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Review

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Taxonomy

Crane fly (Diptera: Tipuloidea) systematics: past, present, and future

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Superfamily Tipuloidea, commonly known as true crane flies, represents a taxonomically and ecologically diverse group within Diptera. Species in this clade are easily recognized by their characteristic long-legged appearance and are widespread across terrestrial and aquatic habitats. This review synthesizes the current state of Tipuloidea systematics, providing an overview of key contributions from the past that have shaped our present understanding. We review the paleontological evidence available for this group and summarize phylogenetic studies that have explored evolutionary relationships across different taxonomic levels. Although significant progress has occurred in documenting global crane fly diversity, opportunities remain to associate conspecific life stages, undertake revisionary taxonomy, and stabilize the classification system through expanded taxon sampling and the use of new genetic markers and mitochondrial genomes in future phylogenetic analyses. Finally, we highlight priority areas for future research to enhance our understanding of Tipuloidea evolution and classification.

Keywords: Tipuloidea, Tipulomorpha, crane fly, taxonomy, systematics.

Scope of the Review and Definition of Tipuloidea

Crane flies (Diptera: Tipuloidea) are one of the most taxonomically and ecologically diverse groups of true flies. With 15,726 described species across 538 genera and subgenera (Oosterbroek 2024), crane flies represent one of the largest and earliest diverging lineages of Diptera. They are globally distributed and commonly found in both terrestrial and aquatic environments and are easily recognizable by the typical long-legged appearance of the adults. Ecologically, both adults and larvae play important roles, such as being key components of soil macrofauna (Frouz 1999), acting as pollinators (Pansarin and Pansarin 2017), a food source for vertebrates, especially birds (Carroll et al. 2015), and as pests in various settings (Moffat 2023).

Crane flies are currently classified under the superfamily Tipuloidea, which is further divided into 4 families: Cylindrotomidae, Limoniidae, Pediciidae, and Tipulidae (Table 1). Some researchers use an alternative classification that consolidates these divisions as a single family, Tipulidae, with the same 4 groups recognized as subfamilies (Alexander and Alexander 1970). Designation as Tipulomorpha is also used when the sister group to Tipuloidea, the

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Table 1. Taxonomic structure of superfamily Tipuloidea

Superfamily	Family	Subfamily	Number of valid species
Tipuloidea	Cylindrotomidae	Cylindrotominae	46
		Stibadocerinae	51
	Limoniidae	Dactylolabinae	58
		Chioneinae	4,307
		Limnophilinae	2,580
		Limoniinae	3,853
	Pediciidae	Pediciinae	471
		Ulinae	28
	Tipulidae	Ctenophorinae	180
		Dolichopezinae	316
		Tipulinae	3,831

Classification structure and species numbers according to Oosterbroek (2024).

family Trichoceridae, is included. Petersen et al. (2010) provide a synopsis of the changes in classification systems used by crane fly taxonomists.

Although much is known about crane flies in general, there are still significant gaps in our understanding of their life history, phylogenetic relationships, and overall taxonomic structure. For instance, while over 15,700 species have been described, only about one-third of the genera and subgenera are known in the immature stages (Oosterbroek and Theowald 1991). A consistent taxonomic framework has been maintained, yet higher-level quantitative phylogenetic analyses suggest that it does not fully reflect the evolutionary relationships within the group (Petersen et al. 2010). As de Jong (2017) noted, higher classification within Tipuloidea is often based on convention rather than evidence of monophyly for all recognized taxonomic groups.

This dichotomy—being well-known but poorly resolved—serves to mask the necessity for research within this group. The goal of this review is to summarize the current state of crane fly systematics, highlighting key research that has shaped our understanding while identifying opportunities for future study. By addressing these gaps, we can overcome taxonomic barriers and advance our understanding of the evolutionary and ecological roles of crane flies.

Diagnosis

Tipuloidea are often confused with, or are superficially grouped alongside other lower Diptera that also have slender bodies and legs longer than their bodies. These groups include Tanyderidae ("primitive crane flies"), Trichoceridae ("winter crane flies"), and Ptychopteridae ("phantom crane flies"). However, Tipulomorpha (Tipuloidea and Trichoceridae) can be distinguished from Tanyderidae and Ptychopteridae by a characteristic V-shaped suture on the mesonotum and the presence of an anal vein extending to the wing margin in the wings. Tipuloidea are distinguished from Trichoceridae by the lack of ocelli in the adult. In the immature stage (Fig. 2), crane flies are identifiable by their hemicephalic head capsule, with about one-third of the compact capsule exposed, and a posterior spiracular disk bordered by a variable number of lobes surrounding the 2 spiracles. Larvae of the previously mentioned families are amphipneusnistc, while Tipuloidea are largely metapneunistc, but with some apneusnistic genera. Taxon identification in Tipuloidea typically relies on a combination of adult characteristics, particularly wing venation and male reproductive structures. Coloration of the body, wings, and legs is also often used in determining species identity. For larvae, head capsule and spiracular disk features are important. Larval identification is typically only possible to genus.

Adult (Fig. 1)

Crane flies with slender bodies that vary from minute (1.5 mm) to large (60 mm); wing length elongate (3 to 50 mm); legs characteristically long with a length that typically surpasses the body length. Overall coloration variable, brightly colored to drab; wing coloration variable, often hyaline but may have darker patterns. Head with large compound eyes present; ocelli absent; vertex of head variable, typically not raised. Antenna variable in length and flagellomere structure (globular, oval, cylindrical, bipectinate); length rarely exceeding body length; typically with 11 to 14 flagellomeres. Anterior head is produced into the rostrum associated with the mouth; typically, as long as head but may be reduced, or twice the head diameter or longer than the entire body; rostrum tipped with a small projection (nasus) in Tipulidae; palpus typically 5-segmented with the terminal segment longer than (most Tipulidae, some Pediciidae) or equal to, or shorter than, previous segments (most non-Tipulidae). Thoracic sclerites variable in construction; mesothorax with a V-shaped transverse suture; meron variable, shape can be diagnostic. Wings elongate, often meeting or exceeding the abdomen length; wing length reduced (brachypterous or micropterous) in a variety of groups; weakly developed anal angle, though rarely enlarged; venation variable, diagnostic at the genus and higher level, stable for intra-generic members. Legs typically elongate and slender, exceeding body length; easily detaching from body at the trochanter-femur suture; apex of tibia with or without spurs. Abdomen elongate, exceeding the length of thorax, cylindrical. Male reproductive structures located at the apex of the abdomen, often complex in construction, and usually diagnostic to species. Female ovipositor located at the apex of the abdomen and forming sclerotized blades, rarely short and fleshy.

