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Review

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Taxonomy

Trichoptera systematics: past, present, and future—making the case for continued caddisfly taxonomic research

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We review the developments in caddisfly (Insecta: Trichoptera) systematics starting with Linnaeus through to the present time. We give a brief introduction to the natural history and biology of the order, survey the contributions of prominent caddisfly taxonomists, explore the history of Trichoptera phylogenetics, define synapomorphies for the major caddisfly clades, identify gaps in our knowledge, and make recommendations for the future research in caddisfly systematics. While the pattern of early evolutionary divergences within the order is becoming clearer with phylogenomic data, much work remains to be done to describe unknown caddisfly diversity and to fully resolve their tree of life. This will require the training of a new generation of Trichoptera systematists, particularly in tropical regions, equipped with broad knowledge in natural history, taxonomy, systematics, genomics, and phylogenetics.

Keywords: Trichoptera, systematics, phylogenetics, caddisfly, freshwater.

Scope of the Review

In this review, we focus on the history and development of systematics research on Trichoptera, commonly known as caddisflies. The insect order Trichoptera is the sister order to Lepidoptera (butterflies and moths), and together, they comprise the extant members of the superorder Amphiesmenoptera. This is one of the strongest sister order relationships within Insecta, supported by multiple phylogenetic studies over the years (eg Hennig 1981, Kristensen 1981, Wiegmann et al. 2009, Misof et al. 2014). While most species of Lepidoptera are terrestrial, nearly all species of Trichoptera inhabit aquatic environments as larvae and pupae, making them an excellent group of insects to study diversification in a freshwater environment (Morse et al. 2019a). Larval caddisflies (Fig. 1) can be diagnosed by 6 well-developed larval legs, small, papilla- or rod-like antennae, absence of external spiracles, and a pair of anal prolegs at the end of the abdomen, each with a single hook (Wiggins 2004). Caddisfly adults (Fig. 2) are often compared in appearance to small moths and are generally gray to brown. Their wings are covered with hairs (hence the name *trichos*-hair, *pteron*-wing) and are held tentlike over their abdomen, though, in some species, the hairs have been secondarily modified into scales (Fig. 2I) (Holzenthal et al. 2007b, 2015).

Succinct Review of Biogeography, Biology, and Natural History

Members of the insect order Trichoptera have captured the imagination of entomologists and naturalists for centuries due to the construction behavior demonstrated by the larvae. Larval caddisflies (or caddisworms) extend their phenotypes in myriad ways by collecting material from the substrate of their aquatic habitats and building

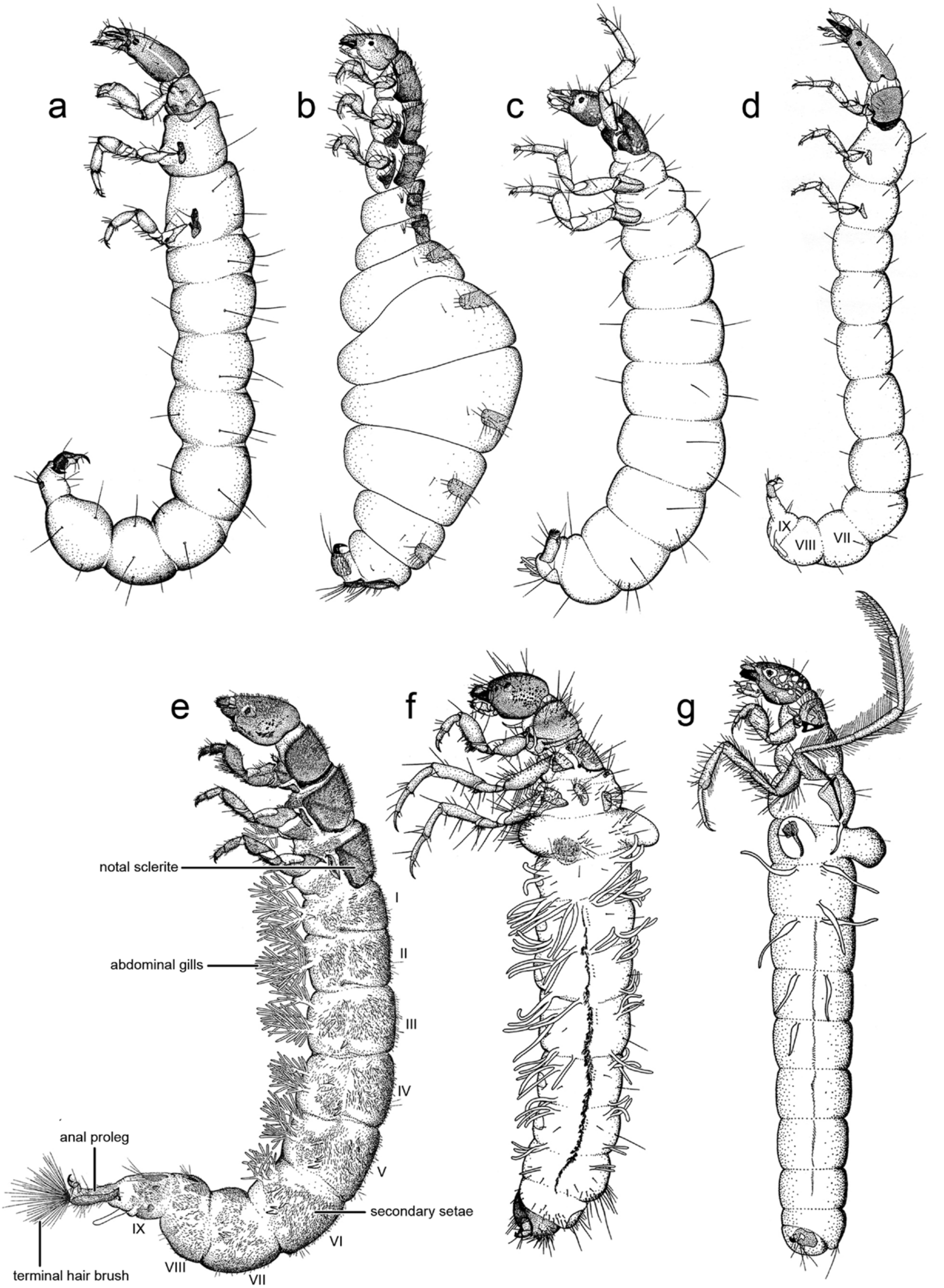

Fig. 1. Trichoptera larvae. A) *Atopsyche* sp. (Hydrobiosidae). B) *Byrsopteryx mirifica* (Hydroptilidae). C) *Protoptila* sp. (Glossosomatidae). D) *Chimarra* sp. (Philopotamidae). E) *Calosopsyche* sp. (Hydropsychidae). F) *Limnephilus* sp. (Limnephilidae). G) *Nectopsyche gemmoides* (Leptoceridae). Illustrations by Ralph Holzenthal and Kris Kuda.

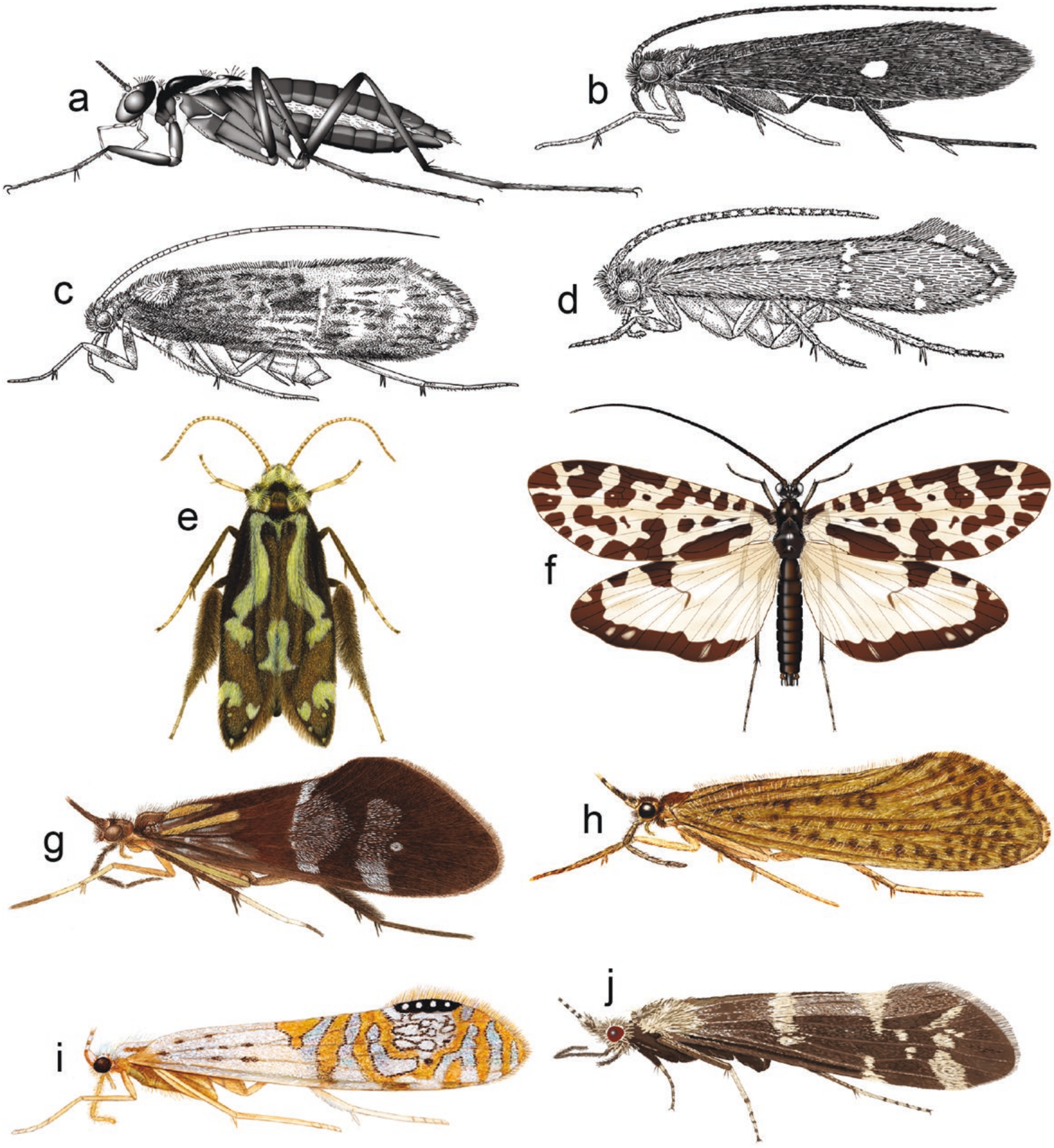

Fig. 2. Trichoptera adults. A) *Dolophilodes distinctus* (brachypterous female) (Philopotamidae). B) *Machairocentron* sp. (Xiphocentronide). C) *Atopsyche* sp. (Hydrobiosidae). D) *Protoptila* sp. (Glossomatidae). E) *Abtrichia* sp. (Hydroptilidae). F) *Semblis phalaenoides* (Phryganeidae). G) *Phylloicus abdominalis* (Calamoceratidae). H) *Banyallarga vicaria* (Calamoceratidae). I) *Nectopsyche flavofasciata* (Leptoceridae). J) *Athripsodes cinereous* (Leptoceridae). Illustrations by Ralph Holzenthal and Julie Martinez.

small structures, either retreats or portable cases, with the use of an underwater-adapted silk (Wiggins 2004) (Fig. 3). The adult form is also well-known to fly fishers who tie flies to mimic adult caddisflies to attract fish. With over 17,000 known species, they are one of the most diverse radiations of aquatic animals (Malm et al. 2013). The biology and natural history of Trichoptera have been reviewed elsewhere in more detail (eg Wiggins 2004, Holzenthal et al. 2007a, 2015, Morse et al. 2019a, b); however, we offer a brief overview here.

