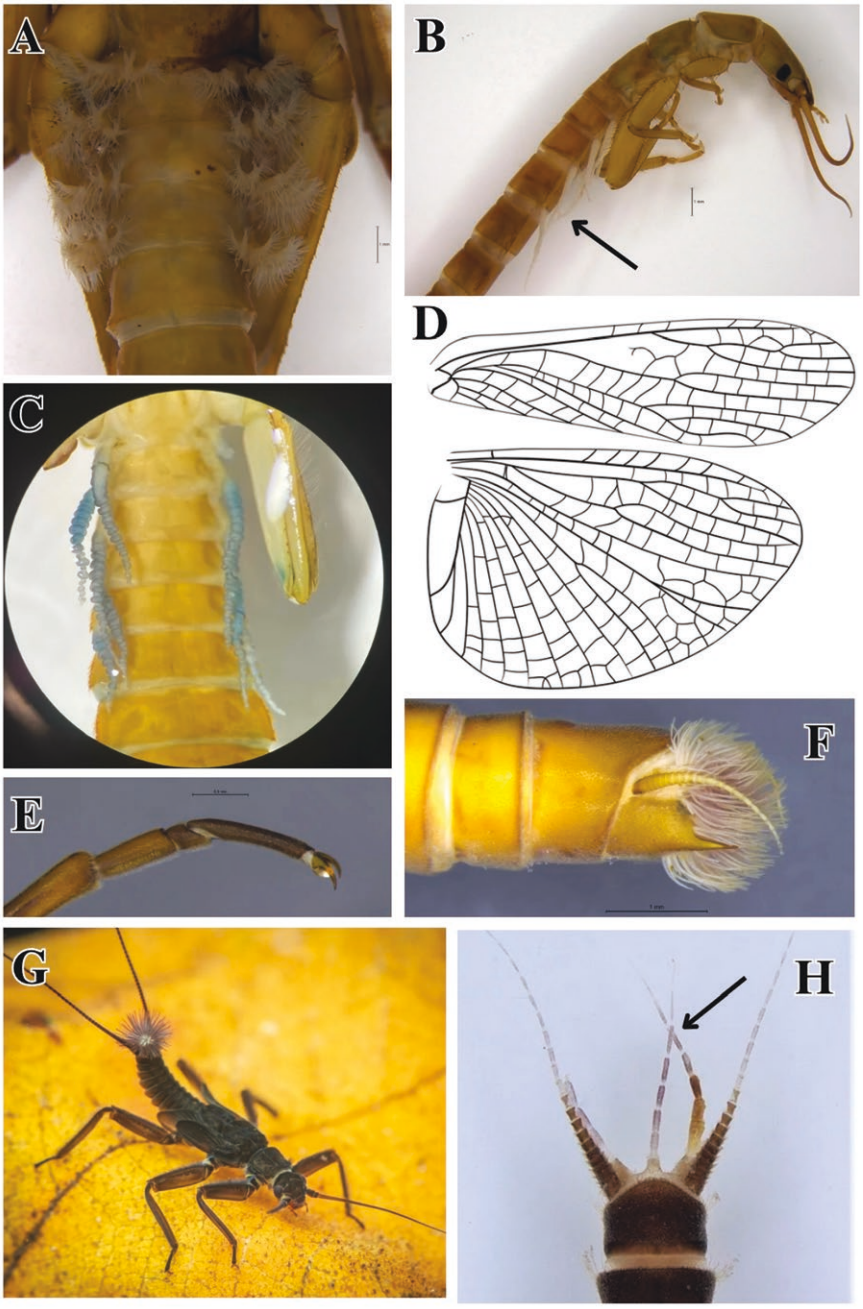

Fig. 4. Main Identifying features of Antarctoperlarian families: A) Diamphipnoidae 4 pairs of complex abdominal gills in Diamphipnoa helgae (Illies 1960), B–D) Eustheniidae. B) Long filamentous abdominal gills (arrowed) in *Neuroperla schedingi* (Navás 1930), C) Structure of filamentous abdominal gills in *Cosmioperla wongoonoo* (Theischinger 1983), D) Rounded hind wing without notch separating the anal region in *Eusthenia costalis* Banks 1913, E–G) Gripopterygidae: E) Loss of tibial spurs in *Pehuenioperla microptera* (Pessacq and Duarte 2020), F) Retractable rosette of fine gill filaments in *Pehuenioperla microptera*, G) Nymph of a *Gripopteryx* sp. with its rosette of gill filaments protruding, Austroperlidae: H) Tube-like gills (arrowed) on Tergite 10 in *Penturoperla barbata* (Illies 1960). Photo credits: A) Tacio Duarte, B) Tacio Duarte, C) Anna Eichert, D) Abigail Kirkaldy, E) Tacio Duarte, F) Tacio Duarte, G) Frederico Salles, H) Tacio Duarte.