Larvae (Fig. 2)

Maggot-like, slender, length much greater than wide. Completing 4 instars. Head capsule usually distinct and sclerotized; with at most 2/3 of head capsule retracted into the prothorax; capsule with variably produced ventral and dorsolateral incisions, in some Chioneinae and

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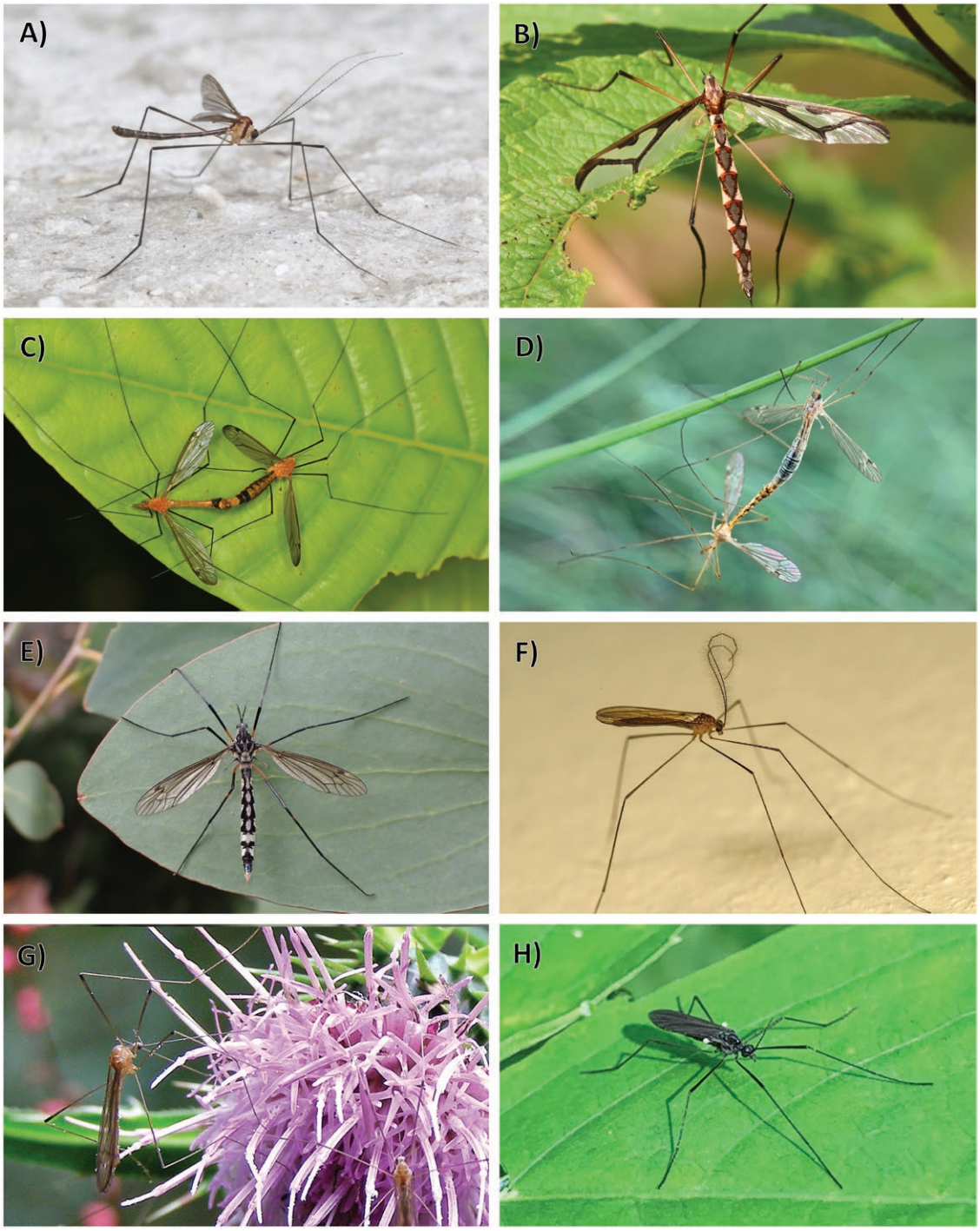

Fig. 1. Habitus of adult crane flies. Representative adult images are shown for Cylindrotomidae: A) *Stibadocerodes zherikhini* Krzeminski (© James Bailey); Pediciidae: B) *Pedicia albivittata* Walker (© mistycal); Tipulidae: C) *Tipula* (*Microtipula*) sp. (Stephen A. Marshall); D) *Tipula* (*Pterelachisus*) *mandan* Alexander (Jon Gelhaus); E) *Platyphasia wilsoni* Alexander (© john eichler); Limoniidae: F) *Polymera* sp. (Stephen A. Marshall); G) *Elephantomyia* sp. (Matt Petersen), H) *Gnophomyia tristissima* Osten Sacken (Jon Gelhaus).

some Limnophilinae causing the capsule to be reduced to rods; mandibles opposed, moving in a horizontal or oblique plane. Abdominal segments smooth or with rows of fine setation; segments may be equipped with transverse creeping welts or fleshy swellings or projections; respiratory system functionally metapneustic, some taxa are apneustic; terminal segment with variably produced lobes that may be partially sclerotized or fringed with setae (commonly 2, 5, 6); anal papillae (as membranous lobes) typically present, variable in length.

Pupae

Slender and elongate, length much greater than wide; obtect, appendages of head and thorax visible; leg sheaths parallel; respiratory system propneustic, peripneustic, or amphipneustic. Thoracic respiratory organs typically present, variably produced; often extended and rod- or spine-like, but may be ear-shaped or branched. Transverse rows of stiff setae or spines variably produced on abdominal segments, may be absent. Genital sheaths often with spines or

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Fig. 2. Habitus of larval crane flies. A) full larva and B) larval head capsule of *Tipula* (*Vestiplex*) sp. (Starkevich et al. 2021); C) immature *Dicranomyia* sp.; D) full larva and E) larval head capsule of *Hexatoma sp.* (Podėnienė et al. 2023).

spine-like tubercles. Pupae typically naked; occasionally enclosed in silken tubes or covered in detritus.

Review of Biology and Natural History

Crane flies are commonly encountered across a wide range of habitats, including forests, grasslands, alpine regions, intertidal marine, managed and cultivated agroecosystems, and urban areas. Pritchard's (1983) review remains the most comprehensive account of crane fly biology to date. While there have been advances since its publication, our understanding of crane fly biology remains significantly limited. As Pritchard noted, "crane flies are virtually unknown to us except as dead adults on pins." This summary presents the current knowledge of crane fly biology, framed within a phylogenetic context to highlight trends across major clades.

Crane flies are holometabolous insects, with most species exhibiting a univoltine life cycle, though bivoltine, semivoltine, and merovoltine life cycles have also been observed. Temperature plays a key role in their development, with shorter life cycles in warmer environments and longer ones in arctic regions (Maclean 1973, Pritchard 1976, 1983). Generally, both adult and larval stages are more common in water-rich environments, though some groups inhabit dry desert habitats (Gelhaus 2005). The egg stage lasts for a few days to several months. The larval stage has 4 instars, with the full larval stage lasting from several months to several years. The second, third, and last instar larvae are very similar morphologically, while the first instar or egg-larvae differ drastically (Podėnienė et al. 2014, 2019). The pupal stage lasts a few weeks, and an adult stage exists from a few days to about a week (Pritchard 1983). Adults are delicate insects, with legs that easily detach when disturbed. Adults are weak fliers, often staying near their larval habitats and resting on nearby vegetation. Feeding during the adult stage is uncommon, though some species may consume water or nectar, and a few possess specialized mouthparts for nectar feeding. Mating is followed by oviposition, with eggs being laid in or near the larval habitats. Habitat requirements tend to be relatively consistent at the genus level. Larvae are found in various environments, including aquatic (marine; freshwater lotic and lentic), semiaquatic (margins of water bodies, algal mats, saturated soils), and terrestrial habitats (dry soils, decaying wood, fungi, leaf litter, vegetation) (Alexander and Byers 1981, Pritchard 1983, de Jong et al. 2008). Their feeding habits are equally diverse, including consuming decaying plant material and associated microorganisms, living plants (mosses and higher plants), diatoms, fungi, or preying on other invertebrates (Pritchard 1983, Gelhaus and Podėnienė 2019).