Biogeography

Caddisflies are distributed worldwide and are found in freshwater habitats on every continent except Antarctica. This distribution was shaped by the breakup of the supercontinent Pangaea around 200 million years ago that led to the widespread distribution of relict fauna and follows patterns observed in other groups of aquatic organisms (Grimaldi and Engel 2005, Holzenthal et al. 2015). Dating estimates suggest that deep divergences in the 2 suborders, Annulipalpia and Integripalpia, occurred 295 million years ago during the existence of Pangaea, with vicariance as an important driver for higher-level diversity (Thomas et al. 2020, 2023, Frandsen et al. 2024), including the emergence of many families during the Cretaceous or Jurassic periods (200–66 million years ago). Thirteen biogeographic regions of Trichoptera are recognized, which broadly reflect the zoogeographic regions of Wallace (1876), but take into account the global distribution patterns observed in caddisflies (de Moor and Ivanov 2008) (Fig. 4). Of the 7 major Wallacean biogeographic regions, the Indo-Malayan region has the highest number of named species and genera, with 5,853 and 207, respectively (Morse

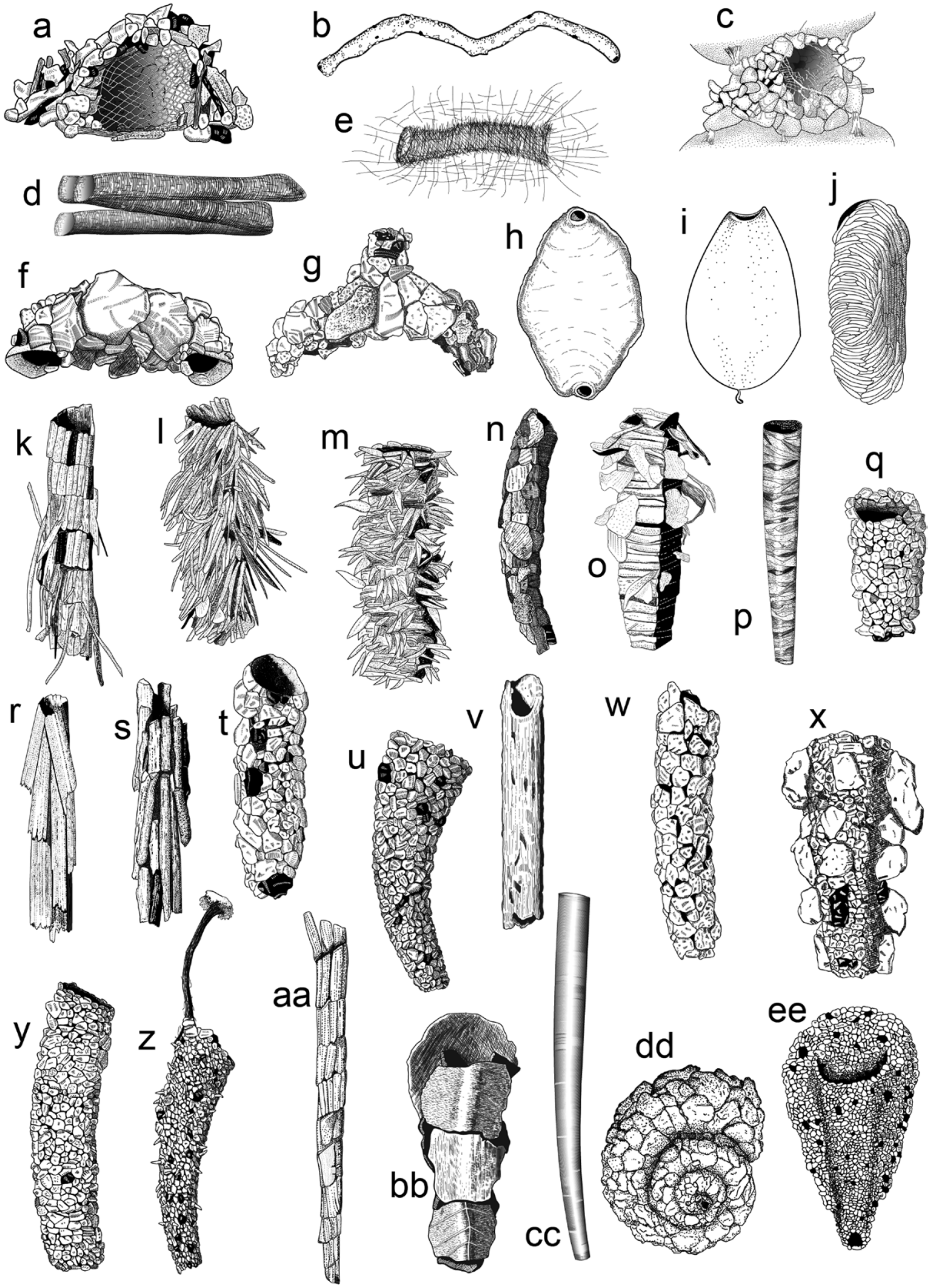

Fig. 3. Larval retreats and cases. A) *Arctopsyche grandis* (Hydropsychidae). B) *Ecnomus* sp. (Ecnomidae). C) *Stenopsyche* sp. (Stenopsychidae). D) *Chimarra* sp. (Philopotamidae). E) *Holocentropus* sp. (Polycentropodidae). F) *Culoptila moselyi* (Glossosomatidae). G) *Protoptila* sp. (Glossosomatidae). H) *Leucotrichia* sp. (Hydroptilidae). I) *Ithytrichia* sp. (Hydroptilidae). J) *Dibusa angat*a (Hydroptilidae). K) *Banksiola dosauria* (Phryganeidae). L) *Fabria inornata* (Phryganeidae). M) *Phanocelia canadensis* (Limnephilidae). N) *Ironoguia sp.* (Limnephilidae). O) *Adicrophleps hitchcocki* (Brachycentridae). P) *Micrasema* sp. (Brachycentridae). Q) *Neotrichia* sp. (Hydroptilidae). R) *Sphagnophylax meiops* (Limnephilidae). S) *Anabolia bimaculata* (Limnephilidae). T) *Dicosmoecus* sp. (Limnephilidae). U) *Pedomoecus sierra* (Apataniidae). V) *Heteroplectron americanum* (Calamoceratidae). W) *Psilotreta* sp. (Odontoceridae). X) *Goeracea genota* (Goeridae). Y) *Rossiana montana (Rossianidae).* Z) *Limnocentropus* sp. (Limnocentropodidae). AA) *Triaenodes tardus* (Leptoceridae). BB) *Phylloicus aeneus* (Calamoceratidae). CC) *Amazonatolica hamadae* (Leptoceridae). DD) *Helicopsyche borealis* (Helicopsychidae). EE) *Eosericostoma inaequispina* (Parasericostomatidae).

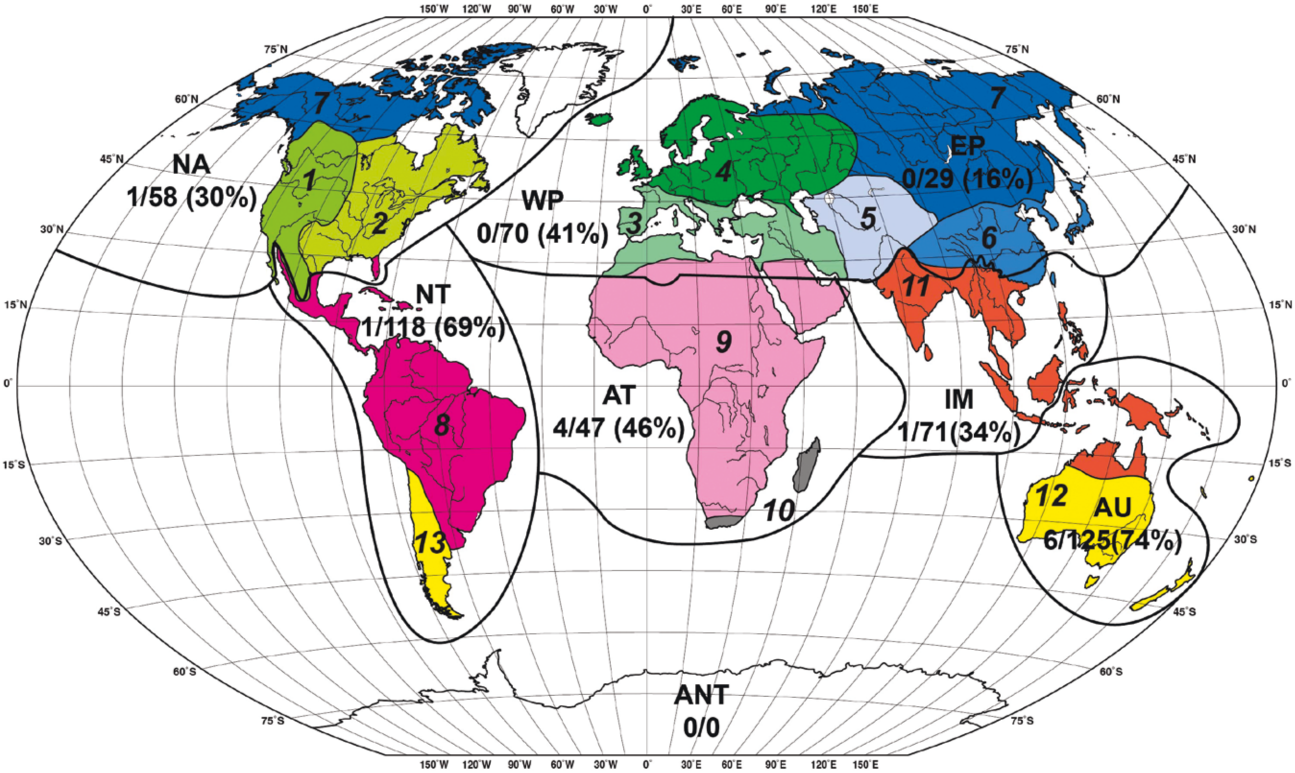

Fig. 4. Trichoptera biogeographic regions of de Moor and Ivanov (2008). (1). West Nearctic. (2) East Nearctic. (3). West Palearctic. (4). Boreal Palearctic. (5). South Palearctic. (6). East Palearctic. (7). Beringian. (8). Neotropical. (9). Afrotropical. (10). Cape South African. (11). Indo-Malayan. (12). Australia and New Zealand. (13). Patagonian. Close biogeographic affinities are indicated by similar colors (redrawn from de Moor and Ivanov, 2008). The number of endemic families, genera, and % endemic genera for Wallace's 7 major bioregions of the world are indicated within the boundaries of those regions: (AT). Afrotropical. (AU). Australasian. (EP). East Palearctic. (IM). Indo-Malayan. (NA). Nearctic. (NT). Neotropical*. (WP). West Palearctic. Antipodoeciidae (AU endemic) is considered a senior synonym of Anomalopsychidae (NT endemic) by some authors; they are considered separate families here.

et al. 2019a). It is followed by the Neotropical region with 3,309 named species in 171 genera. The Australasian region has the highest proportion of endemicity, with 6 endemic families and 125 endemic genera (Fig. 4). Tropical or mountainous areas with significant precipitation levels are known to have high species endemism (de Moor and Ivanov, 2008) and are important areas to explore for continued species discovery.