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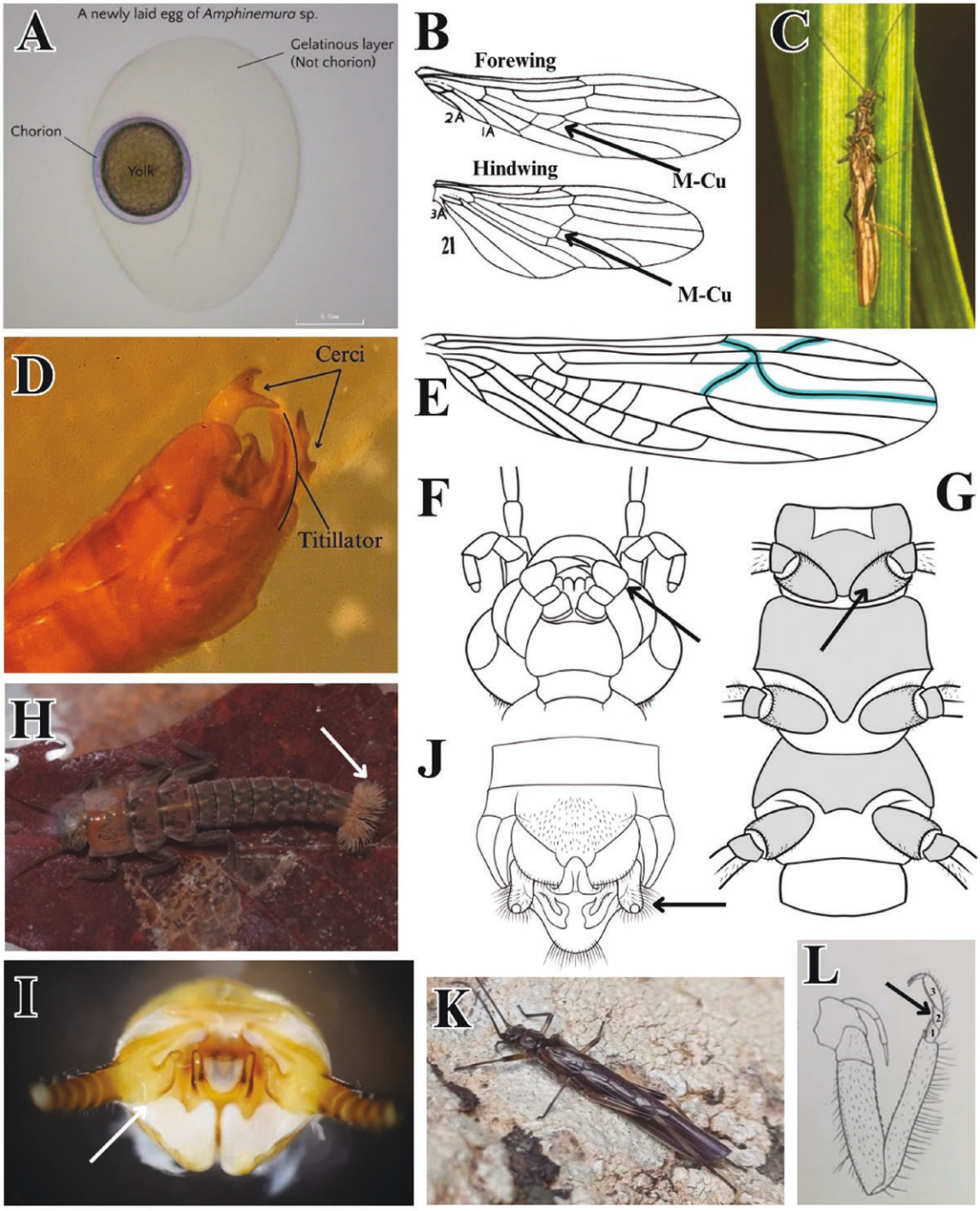

Fig. 5. Main Identifying features of Euholognathan families: A) Euholognathan egg structure, with a soft chorion, B) Capniidae: *Eucapnopsis* sp. M-Cu cross-veins (arrowed) and wing venation, modified from Hanson (1946), C and D) Leuctridae: C) *Perlomyia collaris* (Bank 1906) with rolled wings, D) Modified paraprocts forming titillators in *Leuctra* sp., E–G) Nemouridae: E) Forewing of *Nemoura* sp. showing the "Nemourid X" seen in Nemouridae, and some Notonemouridae, Capniidae and Taeniopterygidae, F) Disk-like terminal labial palpomere (arrowed) in *Soyedina* sp., G) Enlarged, transverse fore-coxae (arrowed) of an Amphinemourinae adult, H and I) Scopuridae: H) Delicate filamentous anal gills in a *Scopura montana* nymph, I) Male basal cercomere with prong in *Scopura montana*, J and K) Notonemouridae: J) Terminalia of a male *Afronemoura amatolae* (Balinsky 1956), showing single segmented cerci (arrowed), K) *Afronemoura amatolae* adult with rolled wings, L) Taeniopterygidae *Taeniopterx nivalis* (Fitch 1847), right hind leg showing elongated second tarsal segment (arrowed), modified from Frison (1935). Photo credits: A) Shodo Mtow, B) John Hanson, C) Richard Baumann, D) Anna Eichert, E) Abigail Kirkaldy, F) Abigail Kirkaldy, G) Abigail Kirkaldy, H) Shodo Mtow, I) Shodo Mtow, J) Abigail Kirkaldy, K) Abigail Kirkaldy, L) Theodore Frison.