The 2 largest crane fly clades, Tipulidae and Limoniidae, exhibit significant variation in larval habitats and feeding ecology. However, the biology of most species in both groups remains undescribed. Most known Tipulidae larvae feed on either live or dead and decaying plant material. These larvae are found in both freshwater aquatic and a wide range of terrestrial habitats, which can be highly specific to a genus and often involve morphological adaptations. For instance, the terrestrial xylophagous genus *Ctenophora* Meigen tunnels in living and dead wood, with modified midguts adapted for consuming woody material (Semenova 1974). In contrast, species of *Tipula* Linnaeus are known to variably inhabit dry or wet soil, feed on plant remains, mosses, roots, stems, and leaves of various grasses (Petersen et al. 2013), or they may be aquatic, feeding on detritus or diatoms (Hall and Pritchard 1975). The biology of Limoniidae is even more diverse than that of Tipulidae, but the general trend of both highly specified and highly generalized taxa is also found here. For example, the larvae of the wingless genus *Chionea* Dalman are specialized and found in rodent burrows, while those of *Dicranomyia* Stephens variably occur in terrestrial or aquatic habitats, including marine and freshwater environments, as well as in decaying wood, fungal bodies, or rotting fruit (Alexander and Byers 1981). Larval feeding behavior is varied but can generally be classified as predatory (Limnophilinae), fungivorous (Limoniinae),

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or phytophagous, feeding on both living and dead plant material (Limoniinae, Chioneinae). Nectar feeding occurs among some groups, and specialized adaptations for this behavior have evolved in at least 3 lineages (eg *Elephantomyia* Osten Sacken, *Geranomyia* Haliday, *Toxorhina* Loew) (Oosterbroek and Lukashevich 2021).

In comparison, the remaining 2 families of crane flies exhibit more consistent biological patterns. Cylindrotomidae larvae are phytophagous, feeding on both terrestrial and aquatic vascular and nonvascular plants. For example, *Diogma glabrata* (Meigen) is known to feed on moss (Peus 1952), while *Cylindrotoma distinctissima* (Meigen) has been recorded feeding on a variety of plants, including *Allium*, *Anemone*, *Trautvetteria*, *Stellaria*, and *Viola* (Imada 2021). Pediciidae ecology can be divided between the 2 subfamilies, Ulinae and Pediciinae. Ulinae larvae are terrestrial and fungivorous, feeding on and inhabiting various fungi. In contrast, Pediciinae larvae are aquatic, typically found in cool springs and headwaters, where they prey on mites, oligochaetes, and small insects.

Contribution from Taxonomists of Past and Present

Carolus Linneaus (Karl von Linne) developed the system of binomial nomenclature we follow today, but in doing so he defacto described the first crane fly species. All of his described crane flies species were placed in the genus *Tipula,* and all were from Europe (Table 2). At present only 4 Linnean species remain in the genus *Tipula*, the others are now placed in 12 other genera, reflecting our better understanding of their evolutionary relationships. Early taxonomists of crane flies following Linnaeus included J. W. Meigen, who described many new genera along with nearly a hundred new species. Later Francis Walker, operating out of the British Museum with specimen holdings built from throughout the British Empire, described over 160 species, although nearly a third have now been synonymized with other earlier described species. The mid to late 1800s saw the work of close contemporaries, Carl Robert Romanovich, Baron von den Osten Sacken (commonly known as C. R. Osten Sacken), and Hermann Loew. Osten Sacken was based for several decades in Washington DC as a diplomat and used his time in the US to make collections of crane flies and other Diptera and to develop American collection resources and young American taxonomists, as well as compiling a catalog of North American Diptera. His description of new species of crane flies was focused on the "Tipulidae brevipalpi" in the present families Cylindrotomidae, Limoniidae and Pediciidae. Loew was based in then Saxony (now part of Poland) and worked on all crane fly families for Europe, however all the North American species he described were obtained through the collecting efforts of Osten Sacken and his correspondents. The bulk of their joint collections reside in the Museum of Comparative Zoology, Harvard University. Elsewhere, the work of Frederick A. A. Skuse described over one hundred species of Australian crane flies in 2 papers published in 1890, as part of a series of papers detailing the Diptera of Australia.

The first few decades of the 1900s saw researchers describing large numbers of species of Tipuloidea from the Nearctic, Indo-Malayan (including Dutch East Indies and India), and Palearctic realms. Rennie W. Doane was principally an economic entomologist in the western United States who took an interest in crane flies and described over a hundred species of Tipuloidea primarily from the western Nearctic (Byers 1976). J. C. H. de Meijere, based in the Netherlands, had his early interest in Diptera stimulated by the respected dipterist F. M. van der Wulp. Meijere subsequently described over a hundred species of Tipuloidea, with most described from Indonesia from material collected by Edward Richard Jacobson (de Jong 2000). Enrico Brunetti, a British citizen, described over 200 species of Tipuloidea from India and surrounding area while he was posted to India as a musician. Most important during these first decades was F. W. Edwards, who was based at the British Museum for 30 years and described nearly 700 species of Tipuloidea from Europe, Southeast Asia, and the Austropacific biogeographic realms. His work was considered of the highest caliber and encompassed, besides Tipuloidea, several other Lower Diptera families (Alexander 1941).

The first decades of the 20th century saw the initial work of Charles Paul Alexander, a researcher who would fundamentally transform our understanding of crane fly taxonomy and classification. At age 16, Alexander took a box of crane fly specimens he had collected to the State Entomologist of New York, E. P. Felt, for identification, and was disappointed when Felt stated "I'm sorry that I cannot help you, but there is no one in this country who can name these flies." (Wheeler 1985). He realized that this group, crane flies, was of great diversity in need of taxonomic expertise. Although he had published his first paper at age 14 on birds, he soon refocused on "tips" (as he often called them), and published his first paper on crane flies at age 20. He went to Cornell University for his PhD and completed a monumental 2 volume dissertation in 1917, with the first volume (Alexander 1919) on adult taxonomy (focused on the New York fauna but with wider applicability) with illustrations of wing and male genitalia (hypopygium). The second volume (Alexander 1920) focused on immature stages and included the first descriptions and illustrations of larval and pupal stages for many crane fly groups. He also included a summary of the worldwide crane fly literature up until that point, making it still of great use today. Soon after his PhD, he focused his research effort on descriptive taxonomy of adult flies and transferred his collection of immature specimens, along with that line of research, to J. Speed Rogers. Over 70+ years, Alexander along with his wife and partner Mabel (*see* Heard 2020) described 11,317 recent and fossil crane fly species in nearly 11,00 papers, a feat not matched by any other researcher in one family group of organisms (Oosterbroek 2022). Byers (1982) noted Alexander had to describe on average a new species every 2 to 3 d during his long career to reach this number, all this while serving as professor and dean at the University of Massachusetts, as well as other roles including President of the Entomological Society of America. Curiously, although he had several graduate students, none studied crane flies, and in addition, he had no coauthors on any new species of crane fly. It was clear that he preferred to work on the crane flies himself.

Alexander described species from all parts of world, except for Europe. It should be noted that he considered all crane flies in the family Tipulidae, unlike the 3 and then recent 4 family approach used by European taxonomists during the same time period (Byers 1992). New crane fly taxonomists need to realize when using the older literature that Tipulidae *sensu* Alexander equals the Tipuloidea as used today. The Alexanders built an unrivaled collection from a combination of their own collecting and from specimens sent by correspondents and paid collectors. They never traveled outside of North America but spent numerous summers collecting in various parts of the United States during the 1930s to 1950s, often in National Parks, where collecting can be restrictive today. The collection, numbering more than 8,000 holotypes, was purchased by the Smithsonian Institution and is housed there now. The collection is of 2 parts, the slides he prepared of wings, genitalia, legs, and antennae, and the rest of the pointed (dry) specimen, which he termed the "carcass." He felt the slides were of utmost value and he used them almost exclusively when identifying a new cache of specimens.