Larvae

Caddisflies are holometabolous, and most species spend their larval stages completely submersed in freshwater before pupating and emerging as winged adults. Caddisfly larvae (Fig. 5) are ecologically important in freshwater environments and have representatives across functional feeding groups (Thorp and Rogers 2015). They are also abundant, with species that are differentially sensitive to pollution, making the order ideal for monitoring the health of freshwater resources (Morse et al. 2019a). The most recent and comprehensive phylogenetic estimates recover 2 suborders within Trichoptera that display divergent uses of silk (Thomas et al. 2020, Frandsen et al. 2024, Ge et al. 2024). These are Annulipalpia, or fixed-retreat makers, and Integripalpia, which includes free-living and case-making caddisflies (Fig. 3). Caddisfly larvae can be hyper-abundant in freshwater streams and not only play a prominent role in freshwater food webs but have also been shown to stabilize stream beds with their thousands of silken nets (Albertson et al. 2014). See Fig. 6 for general larval and pupal morphology.

Pupae

As caddisfly larvae approach the end of their larval stage, they create a shelter that protects them throughout pupation. In free-living families, larvae create a pupal dome consisting of rocks glued together with silk, while most families of tube-case-making caddisflies simply spin silk to cover the tube case opening and attach the tube to rocks or other benthic materials. Caddisfly pupae are exarate (Fig. 5) and some families construct silken permeable or semipermeable cocoons, further protecting the pupa. Nearly all species pupate underwater, except for the few species that are semiterrestrial or that are drought-tolerant (Holzenthal et al. 2015).

Adults

Caddisfly adults are generally inconspicuous and short-lived, but they can be abundant in coordinated emergences. They are most often found on vegetation or, in cold environments, under rocks in the riparian zone and are primarily crepuscular. Feeding is not common in adult caddisflies and is limited to liquids, nectar, or sugary excretions of hemipteran insects due to their reduced mouthparts (Wiggins 2004, Syrnikov et al. 2005). While most adult caddisflies are drab in color, some species have beautifully colored wings (Fig. 2). Most caddisflies are diagnosed to genus or species based on features of the genitalia, though wing venation, leg spurs, ocelli, and maxillary palps are also used. See Fig. 5 for general adult morphology.

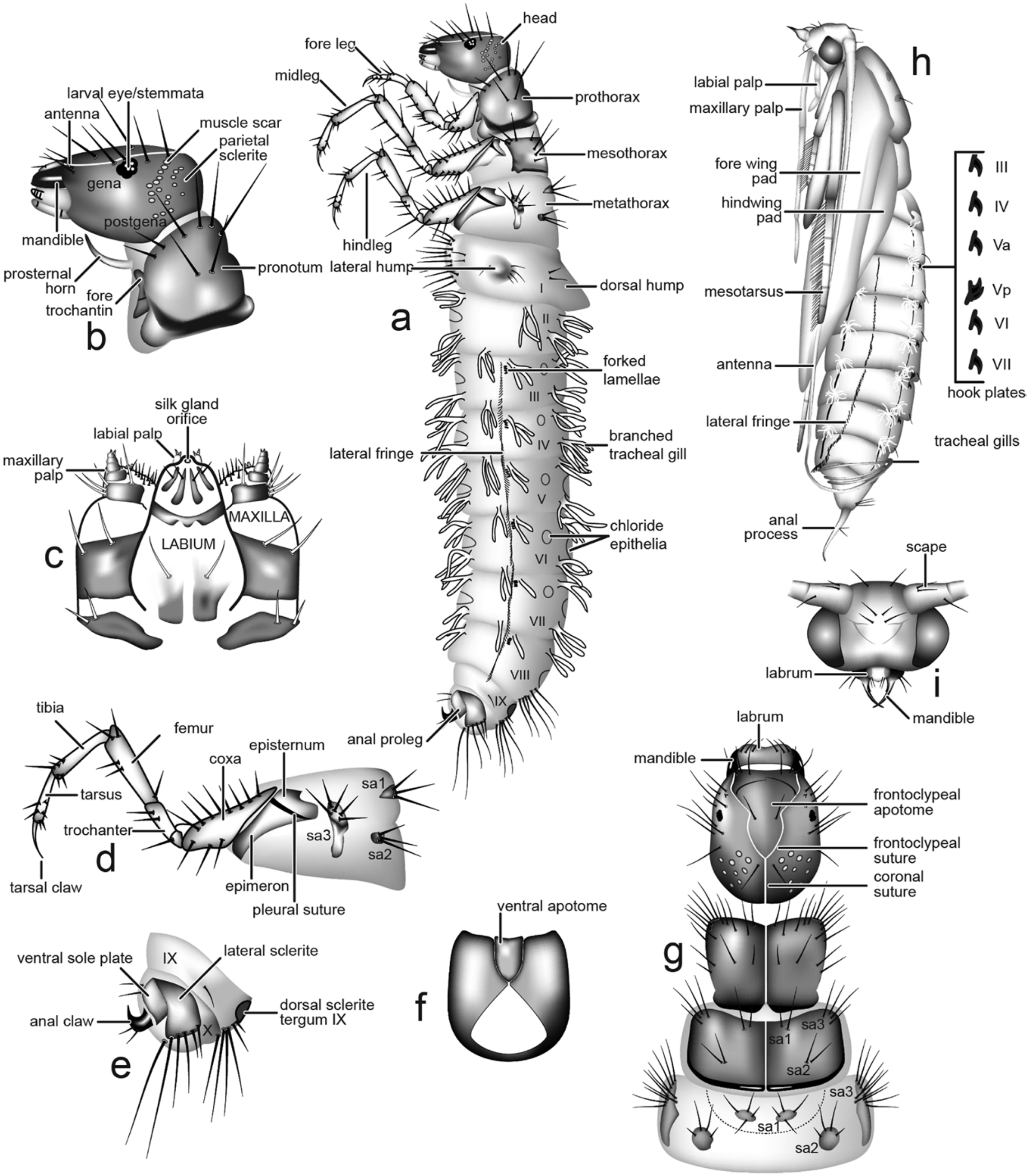

Fig. 5. Trichoptera immature morphology (Phryganides). A). Larva, lateral. B). Head and prothorax, enlarged. C). Maxillolabium, ventral, enlarged. D). Metapleuron and leg, enlarged. E). Terminal abdominal segments, enlarged, F) Head, ventral, enlarged. G). Head and thorax, dorsal, enlarged. H). Pupa, lateral, inset: abdominal hook plates. I). Pupa, head, frontal, enlarged. (Abbreviations: I–X, abdominal segments 1–10; sa, setal area).

A Brief Chronicle of Major Taxonomists Over the Past 265 Years Contributing to the Current Understanding of Species Diversity

Linnaeus (1758) described the first Trichoptera in the genus *Phryganea* in the order Neuroptera, as then broadly defined. Of the 17 species that Linnaeus described, 1 is a megalopteran, 3 are plecopterans, and one of the caddisflies is a *nomen dubium* (Fischer 1968), leaving 12 currently valid species of those originally described. Since then, more than 17,000 species have been described by many additional workers. We include here a table of taxonomists who have described more than 100 species (Table 1). In the

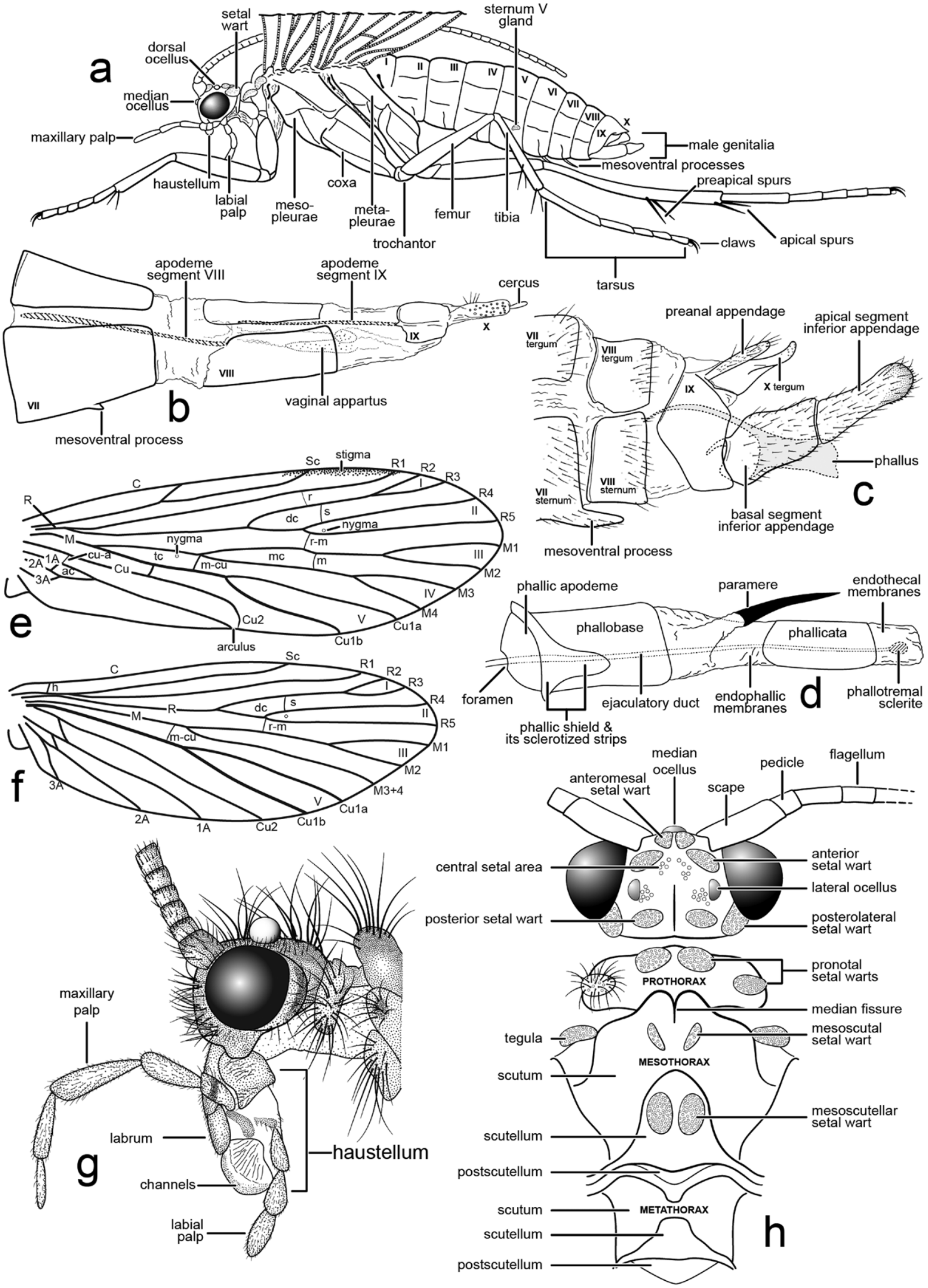

Fig. 6. Trichoptera adult morphology. A) Adult body, lateral (modified and redrawn from Ross, 1944, and Morse et al., 2019). B) Female oviscapt (ovipositor), lateral. C) Male terminal abdominal segments and genitalia, lateral. D) Male phallus, lateral (redrawn from Morse 1975). E) Forewing venation. F) Hind wing venation. G) Head and mouthparts, lateral. H) Head and thorax, dorsal. (Abbreviations: I–X, abdominal segments 1–10; wing venation follows standard Comstock-Needham system).