Capniidae

Capniidae, the Holarctic (Table 3) small winter stoneflies or snowflies currently have 26 genera and 307 accepted species (DeWalt et al. 2024). With unpatterned black or dark brown pigmented bodies (Fig. 1A), adults tend to be between 7 mm and 12 mm (Claassen 1931). Adults can be easily distinguished from

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other families in the Nemouroidea with their usually long many-segmented cerci (Baumann et al. 1977), being a particular exception *Capnioneura* (Ris 1905) with only one cercal segment (Muranyi et al. 2014). Synapomorphies include reduced M-Cu-cross-veins such that no more than 2 are present (Fig. 5B), and no more than one Cu-crossvein. In addition, a number of reproductive structure modifications are distinctive of the family. Female Capniidae do not have a spermatheca but instead have wide oviducts for sperm storage. In males, medial lobes of the epiproct and paraprocts facilitate sperm transfer. The paraprocts merge into a fusion plate, which has a basal opening that is situated above the penis. The epiproct varies in morphology between genera, and when miniaturized, the fusion plate acts as a functional penis during copulation (Zwick 2000). A comparative taxonomic review for many genotypes in Capniidae is elucidated in Hanson (1946).

Leuctridae

Leuctridae are Holarctic (Table 3), with 18 genera and approximately 400 species (DeWalt et al. 2024). Commonly referred to as the rolled-winged stoneflies, leuctrid wings remain rolled around the body at rest (Fig. 5C). Apparent synapomorphies include the bases of both paraprocts forming a common bulbous structure with retractor muscles; the penis is never developed, but instead has modified apices of the inner paraproct lobes that take its role (sometimes these are referred to as titillators or specillums, Fig. 5D); and the presence of sessile seminal receptacles at the front end of vagina, between the entrances of the oviducts (Zwick 2000).

Nemouridae

Nemouridae have a Holarctic distribution (Table 3) and have 800 validated species within 24 genera (DeWalt et al. 2024). These stoneflies are commonly identified by observing the "Nemouridae X" vein in their wing (Figs. 1F and 5E). Autapomorphies of the family are a large, disk-shaped terminal labial palpomere (Fig. 5F), and enlarged, transverse fore-coxae, with protruding median parts that nearly touch (Fig. 5G). The testes are long and resemble a star, and the follicles are all attached to the efferent duct at one singular point. Additionally, unpaired seminal vesicles with tubular ducts entering at the anterior end is a trait that unifies Nemouridae (Zwick 2000). A fused abdominal nerve cord at both ends, with only 5 free ganglia, is a synapomorphy shared with some Notonemouridae (Zwick 2000, Stevens et al. 2018).

Notonemouridae

Notonemouridae are distributed across the Southern Hemisphere (Table 3), where they are represented by 124 species in 24 genera (Illies 1975, McLellan 1991, Fochetti and Tierno de Figueroa 2008, Stevens et al. 2018, DeWalt et al. 2024). The family lacks any clear apomorphies and is instead defined by features shared with their assumed sister group, Nemouridae, although this relationship has been challenged by numerous molecular studies. These include: adult cerci reduced to a single segment (Fig. 5J, Cui et al. 2019, Sroka and Prokop 2023), a forked mesothoracic pleural arm (Zwick 1973, 2000), the penis and retractor muscles are lost (Zwick 1973, 2000), an unpaired muscular ejaculatory duct (Zwick 1973, 2000), and a shortened abdominal nerve cord, with no more than 7 free ganglia (Zwick 2000, Stevens et al. 2018). The "Nemouridae X" pattern in the wing is occasionally present (Fig. 5E) but is the remnant of a plesiomorphic wing vein condition in Nemouroidea (Zwick 2000). Similarly to Leuctridae, notonemourids sometimes have rolled wings at rest (Figs. 1E and 5K).

Taeniopterygidae

Their distribution is Holarctic (Table 3), with 21 genera and approximately 122 species (Fig. 1B, DeWalt et al. 2024). Adults contain a second tarsal segment that is elongated and synapomorphic of the family (Fig. 5L). This second tarsal segment can be longer, or equal in length to the first tarsal segment (Stewart and Stark 1988). In addition, the first segment of the cerci is extended in males and the penis is reduced and eversible. Females have reduced vaginas that are easily visible in the middle of sternite 8 (Zwick 2000).

Scopuridae

Scopuridae (Fig. 1C) comprise a single genus with 8 species (DeWalt et al. 2024), and are found in the Eastern Palearctic within Japan, North Korea, and South Korea (Table 3). *Scopura* species (except in late-instar and adult males) have a delicate terminal filament. A single gill filament originates from the soft inner paraproct base, not from the paraproct tip. Nymphal gills (Fig. 5H) rise from the intersegmental membrane between segments 9 and 10. Other apparent synapomorphies include male epiprocts that have an eversible membranous tube armed with sclerites, and a prong on the male basal cercus segment (Fig. 5I, Zwick 2000).

Characteristics of Systellognatha

Systellognathan eggs have a hardened chorion (Fig. 6A). The reduction of adult mouthparts, especially weak soft mandibles and elongate, sometimes whip-shaped annulate palpi are distinctive of systellognathan species. If adult mandibles are secondarily sclerotized, they are of a derived shape lacking a mola. The Systellognatha groundplan includes a complex male epiproct with modified parts of antecosta 10 sunk into a pouch dividing tergite 10 into hemitergites (Fig. 6B). Atypic intersegmental nymphal swimming muscles are remarkably developed. Females have accessory glands on the receptacular duct (Zwick 2000).