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Table 2. Prominent crane fly taxonomists

Era	Taxonomist	Active publication dates	Species descriptions		Realm
			As first author	As coauthor	
18C	Linnaeus, C.	1758–1767	16	0	WP
19C	Fabricius, J.C.	1775–1805	19	0	A, I, N, NT, WP
	Meigen, J.W.	1800–1838	97	0	WP
	Wiedemann, C.R.W.	1817–1830	42	9	A, I, NT, WP
	Say, T.	1823–1824	15	0	N, NT
	Curtis, J.	1825–1836	6	0	WP
	Macquart, P.J.M.	1826–1855	46	0	A, AO, I, N, NT, WP
	Schummel, T.E.	1829–1833	33	0	WP
	Walker, F.	1835–1865	120	0	A, AO, EP, I, N, NT, WP
	Westwood, J.O.	1835–1881	18	0	AO, EP, I, N, NT
	Zetterstedt, J.W.	1838–1852	27	0	WP
	Staeger, C.	1840–1840	9	0	WP
	Rondani, C.	1842–1875	10	0	A, I, NT, WP
	Loew, H.	1844–1874	118	0	A, AO, EP, N, NT, WP
	Blanchard, E.	1854–1854	5	0	NT
	Osten Sacken, C.R.	1854–1894	190	0	AO, EP, I, N, NT, WP
	Doleschall, C.L.	1856–1859	7	0	I
	Bigot, J.M.F.	1858–1888	6	0	A, NT
	Bellardi, L.	1859–1861	8	0	NT
	Wulp, F.M. van der	1859–1904	25	0	I, NT, WP
	Egger, J.	1863–1863	7	0	WP
	Schiner, J.R.	1863–1868	17	0	AO, NT, WP
	Siebke, H.	1863–1872	7	0	WP
	Mik, J.	1864–1889	14	0	WP, AO
	Philippi, R.A.	1866–1866	38	0	NT
	Westhoff, F.	1879–1882	6	0	WP
	Hutton, F.W.	1881–1902	25	0	AO
	Verrall, G.H.	1886–1888	6	0	WP
	Skuse, F.A.A.	1890–1896	97	0	AO
20C	Bergroth, E.E.	1888–1922	36	0	A, N, WP,
	Williston, S.W.	1893–1900	24	0	NT
	Strobl, P.G.	1893–1910	38	0	WP
	Coquillett, D.W.	1898–1910	21	0	EP, N
	Doane, R.W.	1900–1912	113	0	N
	Grimshaw, P.H.	1901–1901	5	0	AO
	Enderlein, G.	1903–1938	59	0	A, AO, EP, I, NT
	Meijere, J.D.H. de	1904–1924	107	0	WP
	Bezzi, M.	1906–1924	10	0	WP
	Matsumura, S.	1906–1932	15	0	EP
	Lundstrom, C.	1907–1916	18	0	WP
	Becker, T.	1907–1926	7	0	WP
	Speiser, P.	1908–1923	29	0	A
	Johnson, C.W.	1909–1914	19	0	N, NT
	Riedel, M.P.	1910–1933	55	0	WP
	Brunetti, E.	1911–1924	223	0	I

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Table 2. Continued

Era	Taxonomist	Active publication dates	Species descriptions		Realm
			As first author	As coauthor	
	Edwards, F.W.	1911–1939	693	0	AO, I, NT, WP
	Alexander, C.P.	1911–1981	10,835	0	AO, EP, I, N, NT, WP
	Kuntze, A.	1913–1920	11	0	WP
	Dietz, W.G.	1914–1921	43	0	N
	Pierre, C.	1917–1926	29	0	WP
	Nielsen, P.	1919–1966	22	0	WP
	Goetghebuer, M.	1920–1921	8	0	WP
	Tonnoir, A.L.	1920–1926	11	0	WP
	Senior-White, R.	1921–1924	11	0	I
	Santos Abreau, D.E.	1923–1923	6	0	WP
	Lackschewitz, P.	1923–1964	103	0	EP, WP
	Tokunaga, M	1930–1940	7	0	AO, EP, I
	Tjeder, B.	1941–1981	15	2	WP
	Bangerter, H.	1947–1948	11	0	WP
	Mannheims, B.	1950–1973	144	0	A, EP, WP
	Wood, H.G	1952–1952	18	0	A
	Savchenko, E.N.	1952–1989	371	4	WP
	Theowald. Br.	1957–1987	50	23	WP
	Lindner, E.	1958–1958	5	0	A
	Takahashi, M.	1960–1960	7	0	EP, I
	Dobrotworsky, N.V.	1968–1974	27	0	AO
21C	Byers, G.W.	1961–2003	26	1	AO, N, NT,
	Starý, J.	1968–2023	132	9	WP
	Mendl, H.	1971–1994	40	3	WP
	Oosterbroek, P.	1975–2023	64	17	AO, EP, I, WP, NT
	Theischinger, G.	1977–2023	484	26	AO
	Dufour, C.	1981–2003	15	6	WP
	Tangelder, I.R.M.	1983–1987	7	1	EP, N
	Vermoolen, D	1983–1990	6	1	WP
	Geiger, W.	1983–2001	7	5	WP
	Jong, H. de	1984–2021	11	1	A, EP, WP
	Hynes, C.D.	1986–1993	35	0	AO, I, N, NT
	Gelhaus, J.K.	1986–2024	15	21	EP, N, NT
	Brodo, F.	1967–2024	3	4	EP, N
	Young, C.	1987–2023	18	12	AO, I, N, NT
	Yang, D	1987–2023	95	63	EP, I
	Podenas, S.	1993–2023	49	8	A, AO, I, EP, WP,
	Koc, H.	1996–2020	7	6	WP
	Hancock, E.G.	1997–2020	23	0	WP
	Pilipenko, V.E.	1998–2023	10	2	EP, WP
	Vogtenhuber, P.	2002–2012	7	1	WP
	Ribeiro, G.	2002–2018	7	33	NT
	Petersen, M.J.	2004–2019	5	1	I, N
	Freidberg, A.	2007–2012	0	11	WP
	Mao, M.	2009–2019	8	3	EP

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Table 2. Continued

Era	Taxonomist	Active publication dates	Species descriptions		Realm
			As first author	As coauthor	
	Liu, Q	2009–2023	15	17	EP
	Taber, S.W.	2010–2016	7	0	N
	Gavryushin, D.I.	2011–2018	12	1	A, I, EP, NT, WP
	Starkevich, P.	2011–2023	13	11	EP, I
	Zhang, X.	2012–2023	21	12	EP
	Devyatkov, V.I.	2012–2024	15	1	EP
	Byun, W.-H.	2014–2018	0	7	EP
	Mederos, J.	2014–2024	12	0	WP
	Men, Q.	2014–2023	43	8	EP
	Podeniene, V.	2015–2023	1	7	EP
	Kolcsar, L.-P.	2015–2023	7	6	WP
	Ren, J.	2017–2023	5	8	EP
	Billingham, Z.D.	2017–2023	23	28	AO
	Santos, D.	2018–2022	33	0	NT
	Kato, D	2018–2023	25	2	EP
	Zhang, B.	2019–2022	7	4	EP
	Boardman, P.	2020–2020	22	0	A
	Xu, Y.	2022–2024	5	9	EP

Timeframe, biogeographic realm, and number of valid descriptions are given for taxonomist who have described minimum of 5 crane fly species as author and coauthor. Abbreviations: A, Afrotropical; AO, Australian/Oceanian; I, Indo-Malayan; N, Nearctic; NT, Neotropical; EP, Eastern Palearctic; WP, Western Palearctic.