Table 1. Trichoptera researchers who have described 100 or more species through 2022

Researcher	Number species described	Years active	Obituary
Hans Malicky	2,506	1970–present	
Fernand Schmid †	1,358	1947–1998	Weaver and Nimmo (1999), Botosaneanu (1999)
Janus Oláh	1,296	1964–present	
Oliver S. Flint, Jr. †	1,108	1956–2019	Holzenthal and Bueno-Soria (2020), Roble (2019)
Kjell Arne Johanson	827	1990–present	
Ralph W. Holzenthal	707	1982–present	
Porntip Chantaramongkol	704	1983–present	
Wolfram Mey	562	1976–present	
Georg Ulmer †	560	1900–1963	Illies (1964), Kimmins (1963c)
Herbert H. Ross †	538	1938–1978	Unzicker and Wallace (1979a, b)
Alice Wells	529	1978–present	
Nathan Banks †	485	1882–1951	Carpenter and Darlington (1954)
Martin E Mosely †	452	1919–1954	Kimmins (1948), Barnard (2010)
Andreas V. Martynov †	364	1892–1938	Ivanov (1993)
Douglas E. Kimmins †	342	1930–1967	Barnard (1986a, b)
Longinos Navás †	337	1905–1936	Ferrando Más (1938), Bastero Monserrat (1989)
Roger J Blahnik	316	1992–present	
Arturs Neboiss †	307	1957–2003 (2018)	Varzinska and Spuris (1992), McPhee et al (2012)
Robert McLachlan †	307	1862–1903	James and Foote (2004)
Steven C. Harris	273	1977–present	
Donald G. Denning †	270	1937–1989	Resh (1989)
Lean-Fang Yang	257	1987–2017	
Joaquin Bueno-Soria	255	1976–present	
Lazare Botosaneanu †	252	1948–2011	González (2013), Negrea and Nitzu (2012)
John C. Morse	248	1971–present	
David I. Cartwright	189	1982–present	
Füsun Sipahiler	169	1984–present	
Francois-Marie Gibon	163	1982–present	
Jolanda Huisman	133	1989–present	
Brian J. Armitage	127	1983–present	
Herman A. Hagen †	126	1851–1887	Henshaw (1894)
Georges Marlier †	120	1943–1987	
John B. Ward †	117	1990–2009	Patrick (2016, 2017)
John S. Weaver, III	115	1976–present	
Serge Jacquemart †	115	1961–1981	Marlier (1981)
Jorge L. Nessimian	108	2000–present	

† = deceased.
“Years Active” = when first/last Trichoptera contributions were published.

following paragraphs, we further present a synopsis of some of these caddisfly taxonomists and provide selected examples of their contributions grouped by biogeographic regions as defined for caddisflies by deMoor and Ivanov (2008).

Nearctic

Early descriptions of caddisflies in the Nearctic region were provided by Walker (1852), Hagen (1861), and Banks (1900), but the most comprehensive treatment of the fauna began in the late 1930s by Ross (1938, 1941). These works included many descriptions of new species from across the continent, designation of lectotypes from earlier works, and perhaps his most lasting work, *The Caddisflies of Illinois* (Ross 1944), which is still useful today. Important works on the western Nearctic fauna include those of Denning (1954, 1956) and, more recently, Nimmo (1971, 1987) and Ruiter (2000, 2013). Contributions to the knowledge of the eastern Nearctic fauna were provided by Harris (Harris et al. 1991), Rasmussen (Rasmussen and Denson 2000, Rasmussen and Morse 2014), and Morse (Morse et al. 2017) in the southeast and Betten (1934) and Flint (1960) in the northeast. Keys to adult genera across the continent were produced by both Schmid (1998) and Morse et al. (2019b). In addition to contributions to adult taxonomy, Wiggins's *Larvae of the North American Caddisfly Genera* (1996) stands out as one of the most important contributions to our knowledge of North American fauna.

Neotropical and Patagonian

Early intellectual contributions to our understanding of caddisfly evolution and diversification stem from the works of Müller (1879, 1880) in southeastern Brazil; in those same works, he described several of the more iconic representatives of the Neotropical fauna, including *Nectopsyche*, *Marilia*, and *Smicridea* (*Rhyacophylax*). Other early descriptive taxonomic works in the region were provided by Banks (1910, 1913), Ulmer (1905, 1913), and especially Navás, who published over 40 papers describing Neotropical species (1907, 1935). Over the course of his career, beginning in the early 1960s, Flint produced a prodigious amount of work focused on the Neotropical fauna across regions and taxa, including species descriptions (1963, 2008), major taxonomic revisions (1987, 1998), and nomenclatural treatments (1966, 1967). Following Flint's foundational works, Bueno-Soria explored the Mexican fauna (2009); Holzenthal (1988, Holzenthal and Calor 2017), Ríos-Touma (Ríos-Touma et al. 2017), Armitage (Armitage et al. 2024), Blahnik (1992), Harris (1990), Botosaneanu (1980), and Oláh (Oláh and Johanson 2011) increased the taxonomic knowledge across Central and South America and the Caribbean; and Calor (2011), Santos (Santos et al. 2016), Dumas (Dumas and Nessimian 2012), Quinteiro (Quinteiro and Holzenthal 2017), Pes (Pes et al. 2018), and their students and colleagues have contributed important recent information on the Brazilian fauna. Taxonomic knowledge of the Patagonian region was provided in a series of papers by Schmid (1955b, 1964) and has since been expanded by Angrisano (Angrisano and Sganga 2007), Rueda Martín (Rueda Martín et al. 2015), and Sganga (Sganga et al. 2013).

Palearctic

Numerous early workers, largely European, contributed to the knowledge of the Palearctic fauna and their works were cataloged by Fischer (1960-1973), which was itself an important contribution to world Trichoptera literature. More recent contributions include Malicky's *Atlas of the European Trichoptera* (2004) and Schmid's comprehensive revisionary studies of Limnephilidae (1955a). Studies concentrating on more specific regions of the Palearctic include those of González (González et al. 1992) and da Terra (1981) for the Iberian Peninsula and Kumanski (2007) and numerous papers by Kučinić, Previšić, and their colleagues in the Balkans (Kučinić et al. 2016). Moretti, Cianficconi, and their colleagues produced a large body of work on the Italian fauna (Cianficconi et al. 1999) and Malicky published a number of works on the fauna of the Mediterranean region (2005). Additional regional works include those of Sipahiler in Turkey (2016), Nybom (1960) and Salokannel (Salokannel et al. 2011) in Finland, Ivanov in Russia (2011), and Moseley (1939), Kimmins (1966), and Hickin (1967) in Great Britain and the United Kingdom. Martynov (1926) and Lepneva (1970, 1971) were prolific in the Palearctic, as well as other regions globally.

Following Ivanov and de Moor (2008), the East Palearctic consists largely of Eastern Russia, China, Korea, and Japan. Martynov contributed to the description of the Russian fauna (Martynov 1935). Many of the first descriptions of Chinese fauna are scattered among the papers of early European workers, including Ulmer. More focused research on the Chinese fauna includes works by Li (Li and Tian 1990), Sun (2017), Tian (1988), and Yang (Yang et al. 2005), often in collaboration with Morse (Yang and Morse 2000). Similarly, many early European workers described species from Japan. Early Japanese workers included Iwata (1928), Tsuda (1942), and Kobayashi (1964); more recent works have been provided by Ito (2017), Nishimoto (2011), Kuhara (2005), Nozaki (2013), Kuranishi (1999), and Tanida (2002). A series of papers from the early 1990s was published by Kumanski on the caddisfly fauna of Korea (1990, 1991); since then, the fauna has been studied by Park and Bae (1998).

Beringian

The singular focused work on Beringian caddisflies was published by Wiggins and Parker in 1997. Other works on Beringia, as broadly defined by Ivanov and de Moor (2008), include early works by Martynov (1909, 1910, 1914, 1926) and Levanidova (1986, 1989) and more recent works by Arefina (1996) and Ivanov and Melnitsky (2007).

Indo-Malayan

Mosely (1933, 1949), Kimmins (1963b), and Schmid (1987, 1991) provided numerous descriptions of the Indian fauna, along with recent works from Parey (Parey et al. 2023) and Pandeer and Saini (2014); Flint (2001) and Schmid (1958) both also produced focused works on the fauna of Sri Lanka. The caddisfly fauna of Vietnam, Laos, Myanmar, and Thailand has been explored by Arefina and Armitage (2010), Hoang and Bae (2006), Mey (2005), Oláh (1989), Malicky and Chantaramongkol (2007), and Laudee (Laudee et al. 2023), while Wells (1991), Huisman (1993), and Mey (2003) have produced publications adding to knowledge in Indonesia, Malaysia, Papua New Guinea, and the Philippines.

Australia and New Zealand

Mosely and Kimmins provided a comprehensive treatment of the Trichoptera fauna of Australia and New Zealand (1953), while Neboiss provided, among other important works (Neboiss 1981), a key to the families and genera of the region (1986). A plethora of large, descriptive taxonomic works were produced by Wells, largely focused on the family Hydroptilidae (1985, 1990). Additional taxonomic works have been provided by Dean, Cartwright, and St. Clair (Dean et al. 2004, Cartwright et al. 2023). Additionally, fauna of New Caledonia has been described by Espeland, Sjöberg, and Johanson (Espeland et al. 2020).

Afrotropical and Cape South African

Early contributions to our understanding of the fauna of the Afrotropics, probably the least explored biogeographic region, were provided by Jacquemart (1959), Marlier (1943), and Kimmins (1963a). In addition, Andersen (Andersen and Holzenthal 2001) led a research project in West Africa, and Johanson and Oláh have described many African species (2007). The highly endemic fauna of Cape South Africa was initially described by Barnard (1934) and more comprehensively treated later by both Scott (1986, 1993) and de Moor (2007). Similarly, the endemic fauna of Madagascar has been treated by Gibon (2017), Weaver (Weaver et al. 2008), and Johanson (2010).