Chloroperlidae

Commonly referred to as the green stoneflies, or sallflies (Fig. 1H), chloroperlids are found across the Holarctic region with 221 species in 19 genera (Table 3, DeWalt et al. 2024). The family lacks convincing autapomorphies (Zwick 2000), but each subfamily is united by the subsequently listed characters. Paraperlinae (2 genera, 6 species) were previously united by flat thoracic sternites, with parallel furcal pits connected to the posterior edge of the basisternum (Fig. 6C, Zwick 2006). This is shared with *Kathroperla*, and may, therefore, represent a plesiomorphic condition, or was independently derived. Zwick (2006) noted the sister relationship of *Utaperla* and *Paraperla* was supported by the loss of a connection between the spina and furcal pits, which was replaced with a long median internal ridge unconnected to the furcal pits. This can now be considered an apomorphy for the subfamily. The anal lobe is slightly reduced, with only 3 anal veins in the hind wing (Zwick 2006).

Chloroperlinae (17 genera, 215 species, DeWalt et al. 2024) is supported by a reduced anal lobe, resulting in a fore- and hind wing of almost equal size (Fig. 6E), a very small terminal maxillary palpomere, and a shortened, forward-curved epiproct that is fused to the antecosta (Fig. 6D, Zwick 2000, 2006).

Kathroperlidae

Kathroperlidae has a Nearctic distribution (Table 3) and contains 4 species from 1 genus (Fig. 1J, DeWalt et al. 2024). *Kathroperla* adults have a well-developed vesicle on the ninth male sternite, the transverse orientation of the anterodorsal margin of the male genitalia epiproct.

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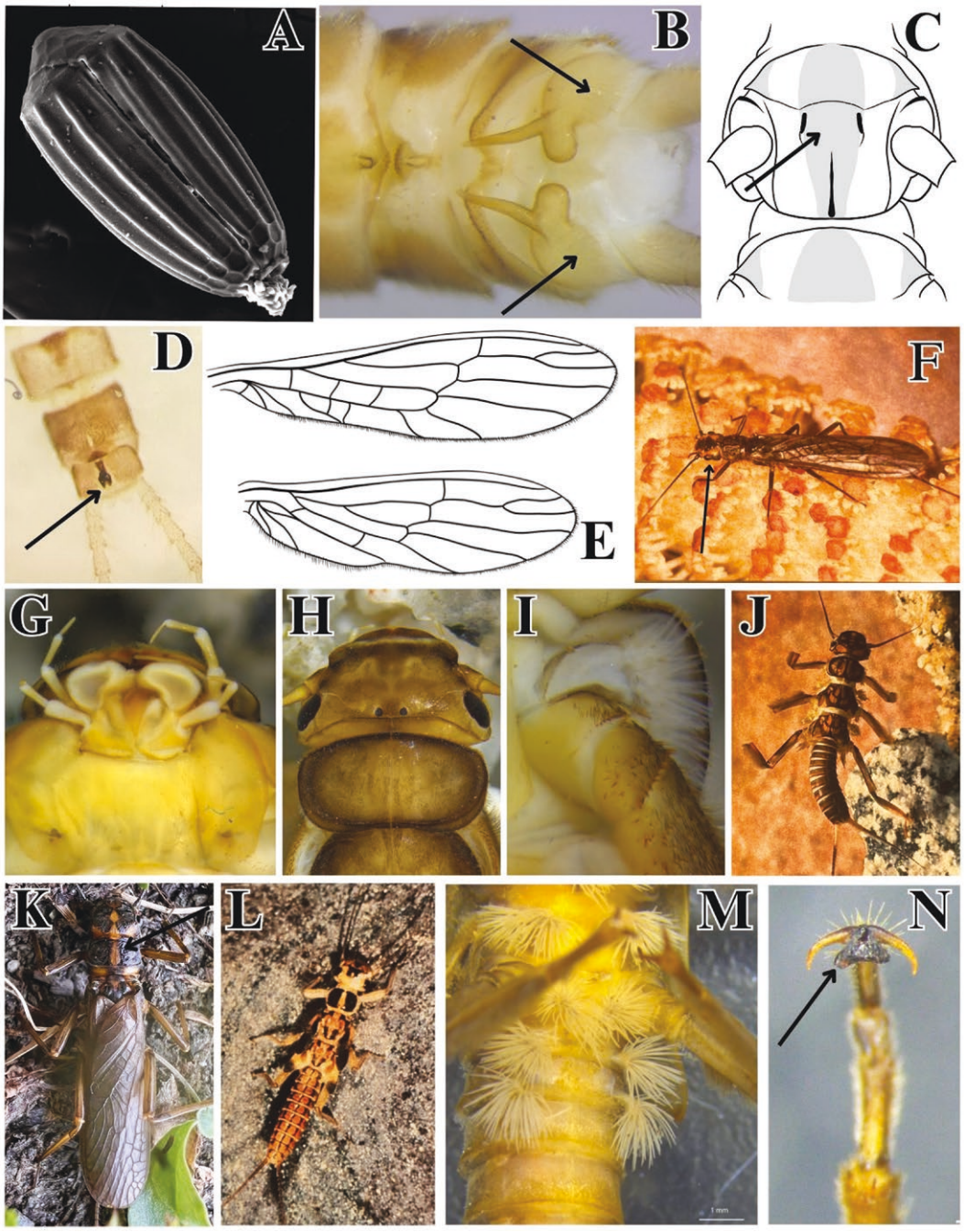