Alexander's taxonomic work was instrumental in documenting crane fly diversity across the world. This overarching influence provides both advantages and challenges. His descriptive work is geographically focused so that a single paper may have new species from a variety of genera. This makes identification of crane flies a challenge, as it requires viewing descriptions for a single genus in numerous papers. Additionally, he rarely produced keys for identification. An advantage though of his work is that his 11,000+ descriptions followed a standard format allowing the user to compare one to another, and often the descriptions were accompanied by illustrations of wings and genitalia (estimated at over 15,000 illustrations; Wheeler 1982). In some larger regional works, he did provide identification keys and a level of synthesis, such as those for California, Northeastern North America, Chile and Patagonia, and sub-Saharan Africa. These are valuable tools for the new as well as the experienced crane fly taxonomist. But for most of the world's fauna of crane flies, a researcher faced (and still faces) a daunting task to identify a crane fly using Alexander's set of papers. It would fall to the next generation of researchers to start the revisionary work at the generic level to provide comparable illustrations and species-level identification keys.

While Alexander was focused on the non-European crane fly fauna, several researchers in Europe and the wider Palearctic realm were making progress documenting that fauna. Most important was Evgeniy N. Savchenko (or Savtshenko), a contemporary of Alexander's who described the crane fly fauna of the vast Soviet Union over his 35-yr career. Like Doane in North America, Savchenko's career was primarily as an economic entomologist, focused on sugar beets and their pests, but after about 20 yr he started publishing on crane fly taxonomy, describing nearly 400 species in over 200 publications (Lantsov 2009). His contributions focused on the fauna of the Ukraine, Caucasus region, Central Asia, and the Russian Far East and included describing immature stages in addition to description of adults. Another major worker during this time in the Palearctic was Bernhard Mannheims, who started his research on taxonomy of Blephariceridae, but after 20 years, discovered the taxonomy of the western Palearctic Tipulidae was understudied and in chaos and set to work to rectify it. He did that in 71 papers describing nearly 150 species, principally Tipulidae (Reusch and Oosterbroek 2009). His most lasting contribution was his synthetic treatment of Tipulidae in "Die Fliegen der Palaearktischen Region."

Beyond descriptive taxonomy, several workers have created important works that emphasized crane fly life history and ecology. In North America, C.P. Alexander started this work before J. S. Rogers extended the knowledge of crane flies by publishing a series of papers describing the first known larvae and pupae for several genera of crane flies (Alexander 1920). He also started incorporating the new field of ecology into crane fly research with papers detailing the seasonal succession of crane fly species at single sites in Florida (1933) and Michigan (1942), with detailed descriptions of larval and adult habitats. Later George Byers, a student of Rogers, produced important monographs of selected genera for North America (*Dolichopeza* Curtis, *Chionea* Dalman), which included species keys, comparative descriptions and illustrations for adults and immature stages, and a wealth of natural history observations. A notable advance was the single monumental monograph of the crane flies of South Africa by Wood (1952) that detailed the first known immatures for a variety of groups along with a number of new species descriptions. Theowald (1957) described the larvae of the Tipulidae for the western Palearctic, and later with Oosterbroek

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used immature characters of Limoniidae for phylogenetic analysis (as discussed elsewhere in this chapter.) Brindle described larvae for Tipulidae and Limoniidae of Great Britain in a series of nearly 20 papers during 1957 to 1967. In Europe, Savchenko (1983) greatly expanded information on Tipulidae ecology. Similar synthetic studies looking at a single genus over large geographic areas include the work of Pjotr Oosterbroek and his student Ida Tangelder in their papers on *Nephrotoma* Meigen for both the Nearctic and Palearctic (Oosterbroek 1980, Tangelder 1984, 1985, 1988). Subsequent studies by others are cited elsewhere in the chapter.

Other important contemporary taxonomists include the work by Jaroslav Starý over 5 decades on the Limoniidae of Europe and the Middle East, describing over 130 species. Gunther Theischinger initially focused on *Tipula* (*Lunatipula*) while in Europe, describing nearly 90 species, but after emigrating to Australia, he focused on the diverse and understudied Tipuloidea fauna there. In particular, he found the genus *Molophilus* Curtis rich in species, describing nearly 180, but also described many species in the genera *Dicranomyia*, *Dolichopeza*, and others, encompassing over 420 species in total.

At present, crane fly taxonomy is in a strong resurgence, with more than 30 researchers active in North and South America, Europe, Central Asia, Russia, Japan, Korea, China, and Australia. As evidence, there were over 130 publications on crane flies in each of 2022 and 2023, with these papers primarily taxonomic in focus. Importantly, new lineages of researchers are being trained in crane fly systematics. Starting in 1960, largely with Broeder Theowald (van Leeuwen) (Table 2) coauthorships on crane fly descriptions greatly increased. In the United States, J.S. Rogers started a new line of crane fly systematists by training 2 crane fly students, C. Dennis Hynes and George W. Byers. Byers continued that lineage with a string of crane fly taxonomists, Fenja Brodo, Jon Gelhaus, Saul Frommer, Chen W. Young, Ernie May, and Steve Teale. Jon Gelhaus has continued this line by training, assisting, and facilitating access to the Alexander Collection of crane flies to a line of contemporary workers, including Solange Akimana, Eduardo Amat, Robert Conrow, Zac Glass, Daichi Kato, Yan Li, Qifel Liu, Matt Petersen, Sigitas Podenas, Virginija Podėnienė, Pavel Starkevich, Maddie Worth and Oyunchuluun Yadamsuren. These lines of researchers and collaborations, in addition to other networks such those developed in China, Mongolia and South Korea, are key steps in developing the expertise needed to address our current knowledge gaps. The extreme diversity and widespread nature of this group can only be addressed with increased collaboration and development of expertise into geographic areas where none currently exist. Areas in need of in situ researchers include sub-Saharan and southern Africa, India, Southeast Asia, and Central America.

Phylogenetic Relationships of Tipuloidea

There is robust evidence supporting the monophyly of Tipuloidea (Hennig 1973, Wood and Borkent 1989, Oosterbroek and Theowald 1991, Petersen et al. 2010). However, the placement of Tipuloidea within Diptera based on morphological data has been somewhat variable. It has most commonly been positioned as the earliest branch of Lower Diptera (Hennig 1973, Wood and Borkent 1989, Courtney 1991), though it has also been proposed as a sister group to Brachycera (Oosterbroek and Courtney 1995) or placed neither particularly basal nor derived (Rohdendorf 1974). Recent studies, combining molecular (Friedrich and Tautz 1997, Bertone et al. 2008, Wiegmann et al. 2011, Zhang et al. 2023) and morphological data (Lambkin et al. 2013), have reached a consensus that Tipuloidea is a basal group and possibly the earliest diverging lineage within Lower Diptera.