How the Phylogenetic Relationships Have Become Clarified Over the Years

A history of phylogenetics research in Trichoptera has previously been treated by Morse (1997) and Holzenthal et al. (2007b), both of which summarized the phylogenetic studies published prior to

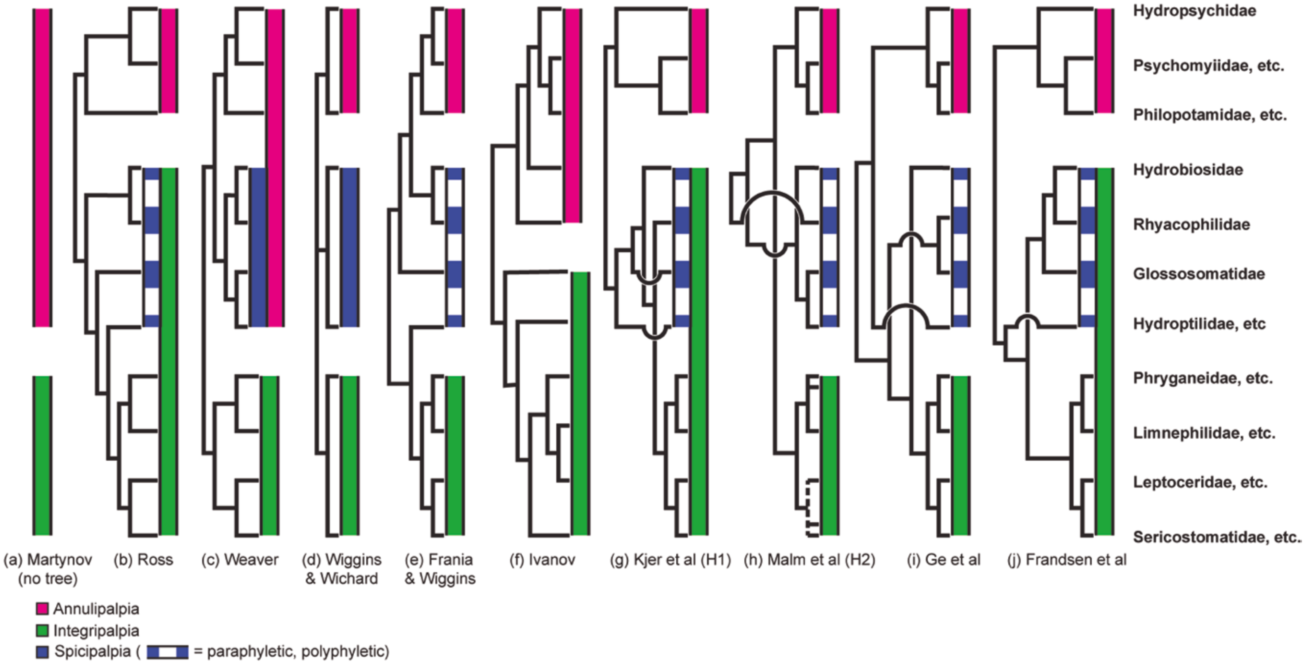

Fig. 7. Hypotheses concerning the deep relationships in Trichoptera (figure adapted from Morse 1997 and, Thomas et al. 2020). These include the suborder classification proposed by Martynov (1924) and phylogenetic hypotheses from Ross (1964), Weaver (1984), Wiggins and Wichard (1989), Frania and Wiggins (1997), Ivanov (2002), Kjer et al. (2001, 2002, 2016), Thomas et al. (2020), Malm et al. (2013), Ge et al. (2023), and Frandsen et al. (2024).

their reviews. To guide the reader, we have summarized the major phylogenetic studies, and the various hypotheses put forward in each study in Fig. 7.

To our knowledge, the earliest evolutionary tree for Trichoptera was published by Ulmer (1912) followed by a highly detailed tree by Milne and Milne (1939), although previous researchers proposed evolutionary relationships without including evolutionary trees (Kolenati 1848, 1859, Krafka 1923, Martynov 1924). These studies predated Hennigian systematics and were based on interpretations of various morphological and behavioral characters. Martynov (1924) classified the order into 2 monophyletic suborders, Annulipalpia and Integripalpia. Later, Ross (1964, 1967) hypothesized a phylogenetic tree in which the order was also split into 2 primary suborders, though he did not initially use Martynov's terminology. Ross further identified 5 'complexes' in 1964, later referred to as "ancestors" in 1967, which were characterized by the larval behaviors of the families belonging to each complex. These were (i) the retreat-making families (included in Annulipalpia by Martynov 1924), (ii) the free-living caddisflies from the family Rhyacophildae, (iii) the tortoise-case makers in the family Glossosomatidae, (iv) the purse-case makers in the family Hydroptilidae, and (v) a "complex" consisting of tube-case-making families. He hypothesized that there were 2 main clades within Trichoptera, the first containing the first "complex," the fixed-retreat makers or Annulipalpia, and the second he called Integripalpia (Ross 1967), which contained the other 4 complexes with a grade of Rhyacophilidae, Glossosomatidae, and Hydroptilidae leading to the tube-case makers. Since the publications of Ross, the monophyly of each of these 'complexes' has never been seriously contested; however, the relationships among these clades have varied across studies (Fig. 7). Ross and other workers at the time considered Hydrobiosidae as a subfamily of Rhyacophilidae. In subsequent studies, where it is considered a family, Hydrobiosidae has been most often placed as sister to Rhyacophilidae, Likewise, 2 genera, *Ptilocolepus* and *Palaeagapetus*, were considered by Ross (1967) to be "primitive" members of Hydroptilidae. These 2 genera are now recognized as the family Ptilocolepidae, which has been subsequently always recovered as allied with Hydroptilidae.

One of the first studies to interpret the phylogeny of Trichoptera using Hennigian cladistics was Weaver (1984). In his paper, he justified each major clade that he proposed with a set of morphological or behavioral synapomorphies. In particular, he split the order into 2 new suborders, Vericloacia and Dicloacia, each of which contained 2 infraorders. In Vericloacia, the 2 infraorders he named were Spicipalpia and Curvipalpia. Spicipalpia contained 4 families, Rhyacophilidae, Hydrobiosidae, Hydroptilidae, and Glossosomatidae. Within Spicipalpia, Rhyacophilidae was sister to Hydrobiosidae, which together were sister to a clade containing Hydroptilidae and Glossosomatidae (Fig. 7). The other infraorder within Vericloacia, Curvipalpia, included the fixed-retreat makers (these families were previously included in Annulipalpia by Martynov 1924). The remaining suborder, Dicloacia, was composed solely of tube-case makers and contained the infraorders Plenitentoria and Brevitentoria. This was the first analysis to place the 4 spicipalpian families together in a monophyletic clade, and the relationships among these families, the clade of fixed-retreat makers, and the clade of tube-case makers have been the primary point of incongruence in subsequent phylogenetic studies.

Later, Wiggins and Wichard (1989) reconstructed the phylogeny of caddisflies based on pupation behavior. Like Weaver (1984), they proposed a monophyletic Spicipalpia (containing Rhyacophilidae, Hydrobiosidae, Hydroptilidae, and Glossosomatidae). However, in contrast to Weaver, they placed this clade as sister to the rest of Trichoptera, including fixed-retreat makers and tube-case makers. The monophyly of Spicipalpia was challenged by Ivanov (1997). Accordingly, for the remainder of this article, we will refer to the "spicipalpian" families (Hydroptilidae, Ptilocolepidae, Rhyacophilidae, Hydrobiosidae, and Glossosomatidae) as the "cocoon-makers" as designated by Wiggins (2004).

The first study to use computational phylogenetics to estimate the phylogeny of caddisflies was published by Frania and Wiggins (1997). In this work, they coded 70 larval and adult characters into a morphological matrix and analyzed it with maximum parsimony. Their analysis was equivocal, and they recovered different trees depending on the characters they analyzed or how the analysis was weighted. Consistent across their analyses, however, were the monophyly of both Annulipalpia (fixed-retreat makers) and their concept of Integripalpia (tube-case makers) with the family Limnocentropodidae sister to all other tube-case makers. Also consistent was the placement of Rhyacophilidae and Hydrobiosidae as allied with Annulipalpia. However, depending on the weighting of characters and the sample analyzed, the placement of Glossosomatidae swapped between being allied with Rhyacophilidae, Hydrobiosidae, and Annulipalpia, or with Hydroptilidae and their Integripalpia (tube-case makers). Subsequently, Ivanov (2002) and Ivanov and Sukacheva (2002) (see also Kozlov et al. 2002) proposed a phylogenetic hypothesis based on morphological synapomorphies (including fossils) that placed Rhyacophilidae and Hydrobiosidae as sister to fixed-retreat makers (Annulipalpia) and Glossosomatidae as sister to a group containing Hydroptilidae and the tube-case makers.

Kjer et al. (2001, 2002) performed the first molecular analysis combined with a reevaluation of the morphological data set generated by Frania and Wiggins (1997). The molecular data set included nuclear DNA sequence data, including rDNA genes (*18S* and *28S*) and *elongation factor 1a* (*EF-1a*), and mitochondrial DNA sequence data from *cytochrome c oxidase subunit 1* (*COI*). They conducted multiple analyses, including maximum parsimony, maximum likelihood, and Bayesian, across both separate (single gene) and combined data sets. They recovered 2 primary clades, one containing the fixed-retreat makers (suborder Annulipalpia) and another with the cocoon-making families forming a paraphyletic grade to the tube-case makers with the exact arrangement of the cocoon-making families differing across trees depending on the analysis and/or data analyzed. They concluded that rDNA genes were optimally suited for the recovery of deep relationships within the order. An expanded analysis with a larger taxon sample was published by Holzenthal et al. (2007b), which recovered a tree similar to those presented in the 2001 and 2002 studies.

Malm et al. (2013) published the first phylogenetic analysis to include divergence time estimates for Trichoptera. To do this they analyzed fragments from 3 nuclear genes, *carbamoylphosphate synthetase* (*CPSase* of CAD), *isocitrate dehydrogenase* (*IDH*), and *RNA polymerase II* (*POL*), and from the mitochondrial *COI* gene. In their study, they characterized the phylogenetic signal present in each codon position of each locus and concluded that, with the exception of *POL*, 3rd codon positions were generally too saturated to be useful in deep phylogenetic studies. They estimated phylogenetic trees with both maximum likelihood and Bayesian methods and estimated divergence times with BEAST (Suchard et al. 2018). In contrast to the previous molecular studies, they recovered the cocoon-making families as a paraphyletic grade at the base of the tree, with Rhyacophilidae as sister to the rest of Trichoptera, followed by a clade of Hydrobiosidae, Glossosomatidae, and Hydroptilidae that was sister to the clade containing the fixed-retreat makers and tube-case makers. They estimated that Trichoptera diverged from Lepidoptera ~243 million years ago and that the first splits in extant Trichoptera occurred ~226 million years ago.

A subsequent study by Thomas et al. (2020) compiled a matrix of new and previously published molecular data, including the nuclear genes *18S*, *28S*, *EF-1a*, *CAD*, *IDH*, and *POL* and the mitochondrial gene *COI*. The phylogenetic tree they estimated from the combined data set was similar to those previously published by Kjer et al. (2001, 2002) and Holzenthal et al. (2007b), while the tree they estimated from solely the protein-coding genes was similar to the tree estimated by Malm et al. (2013). However, when accounting for nucleotide composition bias through RY-coding of 3rd codon positions, a topology more similar to Kjer et al. (2001, 2002) was recovered. Thomas et al. also estimated divergence times using BEAST and recovered older divergence times than Malm et al., with the divergence of Trichoptera and Lepidoptera occurring ~291 million years ago and the first split within extant Trichoptera occurring ~277 million years ago. The authors also made a classification update and subsumed all cocoon-making families into the suborder Integripalpia and used the established name Phryganides as a new name for the clade of tube-case makers (formerly Integripalpia *s.s.*).

Ge et al. (2023) used newly generated and existing mitochondrial genomes to estimate a phylogenetic tree of 28 trichopteran families. They estimated phylogenetic trees based on 13 mitochondrial protein-coding genes (with 3rd codon positions removed) and the rDNA genes using maximum likelihood and Bayesian analyses. In their Bayesian analysis, they used the CAT-GTR mixture model to account for among-site rate variation. In their tree, they recovered Hydroptilidae as sister to the fixed-retreat makers, while the placement of the remaining cocoon-makers was unstable and recovered as either a grade leading to the tube-case makers (in some Bayesian analyses) or at the base of the tree (in maximum likelihood analyses).