Fig. 6. Main Identifying features of Systellognathan families: A) *Neoperla transvaalensis* (Enderlein 1909) egg structure, with the hard *Systellognathan chlorion*, B) Male terminalia of *Neoperla burgeoni* (Navás 1926), with Tergite 10 divided into hemitergites (arrowed), C–E) Chloroperlidae: C) Mesothorax of Utaperla sp. (Paraperlinae) with disconnected furcal pits (arrowed), D) Fused, forward-curved epiproct of *Siphonoperla torrentium* (Pictet 1841) (Chloroperlinae), E) Wings of *Siphonoperla torrentium* with a reduced anal lobe in hind wing, F) Kathroperlidae *Kathroperla takhoma* (Stark & Surdick 1987) elongated head with eyes at mid-point (arrowed), G–J) Perlidae: G) Large, inflated paraglossae in *Neoperla* sp., H). Expanded genae covering mandible bases in *Neoperla* sp., I) Tufted thoracic gills in *Neoperla* sp., J) Tufted thoracic gills in *Doroneuria baumanni* (Stark & Gaufin 1974) nymph, K and L) Perlodidae: K) *Perlodes microcephalus* (Pictet 1833) with the characteristic orange-yellow stripe visible (arrowed), L) Contrasting color patterns in an *Isoperla lata* (Frison 1942) nymph, M and N) Pteronarcyidae: M) *Pteronarcys californica* (Newport 1848) with branched gills on the thorax, and at least 2 abdominal segments, O) *Expanded arolium* (arrowed) in *Pteronarcella badia* (Hagen 1874). Photo credits: A) Abigail Kirkaldy, B) Abigail Kirkaldy, C) Abigail Kirkaldy, D) Abigail Kirkaldy, E) Abigail Kirkaldy, F) Richard Baumann, G) Abigail Kirkaldy, H) Abigail Kirkaldy, I) Abigail Kirkaldy, J) Richard Baumann, K) Anna Eichert, L) Richard Baumann, M) John Sproul, N) John Sproul.

They have an elongation of the head postocularly, with their eyes positioned at the mid-point of their head (Fig. 6F, Baumann et al. 1977, Zwick 2000, South et al. 2021a). While not included in the diagnosis of the family, Stark et al. (2015) recognized an autapomorphic elaborate, tuberculate chorion as diagnostic of the genus.

Perlidae

Perlidae (Fig. 1I), are the most speciose family within Plecoptera, spanning 1397 species in 68 genera (DeWalt et al. 2024) distributed worldwide, except in Australia, New Zealand, and the Antarctic regions (Table 3). Apomorphies of Perlidae are subsequently listed.

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The abdominal nerve cord is fused at both ends, with only 6 free ganglia. The nymphal head has extended genae covering mandibular bases and huge maxillae from above (Fig. 6H), inflated paraglossae (Fig. 6G), and a broad mentum covering the maxillae from below. An additional valve is formed by complex folds in the nymphal proventriculus (Zwick 2000). Their thoracic muscle shows a transfer of *ppm*56 to the posterior sclerite and the presence of *ism*24 (Wittig 1955). The bases of their gills have hairy sclerites, sometimes referred to as gill shields. Perlidae have branched thoracic gills (Fig. 6I and J), which are considered autoapomorphic (Zwick 2000).

Perlodidae

Found across the Northern Hemisphere (Table 3), Perlodidae (Fig. 1G) have 390 species in 57 genera (DeWalt et al. 2024). Perlodidae lack convincing apomorphies, but are instead united by combinations of plesiomorphic conditions (Zwick 2000). Perlodidae have cercomeres that are fused together, with an inner sclerite ring, and without an articular membrane. This is a synapomorphy shared with Perlidae (Zwick 2006). Some phenotypic characters are common, but not universal: most adults have a long yellow stripe on an otherwise dark forebody (Fig. 6K), and nymphs are often yellow with contrasting dark patterns (Fig. 6L, Zwick 2000). Apomorphies of subfamilies Isoperlinae and Perlodinae have been proposed (summarized by Zwick 2000), but their monophyly has not been supported by recent molecular analyses (Letsch et al. 2021, García-Girón et al. 2024).

Peltoperlidae

Peltoperlidae (Fig. 1L) are distributed in the Northern Hemisphere (Table 3), with 13 genera and 83 validated species (DeWalt et al. 2024). Adult forewing lengths tend to be between 6 mm and 17 mm (Stark and Nelson 1994, Stark and Sivec 2007). The prothoracic furca- and spinasternum secure together (Uchida and Isobe 1989, Zwick 2000). Male epiprocts are rod-like in shape. Cross-veins are absent in the anal lobe of the forewings for both sexes (Stark and Stewart 1981).

Pteronarcyidae

Pteronarcyidae (Fig. 1K) is a small, Holarctic distributed family of 12 extant species comprising 2 genera (*Pteronarcella* and *Pteronarcys*) in which most species are exceptionally large (Table 3). Proposed synapomorphies for the family include a laterally expanded arolium of the pretarsus (Fig. 6N, Nelson 1991), reduced sclerotization of thoracic ventropleurites and postfurcasterna (Nelson and Hanson 1968), and a reduced ventral vesicle used by males in drumming (Nelson and Hanson 1971). Pteronarcyidae are easily distinguished from other Holarctic stoneflies by their large body size (eg *Pteronarcys* is 30 to 50 mm, but both *Pteronarcella* species are moderately sized, eg 12 to 18 mm) combined with the presence of branched gills on the thorax and at least 2 abdominal segments in nymphs (Fig. 6M), as well as heavy wing venation in adults (eg see Cui et al. 2016).