The phylogenetic relationships within Tipuloidea have been examined multiple times, however no consensus has been reached. The earliest hypotheses for the group separated crane flies based on the length of the terminal maxillary palpomere. This system divided the "long-palped" crane flies (ie Tipulidae) from the "short-palped" crane flies (ie Limoniidae). Subsequent investigation has determined this trait does not adequately support monophyly of either group. The group was further defined by Alexander (1919, 1920, 1927) and Savchenko (1966, 1979, 1983) based on overall morphology. These qualitative works suggested the first evolutionary hypotheses for Tipuloidea, suggesting distinct Tipulidae and Limoniidae lineages, with Limoniidae further divided into the Chioneinae (as Eriopterinae), Limnophilinae (as Hexatominae), Pediciinae, and Limoniinae lineages. Subsequent morphological analysis of Brodo (1984), Savchenko (1966), and Stáry (1992) sought to examine the relationships among these major taxonomic groups. These studies largely approached the question of Tipuloidea phylogeny through an a priori acceptance of taxonomic structure and largely looked to examine relationships among the groups, rather than scoring individual taxa and defining groups based on evolutionary descent. However, these studies solidified the current taxonomic structure recognizing distinct Limoniidae, Tipulidae, Cylindrotomidae, and Pediciidae family lineages.

Several phylogenetic studies have investigated the phylogeny of Tipuloidea using modern methods that infer relationships among species or genera without a priori assigning higher taxonomic membership to a particular taxon. Oosterbroek and Theowald (1991) scored characters of the larvae and pupae for individual genera across all recognized taxonomic groups. Their findings supported a sister-taxon relationship between lineages corresponding to genera typically contained in the Cylindrotomidae and Tipulidae and provided further evidence of a monophyletic Pediciidae lineage, here placed with Limoniidae genera. A major finding of this work is the recovery of a paraphyletic Limoniidae. While several traditionally maintained clades were recovered as monophyletic (ie Chioneinae, Limnophilinae, Limoniinae), several genera (eg *Dactylolabis* Osten Sacken, *Epiphragma* Osten Sacken, and *Dicranoptycha* Osten Sacken) did not conform to the accepted taxonomic structure. Ribeiro (2008a) then used adult morphological characters to investigate the early patterns of diversification of Tipuloidea, focusing on a broad sampling of Limnophilinae genera and subgenera. This study started with the assumption that Limnophilinae, or a group within Limnophilinae, was the basal lineage of Tipuloidea owing to the abundance of plesiomorphic characteristics present in the group. This study offered the broadest taxon sampling to date, effectively sampling nearly all recognized Limnophilinae genera and subgenera. The recovered phylogeny provided the first evidence of Pediciidae as the sister group to the remaining crane flies. It also recovered a paraphyletic Limnophilinae as the origin of the families Tipulidae and Cylindrotomidae as well as the Dactylolabinae, Limoniinae, and Chioneinae lineages.

The first study to incorporate molecular data was conducted by Ahonen (2008) based on 2 genes, mitochondrial cytochrome oxidase I (CO1) and nuclear elongation factor 1 alpha (EF-1α), and representative taxon sampling of all crane fly families and subfamilies. The resulting phylogeny provided strong relationship among terminal taxa and a poorly resolved phylogeny backbone, likely due to the age of the group and the relatively fast-evolving genes used in the study. These findings, however, largely supported those previously suggested by Oosterbroek and Theowald (1991) and

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Ribeiro (2008). Pediciidae taxa were recovered as the sister group to a paraphyletic Limoniidae (relative to Tipulidae, Cylindrotomidae). Evidence of monophyletic Limoniinae and Chioneinae were recovered, while 2 distinct clades of Limnophilinae genera were found. Petersen et al. (2010) produced the first total evidence phylogeny for the group, combining a matrix of morphology of all life stages with molecular sequence data (28S rDNA, CAD). Their results further supported the recovery of Pediciidae as sister to the remaining crane flies, and a sister group relationship between Cylindrotomidae and Tipulidae. Limoniidae was poorly resolved and not recovered as monophyletic. While taxon sampling represented only 10% of recognized genera and subgenera, they additionally suggested that several genera (*Tipula*, *Limnophila* Meigen) may be polyphyletic and like the results of Oosterbroek and Theowald (1991), many genera do not conform to the conventional 4 subfamily Limoniidae system. More recently a series of higher-level phylogenetic investigations have been produced using complete mitochondrial genomes (Zhang et al. 2016, 2024, Kang et al. 2017, 2023, Song et al. 2023, Xu et al. 2023). These studies opened a new line of data not previously used in Tipuloidea phylogenetics; however, the limited taxon sampling in each study limits their ability to address inter-familiar relationships.

A consensus of these studies provides some phylogenetic resolution but also highlights several persistent questions. The families Cylindrotomidae, Tipulidae, and Pediciidae appear stable and are consistently recovered as monophyletic. Pediciidae is the likely sister group to the remaining crane flies, while a consistent Cylindrotomidae and Tipulidae sister group relationship is supported. The support for a monophyletic Limoniidae is lacking, and this group may instead be defined as the non-Cylindrotomidae, -Tipulidae, and -Pediciidae crane flies. The intra-familiar classification within Limoniidae remains poorly resolved and many genera simply do not conform to the currently recognized taxonomic structure. These trends are all present in the phylogeny produced by Petersen et al. (2010), which presents our best estimation of crane fly evolution to date (Fig. 3).

Phylogenetic studies of crane flies at the genus or subgenus level have provided valuable insights into patterns of evolutionary decent, biogeographic distributions, and associated revision of included species. Such studies, however, are generally rare given the size of the group and the number of taxonomists who have worked on crane fly systematics. Instead, crane fly systematics primarily focused on new species descriptions and regional accounts of species occurrences. Among the studies that have reconstructed phylogenetic patterns, there is a trend towards focusing on regional taxa or less diverse genera, with few having employed modern approaches—such as parsimony, maximum likelihood, or Bayesian methods—that provide explicit support for proposed relationships.

Evolutionary relationships within Tipulidae are among the most studied within Tipuloidea. Oosterbroek (1980), Tangelder (1984, 1985, 1988), and de Jong (1993) investigated the phylogenetic relationships and biogeography of the Holarctic species of *Nephrotoma* based on adult morphological characters. Phylogenetic analyses were conducted for *Prionocera* Loew (Brodo 1987) based on adult morphology and *Angarotipula* Savchenko (Brodo 2018) based on adult morphology and cytochrome *c* oxidase subunit I (COI) sequences. de Jong (1989) conducted phylogenetic studies on the genera *Elnoretta* Alexander, *Valdiviana* Alexander, and *Euvaldiviana* Alexander. Several investigations have used morphological characters of adult crane flies to reconstruct evolutionary relationships and biogeographic patterns within the large genus *Tipula*. Gelhaus (2005) presented a parsimony analysis using adult characters for the evolutionary relationships among 11 subgenera of *Tipula*, a clade he termed the *Lunatipula-Vestiplex* series, which was supported as monophyletic; most subgenera also were supported as monophyletic, but the large subgenus *T.* (*Lunatipula)* was not. Phylogenetic studies within subgenera or species groups of *Tipula* have been conducted for Palearctic *Tipula* (*Tipula*) (Theowald 1984), *Tipula* (*Acutipula*) *maxima* species-group (de Jong 1994a), *Tipula* (*Mediotipula*) (de Jong 1995b) the *Tipula* (*Lunatipula*) *bullata* and *falcata* species groups (de Jong 1995a), and the Holarctic *Tipula* (*Savtshenkia*) (de Jong 1994b). Gelhaus (2005) examined the relationships of the Nearctic *Tipula* (*Eremotipula*), including identifying 16 areas of endemism in western North America and documenting diversification of the group from southern into northern Nearctic deserts.