The first family-level phylogenomic analysis of the order was published by Frandsen et al. (2024). This study used transcriptome or targeted enrichment sequences from over 200 species representing 174 genera and 48 of 52 extant families. This study presented the most expansive data set for caddisfly phylogenetics to date, both in terms of number of taxa sampled and the amount of sequence data for each taxon. The authors estimated a maximum likelihood phylogenetic tree with 2 datasets, one including only those taxa with transcriptome data and another including all taxa (those with transcriptome or targeted enrichment sequence data) in a combined analysis. They also estimated divergence times with MCMCtree (Yang 2007, dos Reis and Yang 2011). They recovered 2 monophyletic suborders with the cocoon-making families allied with the tube-case makers, as in earlier studies by Ross (1964), Kjer et al. (2001, 2002), Holzenthal et al. (2007b), and Thomas et al. (2020) (Fig. 8). The microcaddisfly families (Hydroptilidae and Ptilocolepidae) were sister to the rest of Integripalpia, with a clade containing Glossosomatidae, Rhyacophilidae, and Hydrobiosidae sister to the tube-case makers (Phryganides). This group was recovered as monophyletic across all the analyses of Frandsen et al., but the relationship among families within the clade was incongruent, with Glossosomatidae recovered as sister to a clade containing Rhyacophilidae and Hydrobiosidae in the combined analysis and Hydrobiosidae recovered as sister to a clade containing Rhyacophilidae and Glossosomatidae in the transcriptome-only analysis. However, the authors argued that the recovery of the latter set of relationships was likely due to bias in the transcriptome-only data set, supported by 4-cluster likelihood analysis of permuted datasets and ASTRAL multispecies coalescent analysis. The divergence time analysis revealed that Trichoptera diverged from Lepidoptera ~310 million years ago and that the first splits within extant Trichoptera occurred ~295 million years ago, prior to the breakup of Pangea. Subsequently, an analysis of an independent phylogenomic dataset consisting of 26 families and 71 genera by Ge et al. (2024) recovered a very similar topology, lending further support to this hypothesis concerning the deep splits within the Trichoptera phylogeny.

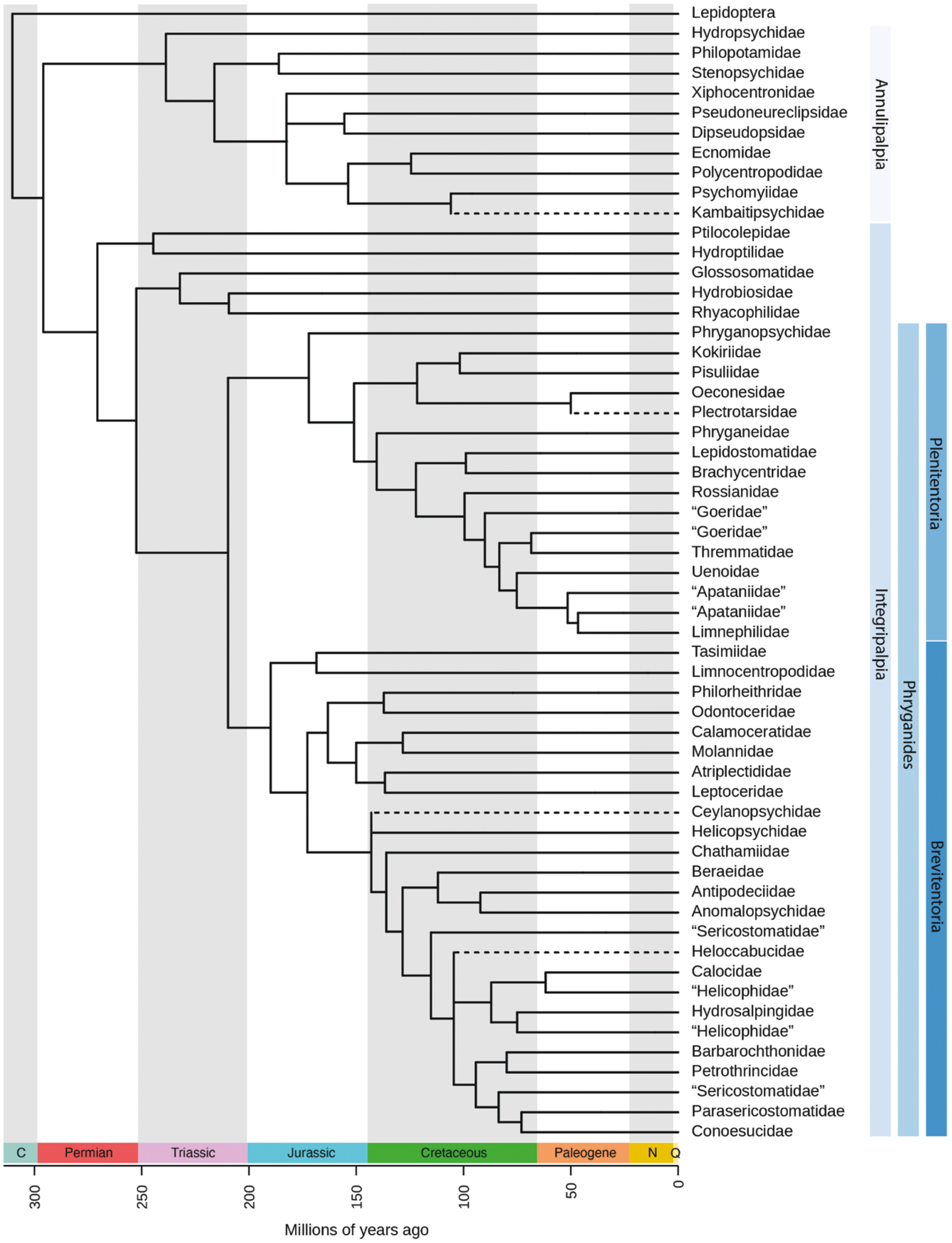

Fig. 8. Phylogeny and estimated divergence times of Trichoptera families, based on Frandsen et al. 2024. Paraphyletic and polyphyletic families are indicated with quotes. Families not included in Frandsen et al. 2024 were placed manually, guided by earlier studies, and are indicated with dashed lines.

Definitions of Major Clades and Synapomorphies

Trichoptera has long been identified as a clearly defined and strongly supported monophyletic group within Insecta. The order is well-established as the closest relative of Lepidoptera in evolutionary studies, whether those studies rely on morphology, genetics, or a combination of both. Holzenthal and Kjer (2020) listed thirteen synapomorphies for the order previously proposed and discussed by other caddisfly workers (Hennig 1981, Weaver 1984, Kristensen 1991, 1997, Ivanov and Sukacheva 2002) (Table 2). Examples include aquatic larvae lacking spiracles, but with epidermal respiration often aided by filamentous larval gills, and adults with nonfunctional mandibles, but with the presence of a "haustellum" composed of fused hypopharynx and prelabium that aids in the uptake of liquids.

The order contains 2 monophyletic suborders: Annulipalpia, the fixed retreat and net spinners, and Integripalpia, which includes free-living species and various case makers. The 2 suborders were originally defined by the presence (Annulipalpia) or absence (Integripalpia) of cuticular annuli on the last segment of the maxillary and labial palps (Fig. 9A). The lack of annulate palpi is plesiomorphic; however, several other synapomorphies have been identified that define Integripalpia, including female and larval characters and additional modifications of the haustellum (Ivanov 2002). While Ross (1967) provided an early phylogeny in which morphological characters for the major clades were included, this phylogeny was not based on cladistic principles. The most recent assessment of morphology, including an assessment of characters for all major lineages, was presented by Ivanov (2002) and these characters are included in Table 3 and are illustrated in Figs. 1, 3, 5, 6, and 9. The major lineages further defined by Ivanov (2002) in his morphological analysis are also largely recovered with molecular data in the most comprehensive phylogeny of Trichoptera published to date (Frandsen et al. 2024).

Taxonomic Databases

The primary taxonomic database for caddisflies is *The Trichoptera World Checklist* (Morse 2011, 2024). The checklist was initiated in 1990 by John C. Morse, using sources such as Fisher's catalogs (1960–1973), Zoological Record, and other sources as a starting point (Morse 2011). It contains information from the major biogeographic regions of the world: Afrotropical, Australasian, East Palearctic, Nearctic, Neotropical, Oriental, and West Palearctic Regions. As of August 2024, this electronic resource reports a total of 17,279 species, 51 families and 630 genera of caddisflies (Morse 2024). In its current form, the database includes a search page where the checklist can be searched by taxon, country, or biogeographic region. Each species is represented by a web page that contains its classification hierarchy and can contain additional information on distribution, location, and a list of papers that mention the species. The database is currently in the process of being moved to TaxonWorks (taxonworks.org), which will add additional functionality (a committee is currently being formed for this task). A DNA barcode database is also available for caddisfly species on the Barcode of Life Data System (Ratnasingham and Hebert 2007); this database is well-established for the Nearctic, Palearctic, and Australasian regions, but there are clear holes that need to be filled for other parts of the world (Fig. 10).

Regional taxonomic databases are somewhat sparser (Table 4). In the Palearctic region, there is a regional database for Europe (Graf et al. 2008, 2024, Schmidt-Kloiber and Hering 2015) and several countries offer online species lists, including Italy (Stoch 2003) and Spain (González 2024). Similarly, Viljanen (2021) provided an online list of caddisfly species for the Fennoscandia region. For the Afrotropical and West Palearctic, the "Caddisflies of the West Palearctic and Afrotropical regions of Africa" provides information on species and genera occurring in both regions, the geographic distribution of the species, and identification keys for both regions (Tobias and Tobias 2007). Finally, for the Americas, baseline data and information are available for the US and Canada (Rasmussen and Morse 2014), Brazil (Santos et al. 2024), Argentina and Uruguay (Sganga et al. 2024), and Mexico (DGRU-UNAM 2024).

Table 2. Trichoptera ordinal level apomorphies (from Holzenthal and Kjer, 2020, and authors cited therein)

1. Larvae aquatic, apneustic (no open spiracles), respiration epidermal, often by filamentous abdominal gills (Fig. 5A)
2. Larvae living in silken retreats in oxygenated water of streams (Ivanov and Sukatcheva, 2002: 209) (not present in all Trichoptera, although all extant species construct a pupal shelter, larval retreat, or larval case; production of silken larval and pupal structures also occurs in Lepidoptera).
3. Larval tentorium reduced, delicate.
4. Larval antennae greatly reduced (at most 2-segmented) and without extrinsic muscles (Fig. 5B).
5. Larval abdominal segments I–IX without prolegs (possibly apomorphic for a more inclusive clade, such as Amphiesmenoptera or Endopterygota).
6. Larval anal prolegs well developed (Fig. 1).
7. Larval abdominal segment IX with dorsal tergite (Fig 5E).
8. Pupation aquatic in attached dome-shaped pupal structure of sand grains to protect pupa and enclosing an osmotically active semipermeable cocoon filled with special ionically active liquid to aid respiration (Ivanov and Sukatcheva, 2002: 209). (Not all Trichoptera have semipermeable fluid-fill cocoons, although almost all extant species pupate underwater in a pupal structure, except for a few semiterrestrial species.)
9. Adult mandibles reduced, with loss of mandibular articulation (Fig. 6G).
10. Adult prelabium joined with hypopharynx to form a unique protrusible/ eversible 'haustellum' which serves as a lapping/sponging organ (Crichton, 1957, Kristensen, 1997, Holzenthal et al., 2007) (Fig. 6G).
11. Maxillary and labial palps well developed, with subterminal sensory organs (Ivanov and Sukatcheva, 2002: 209; Figs. 6G and 9A).
12. Mesonotum with distinct warts along lateral sutures (Ivanov and Sukatcheva, 2002: 209) (Fig. 6H).
13. Forewing vein Cu2 with strong apical bend (Fig. 6E) (listed as a potential autapomorphy by Kristensen 1997, but several extant species have straight Cu2 apex).