Styloperlidae

Styloperlidae (Fig. 1M) are found throughout the Eastern Palearctic and Oriental regions (Table 3) and have 12 species in 2 genera (DeWalt et al. 2024). Both included genera (*Cerconychia* and *Styloperla*) have a dense setal brush on male sternite 9 where other Arctoperlarian male vesicle and hammers exist. Styloperlidae have a unique "X" shaped sclerotization of male sternite 10. Nymphs lack spurs but have trifurcates and other strongly modified setae on the tarsi and tibial apex. The epiproct is reduced and unsclerotized. Nymphs are slender and gill-less, the pro-spinasternum is free (Zwick 2000).

Taxonomic Databases

The Plecoptera Species File provides an extensive, invaluable, and comprehensive overview on global stonefly species diversity, distribution, nomenclature, and literature for researchers and enthusiasts. Detailed species descriptions and images are available to allow the reader to explore taxonomic hierarchies and geographic distributions. It yields a unique opportunity to observe and track historical changes in taxonomy within Plecoptera and is an invaluable resource to survey archival publications. Every citation for changes in taxonomy for species is hyperlinked for ease of access to researchers, and the website is continually updated and maintained by the Plecoptera Species File group. For each major group there is a map that accompanies search results to allow the user to visually observe estimated range distributions. For more information about the history of the database, visit https://plecoptera.speciesfile.org/about (DeWalt et al. 2024).

Regions in Need of Biodiversity Exploration

Of the almost 4,000 stonefly species that have been described worldwide, North America has 765 species whilst Europe has 489 species (DeWalt and Ower 2019). Although there is abundant literature on North American and European stonefly fauna, there is still much work that must be accomplished to fully understand plecopteran biodiversity. For instance, the Southern Appalachian region in the United States is regarded as a biodiversity hotspot that has continued to yield new stonefly species (Metzger and Grubbs 2023), while the Balkans and Eurasian Caucasus Mountain Ecoregions similarly report high diversity rates for stoneflies (Kazanci et al. 2017; Rušiti-Dauti et al. 2024). Australia (including Tasmania) and New Zealand have relatively well-known stonefly diversity, with 191 and 104 documented stonefly species, respectively (DeWalt and Ower 2019).

Central and South America collectively boast one of the highest rates of species descriptions (DeWalt and Ower 2019). In Froehlich's *Catalog of Neotropical Plecoptera* (2010), 508 valid species names are listed, while the Neotropical species list by Pessacq et al. (2019) expands this to 596 valid names. An additional 21 new species have been described between 2019 and 2024, leading to a total of about 620 species. However, despite advances in taxonomy in this region over time, extensive geographical regions of South and Central America remain unexplored (Kondratieff and Armitage 2019, Castillo-Velásquez et al. 2023, Duarte and Lecci 2023, Rippel et al. 2023). For instance, only one genus (*Anacroneuria*) is found in Central America. It is hypothesized that the thinner eggshell layers and unique features of *Anacroneuria* eggs may allow this genus to survive in neotropical waters, which are characterized by high temperatures and relatively low dissolved oxygen (Fenoglio and Rosciscewska 2003).

In Brazil, vast regions still need to be surveyed for Plecoptera, with no official records of this order in Alagoas, Paraíba, and Rio Grande do Norte (Duarte and Lecci 2023). Historically, research efforts and funding have been concentrated in the southeast and south, resulting in a higher number of recorded Plecoptera species there than elsewhere (Duarte and Lecci 2023). This suggests that many new species and unrecorded occurrences are yet to be discovered (Duarte and Lecci 2023). The situation is exacerbated by relentless threats from human activity throughout South America, particularly in Brazil (Agostinho et al. 2005, Ribeiro et al. 2009).

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Several factors contribute to these taxonomic challenges. The scarcity of associated nymphs and adults (the Hackealian shortfall) for most stonefly groups limits opportunities and hinders scientific progress in many areas. This limitation has prevented more in-depth studies of some groups of South American stoneflies, such as inferring phylogenetic relationships based on morphological data and developing more comprehensive diagnoses for genera and species using nymphal characteristics—an essential step for ecological research (Duarte and Lecci 2023, Almeida et al. 2024). Additionally, the lack of molecular data on South American species presents a significant gap. Currently, only 49 out of 212 Brazilian species have molecular data (such as *COI* sequences) available in databases such as GenBank (Duarte and Lecci 2023, Almeida et al. 2024).

Plecoptera diversity in Africa is low; until recently, fewer than 100 species were described across the continent (DeWalt and Ower 2019). Approximately half of these species (15 genera, 7 families) are limited to Morocco, Algeria, and Tunisia in the north (DeWalt et al. 2024), leaving just 41 species from 2 families in the Afrotropical region (40 Notonemouridae in South Africa and Madagascar, with one widespread Perlidae). This low diversity is potentially due to the warm and dry climate across the region (Hynes 1976, Fochetti and Tierno de Figueroa 2008, DeWalt and Ower 2019).

However, recent research indicates that the diversity of stonefly species in Africa has been significantly underestimated (Zwick and Zwick 2023). The widespread genus *Neoperla* has long been considered a single species (*Neoperla spio* sensu lato) after the African taxa were synonymized (Hynes 1952). Hynes (1952) recognized that many established species were based on unreliable habitus characters, but interpreted differences in genitalia as a developmental series, leading to the formation of a highly variable species complex (Zwick 1976, Picker 1980). Recently, Zwick and Zwick (2023) recognized 82 valid *Neoperla* species from sub-Saharan Africa.