Several studies have examined evolutionary relationships of cylindrotomid crane flies. Ribeiro (2008b) examined the relationships of Neotropical genus *Stibadocerina* Alexander and Trans-Pacific biogeography of the subfamily Stibadocerinae based on morphological characters of the adult. Convincing evidence was provided to suggest that Neotropical genus *Stibadocerina* Alexander is sister to the Indo-Malayan genus *Stibadocerella*. Kania-Kłosok et al. (2021) examined the placement of the extinct genus *Cyttaromyia* Scudder within the greater Cylindrotomidae phylogeny based on wing characteristics. They recovered *Cyttaromyia* as the sister group to the extant genera of a paraphyletic Cylindrotomidae. Cylindrotominae appeared paraphyletic in respect to the Stibadocerinae, thus calling into question the subfamily structure of this family. Kolcsár et al. (2022) produced a partial revision for the Japanese species in the family based on a mitochondrial cytochrome oxidase (CO1) and a maximum likelihood analysis. This analysis provided new insight into the taxonomic status of several Japanese Cylindrotomidae species.

Few investigations have been conducted on the evolutionary relationships within Pediciidae. Petersen et al. (2010) provided limited evidence for the maintenance of the 2 recognized subfamilies. Dénes et al. (2016a, 2016b) produced a revision and phylogenetic analysis for the *Pedicia* (*Crunobia*) *staryi* species-group in Ukraine and Romania based on mitochondrial cytochrome c oxidase subunit I (COI) sequences.

Within Limoniidae, phylogenetic investigations have occurred across all subfamilies except Dactylolabinae. Within Chioneinae, studies have focused on several Neotropical genera and subgenera. Ribeiro (2003) conducted a phylogenetic revision of Neotropical species in the genus *Styringomyia* based on adult characters, resulting in a phylogeny and identification of morphological synapomorphies for the recovered clades. de Jong and Ciliberti (2014) used adult morphological characters to study the phylogeny of *Chionea* Dalman, revealing 2 major clades: the strictly Palearctic clade and the combined Nearctic-Palearctic clade, with an initial distribution likely extending into the Eastern Palearctic. Santos et al. (2019) provided a comprehensive phylogenetic revision of the endemic Chilean genus *Maietta* Alexander, including a phylogeny based on adult characteristics and a discussion of the evolution of the interbase of the adult male hypopygium within this clade. Santos et al. (2022) conducted a phylogenetic study on the genus *Amphineurus* Skuse using adult morphological characters, finding that the subgenus *Amphineurus* (*Rhamphoneurus*) Alexander was supported as a monophyletic group, with its closest relatives being taxa currently distributed in New Zealand. The Australasian taxa were found to be paraphyletic with respect to the Neotropical clade. Santos and Ribeiro (2018) examined the relationships of *Aphrophila* Edwards based on adult characters, providing evidence that the South American fauna is more closely related to species from New Caledonia than to those from New Zealand.

Within Limnophilinae, Ribeiro (2008) used adult morphological characters to investigate the early patterns of diversification

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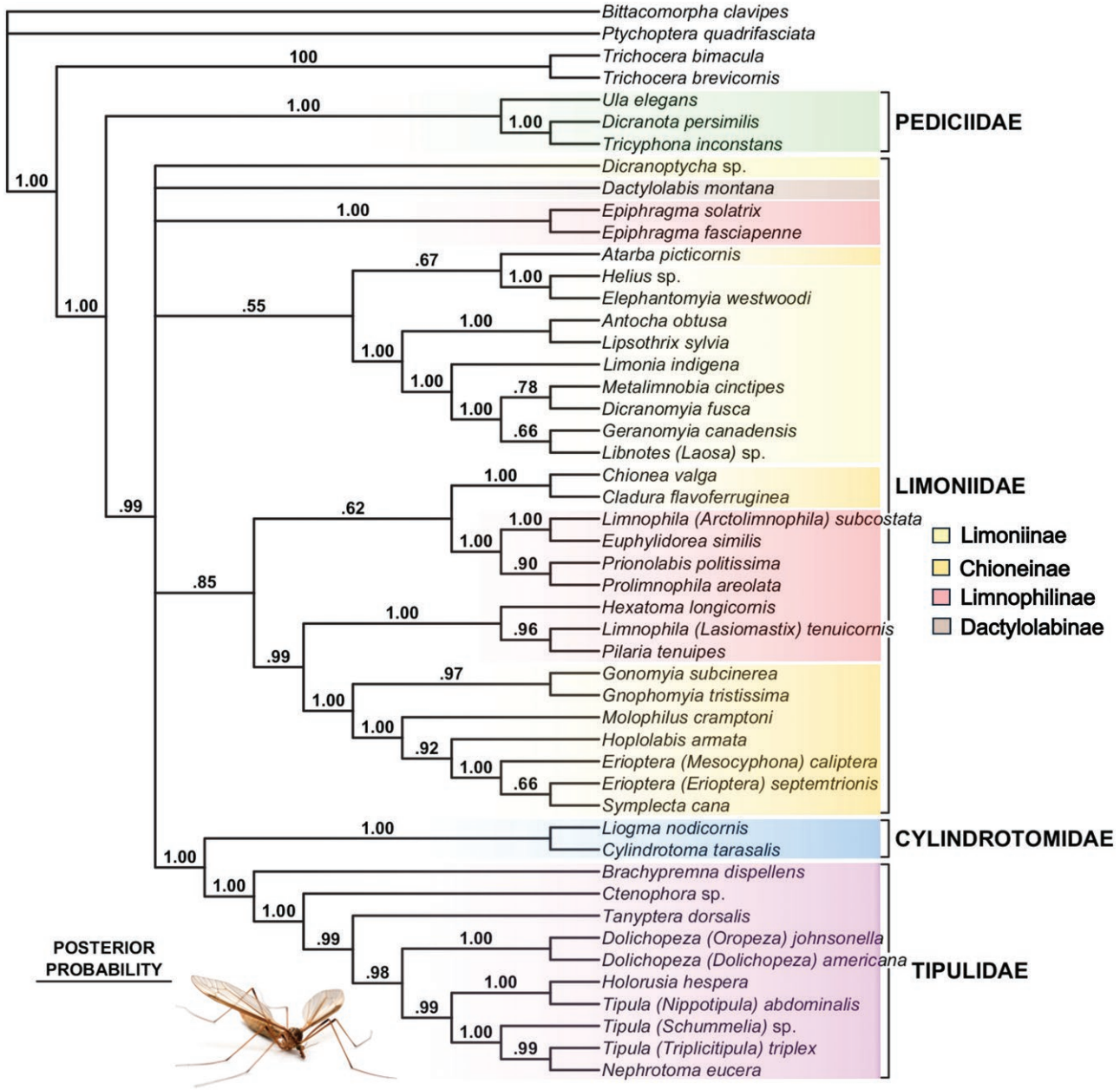

Fig. 3. Proposed phylogenetic relationships and classification of Tipuloidea. The presented phylogeny is based on the Bayesian analysis of a total evidence dataset (morphology + 28S + CAD) in Petersen et al. (2010). Posterior probabilities are shown above the branches.

of Tipuloidea, focusing on a broad sampling of Limnophilinae genera and subgenera. Details of adult character evolution within Limnophilinae are discussed. Petersen (2010) applied a molecular approach (COI, COII) to study the phylogenetic relationships of the North American genus *Neophylidorea* Petersen. The study reconstructs diversification in the genus but also suggests incomplete lineage sorting between the sister taxa *N. columbiana* and *N. adusta*. Santos and Ribeiro (2024) conducted a phylogenetic analysis on *Eloeophila* and *Idioptera* based on adult morphological characters. The results showed that *Idioptera* formed a clade within *Eloeophila*, necessitating synonymy of *Eloeophila* with *Idioptera*.