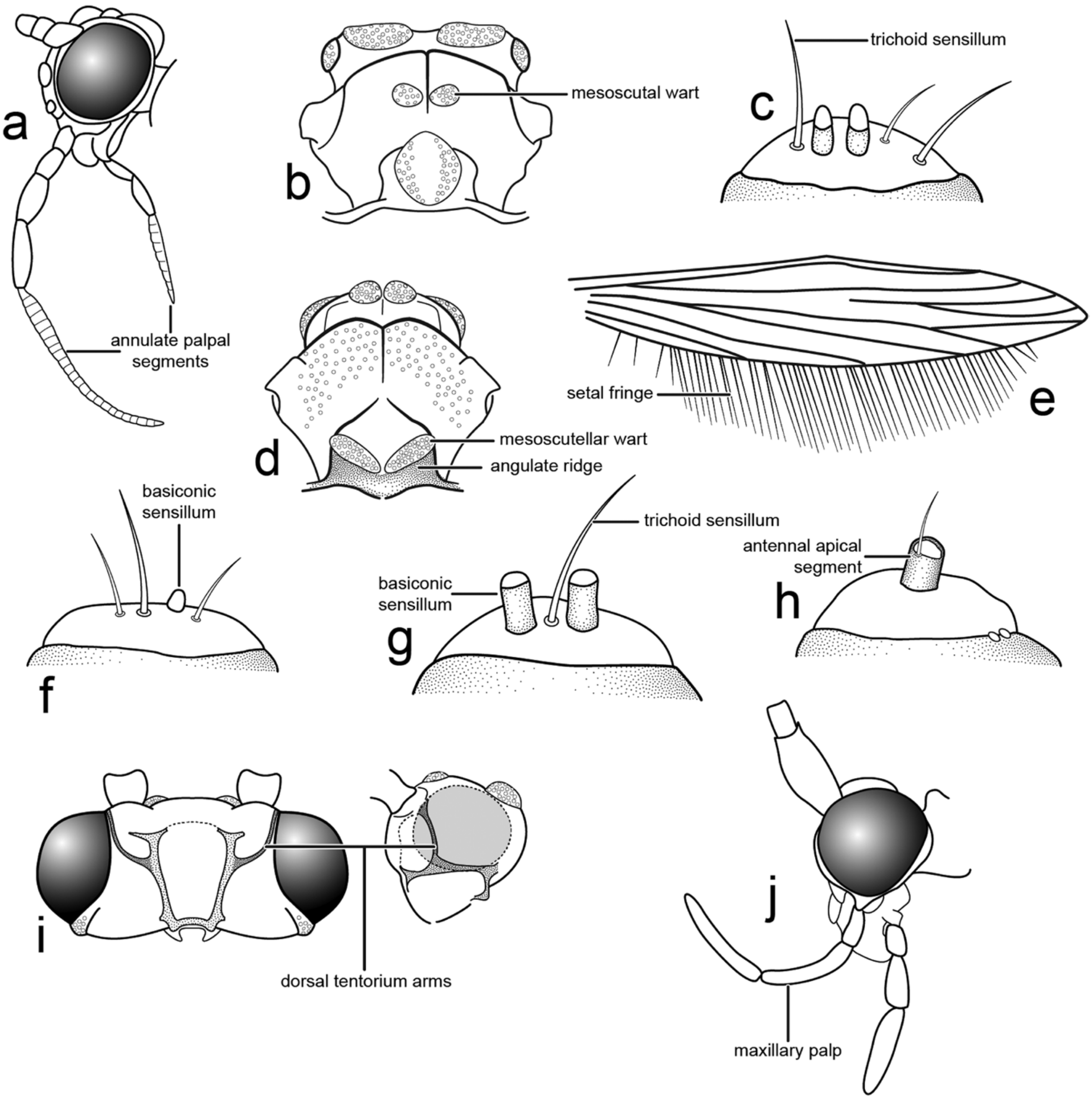

Fig. 9. Adult and larval morphological structures (indicting apomorphies of various clades, see Table 1). A) Adult head, lateral (Ecnomidae). B) Adult pro- and mesothorax, dorsal (Polycentropodidae). C) Larval antennal detail (Stenopsychidae). D) Adult pro- and mesothorax, dorsal (Hydroptilidae). E) Hind wing (Hydroptilidae). F–H) Larval antennal details (Polycentropodidae, Rhyacophilidae, Phryganeidae, respectively). I) Adult head, showing tentorium (Lepidostomatidae). J) Adult head, lateral (Brachycentridae). (Figures A), B), D), E), and J) modified from Morse et al. 2019, figures C), F), G), and H) modified from Frania and Wiggins, 1997, figure I) modified from Neboiss, 1991).

Regions in Need of Biodiversity Exploration and Documentation

The diversity of Trichoptera is underestimated in the Afrotropical, Neotropical, and Oriental faunas. According to hypotheses made by de Moor and Ivanov, the number of Trichoptera species described likely represents 25%–30% of the total diversity in the order (2008). Malicky (1993) suggested that global Trichoptera diversity could exceed 50,000 species. Nevertheless, species discovery rates highlight regions requiring extensive biodiversity exploration. From 2008 to 2019, the Afrotropical region recorded a 14.2% increase in described caddisfly species, whereas the East Palearctic and Indo-Malayan regions experienced larger increases of 31% and 23.5%, respectively. As with many insect taxa, caddisflies are most diverse in the tropical regions of the world, many of which are poorly studied, indicating that those regions should be the focus of future taxonomic studies (de Moor and Ivanov 2008). For example, in the GBIF database for Trichoptera records, there are large gaps in tropical Africa and South America

Table 3. Morphological synapomorphies for the major clades of Trichoptera as presented by Ivanov (2002) with slight modifications to certain terminology and to conform to the phylogeny presented by Frandsen et al. (2024). To save space, figures are referred to as "F"

Taxon	Synapomorphies	Included families
ANNULIPALPIA[a]	*Adult*: palps 'annulate' (F9a); male parameres lost; forewing Cu1 base shifted distad. *Larva*: anal proleg base elongate (F1e); segment 10 reduced; antenna with 3 trichoid sensilla (F9c).	
Hydropsychoidea	*Larva* (F1e): secondary notal sclerites; dense secondary setae on body, especially abdomen; abdominal branching gills; anal proleg terminal hair brush; silken net with regular mesh (F3a).	Hydropsychidae
Psychomyioidea	*Adult*: mesoscutal warts rounded (F9a). *Larva*: pronotal hind angle joins sternite behind coxa; hypopharynx sclerotized dorsally; prementum not discernable; spinneret long; larval body flat; cuticle hydrophorous; antenna with 1 basiconic sensilla (F9f).	Dipseudopsidae, Ecnomidae, Kambaitipsychidae, Polycentropodidae, Pseudoneureclipsidae, Psychomyiidae Xiphocentronidae
Philopotamoidea	*Larva*: abdominal tergum IX membranous, all setae inconspicuous (F1d)[b]	Philopotamidae, Stenopsychidae
INTEGRIPALPIA[c]	*Adult*: Hind wing crossvein *cu-a* thin, perpendicular to veins. *Larva*: head secondarily hypognathus (F5b); spinneret opening with wide dorsal lobe, silk thread flat; anal prolegs short, stout (F5e).	
Hydroptiloidea	*Adult*: small size; mesoscutellar warts transverse, meet mesally to form angulate ridge (F9d); hind wing narrow, acute, with posterior setal fringe (F9e).[d] *Larva*: hypermetamorphosis; purse case (F3h-j,q); algal feeders.	Hydroptilidae, Ptilocolepidae
Glossosomatoidea[e]	*Larva*: tortoise case (F3f,g).	Glossosomatidae
Rhyacophiloidea	*Larva*: antenna with 2 basiconic sensillae and 1 trichoid sensilla between them (F9g); carnivorous; silk produced only prior to pupation.	Rhyacophilidae, Hydrobiosidae
Phryganides[f]	*Adult*: haustellum apex with parallel channels covered with asymmetrically branching microtrichia (F6g); female ovipositor (oviscape) reduced, apodemes lost, cerci reduced; eggs laid in proteinaceous matrix; forewing M4 tending to reduction *Larva*: antenna with modified apical sensilla (F9h); sternite bearing paired glands; abdominal segment 1 with lateral projections (humps) (secondarily reduced in some families) (F5a); abdominal lateral fringe and forked lamellae (F5a); abdominal prolegs short (F5e); portable tube case (F3k-p, r-ee).	
Plenitentoria	*Adult*: male maxillary palps turned upwards and usually with less than 5 segments(F9j); dorsal tentorial arms secondarily developed (F9i). *Larva*: prothorax with Gilson's gland opening on prosternal horn.	Kokiriidae, Apataniidae, Goeridae, Limnephilidae, Rossianidae, Thremmatidae, Uenoidae, Brachycentridae, Lepidostomatidae, Oeconesidae, Phryganeidae,Pisuliidae,Plectrotarsidae
basal brevitentorian families	Molecular characters only, although predaceous larvae are a possible synapomorphy.	Tasimiidae, Limnocentropododae
Brevitentoria	*Larva*: forked lamellae on abdominal segment 8 only, Gilson's gland reduced; hind legs adopt sensory function and held upwards (F1g).	
Leptoceroidea	*Adult*: base of forewing 2A separated by jugal fold from rest of anal loop.	Atriplectididae, Calamoceratidae, Molannidae, Leptoceridae, Odontoceridae, Philorheithridae
Sericostomatoidea	*Larva*: pronotum desclerotized caudally (ie lacks prominent posterior transverse ridge seen in Limnephilidae and related families, see Wiggins 1996); abdominal seta 7 displaced dorsad to the claw base; abdominal tergum 9 membranous.	Anomalopsychidae, Antipodoeciidae, Barbarochthonidae, Beraeidae, Calocidae, Celanopsychidae, Chathamiidae, Conoesucidae, Helicophidae, Helicopsychidae, Heloccabucidae, Hydrosalpingidae, Parasericostomatidae, Petrothrincidae, Sericostomatidae

[a] Hydropsychina of Ivanov (2002) and including Rhyacophiloidea.

[b] Frania and Wiggins (1997).

[c] Phryganeina of Ivanov (2002) excluding Rhyacophiloidea. Characters listed by him apply to Integripalpia of Frandsen et al. (2024) exclusive of Rhyacophiloidea.

[d] Interpreted from Wiggins (2004).

[e] Not listed by Ivanov (2002), but several possible apomorphies discussed by Frania and Wiggins (1997).

[f] Dicloacia of Ivanov (2002).

(Fig. 11) (GBIF 2024). The difference evident in records between the regions underscores the need for increased taxonomic research and biodiversity documentation efforts in understudied areas, such as the Afrotropical region to understand better and conserve its unique ecosystems.

Areas of Taxonomic Impediments and Challenges in Advancing Systematic Research

Lack of Standardization of Genitalic Terminology

Standard characters traditionally used in the identification of families and genera of adult Trichoptera include antennal length, presence or absence of ocelli, structure of maxillary palps, setal warts on the head and thorax, wing venation, and number of tarsal spurs. Terminology used for these structures is generally consistent across the order. However, species-specific characters are largely tied to the male genitalia; these genitalic structures are hyperdiverse and an assessment of their homology has never been performed across the entire order. Additionally, numerous sets of terminology for referring to these structures have accumulated over time, adding confusion to the already confounding variation (Ross 1956, Nielsen 1957, Schmid 1970, Tuxen 1970, Marshall 1979, Oláh and Johanson 2008). This lack of standardization occurs between the older literature and current literature, and within current literature as well. For example, the ancestral appendicular structures of the IXth segment of the male genitalia have been variously referred to as claspers, inferior appendages, gonopods, and coxopodites (*op. cit*).