Despite this landmark contribution, significant gaps in our knowledge of the African stonefly fauna remain, with many species remaining undescribed. Novel species of *Neoperla* continue to be found (P. Zwick, pers. comm., A. Kirkaldy, in prep), and Stevens et al. (2018) recently identified cryptic species in the South African Notonemouridae, mainly within the *Aphanicerca capensis* Tillyard species complex. Furthermore, distribution data for most species is lacking, and there are no published records of stoneflies from several countries, including Botswana and Mozambique. The latter has a single specimen identified on the citizen science platform iNaturalist. Outside of South Africa, much of Africa remains poorly studied, and further research is needed to understand the diversity and ecology of Plecoptera across the continent.

Many African stoneflies appear to be localized endemics, with almost a third of the South African Notonemouridae only known from type localities (Stevens et al. 2018), and many of the newly described *Neoperla* species identified from only a few historical collections (Zwick and Zwick 2023). The ecological requirements of most species are unknown, and these isolated species may already be in danger of extinction.

China has a diverse stonefly fauna, with 545 species described in the Chinese species catalogue of Yang and Li (2018). However, the number of stonefly species in China has been growing at a rapid rate, with 268 additional species described between 2019 and 2024. DeWalt and Ower (2019) suggest that China will have almost one thousand described species by 2050. There are likely many undescribed stonefly species that are endemic to regions within Central Asia and the Indian subcontinent (Fochetti and Tierno de Figueroa 2008). A recent survey in India found that 93 of 124 species were endemic, but there are still many regions within India that have not been surveyed (Babu et al. 2019). Even though substantial work has been accomplished by Russian taxonomists, 27 species and 1 genus were recently recognized as endemic to the Russian Far East (Teslenko 2009).

The Arctic is one of the most warming biomes in the world due to climate change (Kattsov et al. 2005), yet there is little research to understand the impacts of these environmental changes on aquatic insect populations in this region. Generally, efforts to study stonefly diversity in the Arctic have been restricted to areas with well-established infrastructure, such as maintained roads that allow for accessible sampling (Patenall et al. 2024). Little is known about the thousands of kilometers of freshwater environments in the tundra where stoneflies likely live but have never been surveyed before within the Arctic circle region. To more easily elucidate the responses of stoneflies to climate change in the Arctic, long-term research efforts to understand species diversity, range, and population dynamics must be founded now. By delving into genetic diversity within and between populations, one can hypothesize on the susceptibility of entire populations becoming regionally extinct.

Another priority area for plecopteran biodiversity research is high-elevation mountain ecosystems. Upland species often have unique adaptations that allow them to survive in the harsh alpine conditions (McLellan 1977, 1993, McCulloch et al. 2019a, 2019b) and may have very narrow geographic ranges (McCulloch et al. 2022, Tsyrlin et al. 2022). Globally, mountain habitats are being rapidly altered by climate change (Pepin et al. 2022). These changes include declines in seasonal snowpack, uphill shifts of treelines, increasing water temperatures, and ever-growing risks of flow intermittency (Hotaling et al. 2017).

To clarify how climate change will impact mountain stream and lake ecosystems, an improved taxonomy for resident Plecoptera is needed since stoneflies are often one of the most common taxonomic groups in these ecosystems. For instance, in alpine streams of Glacier National Park, USA, *Lednia tumana* (Nemouridae) comprises more than 60% of the total invertebrate density (Giersch et al. 2017). Due to this distribution and associated climate threats, *Lednia tumana* has been listed as Threatened under the US Endangered Species Act. In the same streams, another nemourid—*Zapada glacier*—is also listed as Threatened under the US Endangered Species Act, but its distribution and taxonomy are more complicated than *L. tumana* because *Z. glacier* co-occurs with congenerics, and as nymphs, it can only be distinguished from other taxa in the group via molecular barcoding (Hotaling et al. 2019). In a limited barcoding effort for *Zapada* in alpine streams of the Rocky Mountains, USA, Hotaling et al. (2019) identified at least 4 potential cryptic lineages of the genus. Thus, between conservation needs and taxonomic uncertainty, stoneflies residing in mountain streams warrant considerably more systematic focus going forward.

Challenges in Advancing Systematic Research

Stoneflies have a global distribution, and we need more effort to expand the capacity for Plecoptera systematics globally. How can we diversify who has access to stonefly collections, who is trained in stonefly systematics, and who is a member of the stonefly research community?

Much great taxonomic and systematic work has been undertaken on stoneflies, but as in other areas of entomology and science more broadly, these works are often published in journals behind paywalls (Packer 2024), and specimens are housed in museums that may be inaccessible to those from other nations for a variety of reasons (Konstantinov and Namyatova 2019, Pinedo-Escatel et al. 2024). Efforts to digitize collections of stoneflies have been slow,

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and in many cases, available digital images are not diagnostic in the nature of the images (ie some taxa may require dissection for proper identification), preventing one from using them in lieu of trips to North American or European museums. Although a massive undertaking, the digitization of existing stonefly records within museums into publicly available databases would be incredibly valuable in accelerating taxonomic studies, as well as other disciplines within biology, such as species distribution modeling (Short et al. 2018).

There are unfortunate inequalities that exist for systematic researchers that work in the Global South when compared to the Global North. For instance, the English language has become a qualification for publishing and scientific discourse in academia, proving as a barrier to the expansion of knowledge in non-English countries. The limited accessibility to next-generation sequencing centers (Helmy et al. 2016) and a lack of institutional support or funding (Meirmans et al. 2019) directly challenge the advancement of biological research in the Global South (Soares et al. 2023, Turba et al. 2025). As evolutionary biologists and plecopterologists, it is of utmost importance to share scientific resources (ie use open-source software and/or open-access publishers), foster an environment that supports linguistic diversity and perspectives, and advocate for the participation of researchers from all over the globe (Turba et al. 2025).

The number of labs specializing on stonefly research around the world is small in number (DeWalt and Ower 2019), relative to the number of labs studying conventionally charismatic insect taxa, such as butterflies or beetles. Financially supporting labs and public education programs that focus on aquatic insect systematics goes hand-in-hand with conserving our freshwater resources and biodiversity (Contador et al. 2012, Miličić et al. 2021). Understanding the phylogenetic processes that led to the diversification in Plecoptera will only aid in the ability to protect species that are being negatively affected by climate change or anthropogenic influence (Dijkstra et al. 2014, González-Orozco et al. 2016).

Future of Plecoptera Systematics

The advent of molecular data, including phylogenomic approaches, has significantly advanced our understanding of the Plecoptera Tree of Life (Letsch et al. 2021, South et al. 2021b). However, as outlined here, there are still challenges in determining the limits and placements of certain extant lineages. To further leverage phylogenomics, collaborative efforts to generate new genomic and transcriptomic resources are needed to improve taxon sampling of key lineages and better represent global diversity.

Given the rate of new stonefly species discovery (DeWalt and Ower 2019) and their tendency toward local genetic differentiation (Sproul et al. 2014, McCulloch et al. 2019b, 2022, Tsyrlin et al. 2022), much future work should continue to aim at new species discovery, documentation, and resolving phylogenetic relationships at finer evolutionary scales. To this end, there should be a concerted effort to efficiently survey multilocus molecular diversity using low-cost methods that can maximize species-level sampling (eg Sanger, Illumina amplicon sequencing). The current imbalance in gene coverage on GenBank NCBI, where species are predominantly represented by *COI* sequences, underscores the need for broader gene representation across species in this effort. Researchers designing new molecular studies should consider engineering compatibility with existing data sets (eg legacy genes described in *The History of the Systematics of Plecoptera* section above, published phylogenomic probe sets) as the constraints of their studies allow. Given the success of PCR and short-read sequencing technology even with marginal-quality ethanol-collected material, natural history collections should play a central role in efforts to survey molecular diversity.

Furthermore, the field must continue to recognize the reciprocal illumination between morphology and DNA data. There should be a strong focus on developing a comprehensive morphological-based matrix covering extinct and extant Plecoptera. In addition to helping elucidate relationships within extant lineages, morphological data are a prerequisite for incorporating valuable fossils into phylogenetic analyses. Recent methodological refinements, such as the fossilized birth-death process (Heath et al. 2014, Zhang et al. 2016) and the total-evidence approach (Pyron 2011, Ronquist et al. 2012), have helped to revise the previous placements and time divergence estimate of numerous lineages while better accounting for the fossil record (Vea and Grimaldi 2016, Spasojevic et al. 2021). However, these approaches have never been used for Plecoptera, likely because they require extensive morphological and/or fossil data (Klopfstein 2021).

In addition, relatively few studies have been conducted on reproductive systems, and spermatozoa (Fausto et al. 2001, Rościszewska and Rzońca 2009, Li et al. 2014), gill sensilla (Kapoor and Zachariah 1978), or antennae (Rebora et al. 2016). Despite their limited number, these studies have provided valuable insights into the biology of the group and their evolutionary relationships. However, these characters have never been employed in quantitative cladistic analyses to effectively test for character congruence. Therefore, further studies on external and internal morphology using SEM, TEM, and micro-CT, along with morphometry and behavioral studies (eg drumming), are necessary to generate independent, informative data for reconstructing character evolution at the phenotypic level. Hence, we believe that increasing accessibility to microscopy techniques and employing all these methodologies will be indispensable for comprehensively unraveling the evolutionary histories of Plecoptera. The fate and pace of this work rests on the health of the community of plecopterologists, the strength and breadth of its collaborations, and the effective transfer of knowledge and passion to new generations of researchers.

Work to increase participation by researchers across the globe on stonefly evolution and systematics will require recruitment, retention, and activism efforts. We need to recruit people first by introducing stoneflies to the public and educating students early on about these remarkable taxa (Birrell and Frakes 2023). Recruiting students as high schoolers and undergraduates into existing research programs and citizen science initiatives is key, and we should consider ways to recruit from audiences beyond our own lived experiences (New 2024). Connecting with existing programs and scientific societies known to promote ethnic and racial diversity, such as the Entomological Society of America, Entomologists of Color (EntoPOC), or those who work with the engagement of military veterans, such as Anglers of Honor, or affinity groups like 500 Queer Scientists or oSTEM, would allow the stonefly systematics community to broaden participation in our field.

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provide the foundation in unraveling the evolutionary histories and ecological significance of Plecoptera. Many thanks are owed to the Plecoptera Species File group who continually provide invaluable accessible data that largely helped make this review possible.

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Supplementary material

Supplementary material is available at *Insect Systematics and Diversity* online.

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