Female Identification

In Trichoptera, as in many other taxa, characters of the male genitalia are often structurally complex and host numerous species-specific features, hypothesized to be driven by sexual selection (Eberhard, 2015). Because of this, species-level taxonomy of caddisflies has traditionally been based on males, while descriptions of females are largely lacking. Female genitalic characters at the macromorphological level appear simple and are more uniform across species—however, when often studied in detail, especially with internal sclerotized structures, species-specific characters are often discernible (Nielsen 1980). Additionally, females are usually associated with males indirectly by, for example, assuming that males and females collected together at the same time and place and with the same morphotype are conspecific. This is appropriate in some instances, but at sites with many members of different species, especially in the same genus, it is problematic. Collection of *in copula* pairs is rare and adult rearing from larvae is hindered by a lack of species knowledge of the larval stage.

Larval Identification

A similar situation occurs with species identification of larvae. First, in situations where larvae have been associated with adults, it is the fifth (final) instar that is typically described. Earlier instars are generally unidentifiable to species (especially in species-rich genera), and sometimes even to genus. Secondly, within a genus larvae are often very uniform morphologically and characters used to separate the species are often difficult to discern. Standard characters traditionally used in the identification of families and genera of larval Trichoptera include abdominal gills, anal prolegs, antennal length, thoracic sclerites, and structures of the legs (Wiggins 2004, Morse et al. 2019b). However, larval characters at the species level in many instances are based on fine details of setal morphology (chaetotaxy) and, within some genera, color patterns on the head capsule, which can be variable within a species (Schefter and Wiggins 1987).

DNA Barcoding

The Trichoptera Barcode of Life project (Zhou et al. 2016) has been extremely successful at generating DNA barcodes for caddisflies with 6,447 species represented by more than 86,000 DNA barcode sequences (Ratnasingham and Hebert 2007). This represents coverage for nearly 40% of named caddisfly species. These sequences have also been useful for associating larval and adult caddisflies (eg Ruiter et al. 2013). Further, as biomonitoring studies using environmental DNA or bulk tissue metabarcoding become more common, a reliable reference database of DNA barcodes is even more essential. While the coverage of the database is impressive, it is currently patchy with bias towards Canada, the United States of America, Europe, Japan, Australia, and New Zealand. Thus, additional efforts to improve the DNA barcoding reference database in under sampled areas of the globe are essential (Fig. 10).

Future of the Systematics of Trichoptera

The deep splits within the caddisfly phylogeny converging upon resolution in the most recent phylogenomic analyses. However, more research is needed to clarify the phylogeny at the superfamily and family levels. Multiple research groups are now beginning phylogenomic work on some of the most diverse families (Thomson et al. 2022, Pauls et al. 2023). These advances are exciting, and we hope work continues across more caddisfly families as sequencing costs continue to decline and as new caddisfly researchers enter the discipline.

The training of new caddisfly researchers should be a major goal moving forward, especially in the tropical regions of the world where caddisflies are species-rich and understudied. As is the case with taxonomic researchers of other groups, many caddisfly taxonomists are retired or reaching retirement age, leaving a profound gap in taxonomic expertise in the group. Closing this gap should be a priority in our training and future research goals. Given the competitive academic environment, we should also work to ensure that students are receiving the most up-to-date education in disciplines related to systematics, including bioinformatics, genomic analysis, evolutionary biology, and taxonomy. As the caddisfly phylogeny continues to be resolved, more questions concerning the evolution of biological traits and biogeography can be answered. Building productive global collaborations among caddisfly researchers will be key to generating hypotheses and data sets to test them.

While new genetic-based technologies have revolutionized insect and caddisfly systematics, fundamental knowledge in natural history, access to and curation of collections, descriptive and revisionary taxonomy, nomenclature, online catalogs, databases and identification resources, illustration and photography, knowledge of historical literature, etc. should not be forgotten as these are vital components to understand and ultimately protect the world's caddisfly fauna.

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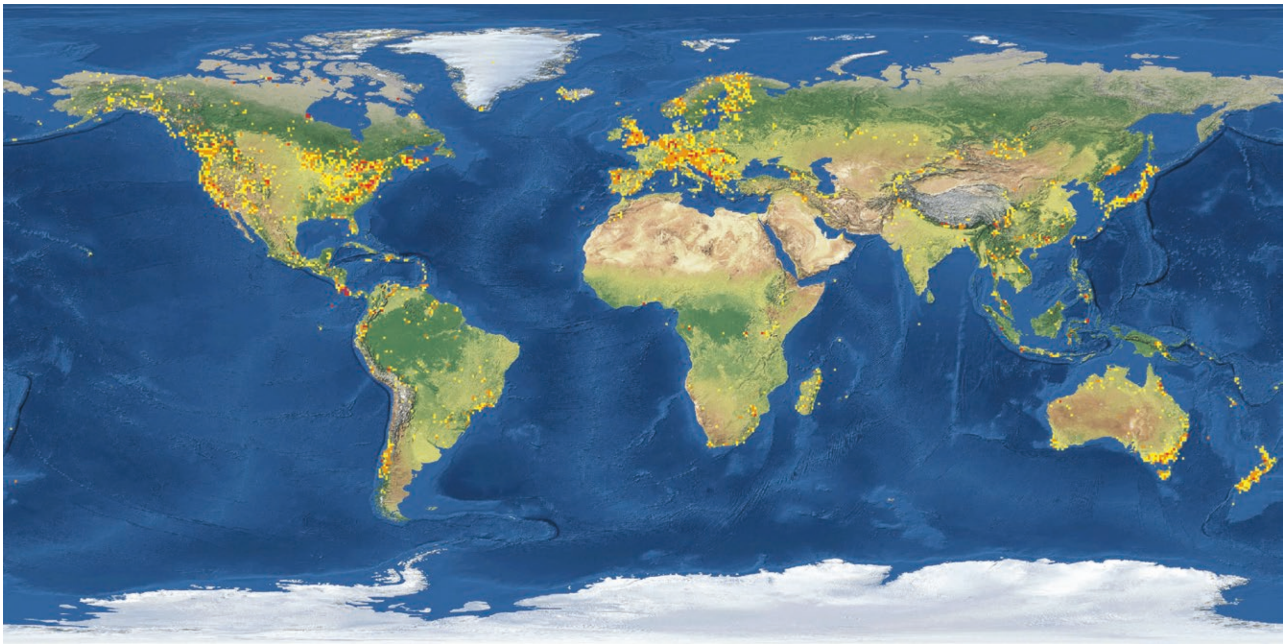

Fig. 10. Heatmap of global representation of DNA barcode sequences for Trichoptera in the Barcode of Life Data System. Density is shown from low (yellow) to high (red).

Table 4. Databases for Trichoptera, including regional coverage and website

Coverage	Database	Reference
Worldwide	The Trichoptera World Checklist: https://trichopt.app.clemson.edu/welcome.php	Morse (2011), Morse (2024)
Palearctic	Fresh Water Ecology: www.freshwaterecology.info	Schmidt-Kloiber and Hering (2015), Graf et al. (2024)
West Palearctic	Checklist of the species of the Italian fauna: https://www.faunaitalia.it/checklist/introduction.html	Stoch (2003)
West Palearctic	El Reino Animal en la Península Ibérica y las Islas Baleares: https://www.fauna-iberica.mncn.csic.es/faunaib/index.php	González (2024)
West Palearctic	Trichoptera from East Fennoscandia in the Finnish Museum of Natural History (MZH/FMNH/Luomus): https://tietopankki.luomus.fi/	Viljanen (2021)
West Palearctic and Afrotropical	Caddisflies of the West Palearctic and Afrotropical regions of Africa: https://trichoptera.senckenberg.science/Trichoptera%20africana/introduction.htm	Tobias and Tobias (2012)
Neotropical	Trichoptera in Catálogo Taxonômico da Fauna do Brasil: http://fauna.jbrj.gov.br/fauna/faunadobrasil/278	Santos et al. (2024)
Neotropical	Colecciones Universitarias, Trichoptera: https://datosabiertos.unam.mx/biodiversidad/	DGRU-UNAM (2024)
Neotropical	TRICHOPTERA species from Argentina and Uruguay: https://biodar.unlp.edu.ar/trichoptera/	Sganga et al. (2024)
Nearctic	Trichoptera Nearctica: https://trichoptera.org/	Rasmussen and Morse (2014)

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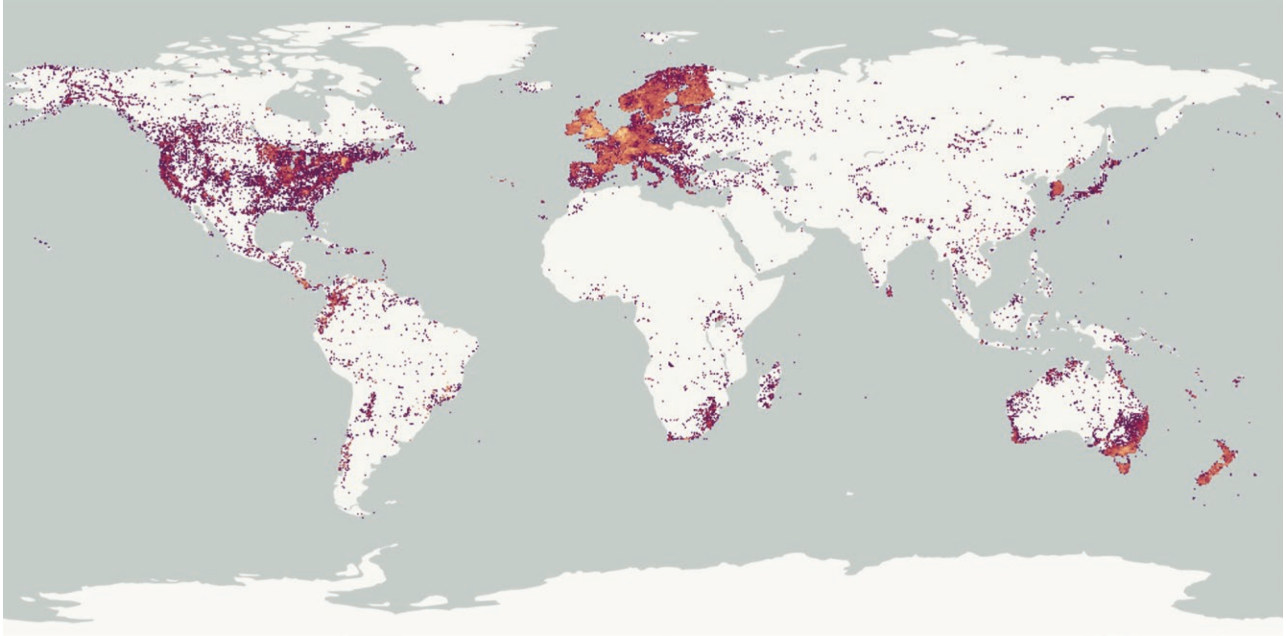

Fig. 11. Heatmap of records for Trichoptera collections from 1738 to 2024 stored in GBIF show unequal coverage across the globe. Density is shown from low (purple) to high (gold).

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