Within Limoniinae, Petersen (2015) studied the phylogenetic relationships and biogeography of the 32 species in the genus *Lipsothrix* Loew based on morphology of the adult. The origin of *Lipsothrix* likely occurred in the Western Palearctic realm during the Eocene. Multiple dispersal events likely then occurred before major diversification into the Indo-Malayan and Eastern Palearctic + Nearctic realm. Nitta and O'Grady (2008) studied the relationship between species of endemic *Dicranomyia* (*Dicranomyia*) in Hawaii using a multigene dataset. Findings suggest that at least 2 colonization events led to the diversification of the genus in this region. Goodman and O'Grady (2013) further examined this diversification and found that colonization of Hawaii is estimated to have occurred at 6.9 MYA. Importantly, *D. variabilis* was recovered as paraphyletic relative to *D. kraussi* and *D. stygipennis*. This investigation was the first to suggest the maintenance of ancestral species during the formation of novel crane fly species. Kang et al. (2023) supported the monophyly of the tribe Elephantomyiini by using complete mitochondrial genome data, as the genera *Elephantomyia* and *Helius* form a strongly supported clade, which represents a significant origin of flower-visitation in Limoniidae.

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Paleontological Evidence

The fossil record of the insect order Diptera, known for its remarkable diversity, is well-documented and extensive (Kovalev 1990, Krzeminski and Ansorge 1995, Krzeminski 1992a, 1992b, Krzeminski and Evenhuis 2000, Krzeminski and Krzeminska 2003, Rasnitsyn and Quicke 2002, Grimaldi and Engel 2005, Blagoderov et al. 2007, Lukashevich 2009, Ponomarenko et al. 2014, Ribeiro and Lukashevich 2014, Kopec 2017, Kopec et al. 2018, Lukashevich and Ribeiro 2019, Kopec et al. 2021, Krzemiński et al. 2021). Fossil evidence shows that the earliest Diptera specimens date back to the Middle Triassic period, approximately 242 to 247 million years ago, found in northeastern France (Krzeminski et al. 1994, Lukashevich and Ribeiro 2019). These ancient lineages include extinct genera from the superfamily Tipuloidea. The classification of Triassic representatives from this group suggests that the origin of Tipulomorpha (including Trichoceridae and Tipuloidea) occurred during the Triassic period. However, fossil records for the families Trichoceridae, Pediciidae, and Tipulidae only appear in the Early, Middle, and Late Jurassic periods, respectively. Notably, the earliest Cylindrotomidae fossils are from the Paleogene (Kania-Kłosok et al. 2021). Despite the absence of earlier Cylindrotomidae fossils, the presence of the closely related Tipulidae in the Late Jurassic, as evidenced by the Jurassic genus *Tipunia* (Krzeminski and Ansorge 1995), supports the hypothesis that Cylindrotomidae also shares this extended temporal range, as suggested by the phylogenetic analysis of Lukashevich and Ribeiro (2019). A recent study on the Tipulidae from the Mesozoic Crato Konservat-Lagerstätte (Aptian of Brazil) (Santos et al. 2023) revealed an impressive variety of fossil species from that location, indicating that there are probably many more species yet to be found and researched globally.

The significance of fossil crane flies within the phylogenetic framework of the Diptera is paramount for addressing specific evolutionary inquiries. In particular, the examination of wing vein homologies—key characteristics utilized for interpreting fossil taxa and understanding the evolutionary transition from a "Mecoptera-like" wing to a "Diptera-like" wing—highlights the critical role of craneflies. It is overly simplistic to assume that the phylogenetic relationships among various lineages of Mecoptera and Diptera, which encompass numerous scientifically valuable fossils, can be resolved without a comparative analysis of wing venation traits. The wing vein structure of the Tipulomorpha exhibits significant comparability to that observed in mecopteroid groups, making it essential to identify wing vein synapomorphies that link early mecopteroid fossils to Diptera. This endeavor is particularly relevant for clarifying the systematic placement of fossils with ambiguous affiliations. The systematic placement of Tipulomorpha as either a sister group or positioned near the base of the Diptera phylogenetic tree (Zhang et al. 2023) is a recurring theme, indicating an intrinsic relationship between the early evolutionary trajectories of Tipulomorpha and Diptera. This interrelationship encompasses not only the understanding of character systems, such as wing vein homology and evolution but also the systematic positioning of certain obscure fossil taxa, which have been assigned to various extinct families of Diptera or even to Mecoptera.

Given the numerous unresolved details concerning the phylogenetic relationships among the primary lineages of Tipuloidea, along with the exceptional diversity of this group in the fossil record, several significant challenges remain to be addressed. What are the systematic affinities of the earliest Tipuloidea? At what point did the modern lineages begin to diverge from their earliest forms? How do the numerous extinct lineages relate to the extant and other extinct ones? What factors drove the impressive diversification of the group and when? These questions largely remain open yet newer methods, such as combining genomic data for examining phylogeny coupled with lineage dating using fossils offers an exciting area of research.

Synapomorphies of Major Clades

It is possible to separate major taxonomic groups of crane flies (Table 1) based on morphology of the adult and immature stages, but there is a lack of consensus for clear morphological synapomorphies by which these groups are defined. This is particularly true for Limoniidae. Overall, there appears to be significant homoplasy in both adult and immature characters. In many cases, this homoplasy results from convergent evolution related to immature behavior or adult character loss, such as in the arrangement of the radial section of wing veins. Here, we focus on clades that have been consistently recovered in phylogenetic analyses with broad sampling of crane fly taxa (Oosterbroek and Theowald 1991, Ribeiro 2008a, Petersen et al. 2010, Lukashevich and Ribeiro 2019). Lukashevich and Ribeiro (2019) offer a recent review of Tipulomorpha relationships based on an analysis of both extinct and extant genera, and they provide an overview of synapomorphies previously used to support major crane fly clades.

Tipuloidea

Tipuloidea monophyly is supported by adult characters, including the absence of ocelli and the postgenae meeting medially without being separated by a membranous area (Lukashevich and Ribeiro 2019, Fig. 4). The loss of ocelli is consistent across the group, whereas the evolution of the posterior margin of the head remains less clearly resolved as an unambiguous character (Ribeiro 2008a). Oosterbroek and Theowald (1991) considered the characters of metapneustic respiration, hemicephalic head capsule, the posterior genae extending anteriorly and posteriorly incised, pupal sheaths side by side (considered weak by the authors), and an anteriorly toothed hypostoma to be synapomorphies for the group (Fig. 2). Neugart et al. (2009) additionally considered the condition of the hypostoma and the moderately retracted head into the prothorax (ie hemicephalic), as apomorphies for the group.

Pediciidae

Pediciidae is consistently recovered as the sister group to the remaining crane flies. A prominent diagnostic feature of this group is the presence of setose eyes in the adult, which is absent in all non-Pediciidae crane flies. Some consider this feature a synapomorphy for the group (Starý 1992, Lukashevich and Ribeiro 2019), while others regard it as a symplesiomorphy (Oosterbroek and Theowald 1991), as it is present in other Lower Diptera. Starý (2021) also noted the length of the coxae, which are reported to be distinctly longer than in other Tipulomorpha families, approximately 3 to 4 times the length of the trochanters. This character may prove informative but is currently more suggestive than quantitative. Neugart et al. (2009) examined the shape of the larval mandible, which is distally elongate and sickle-shaped. This character is also shared by some Limnophilinae (Limoniidae) taxa (Fig. 2) and may instead suggest an adaptation to predatory behavior in these groups.

Tipulidae

Tipulidae has long been recognized as a distinct taxonomic group. The common name for the group, long-palped crane flies, refers to the length of the terminal segment of the adult palpus, which is

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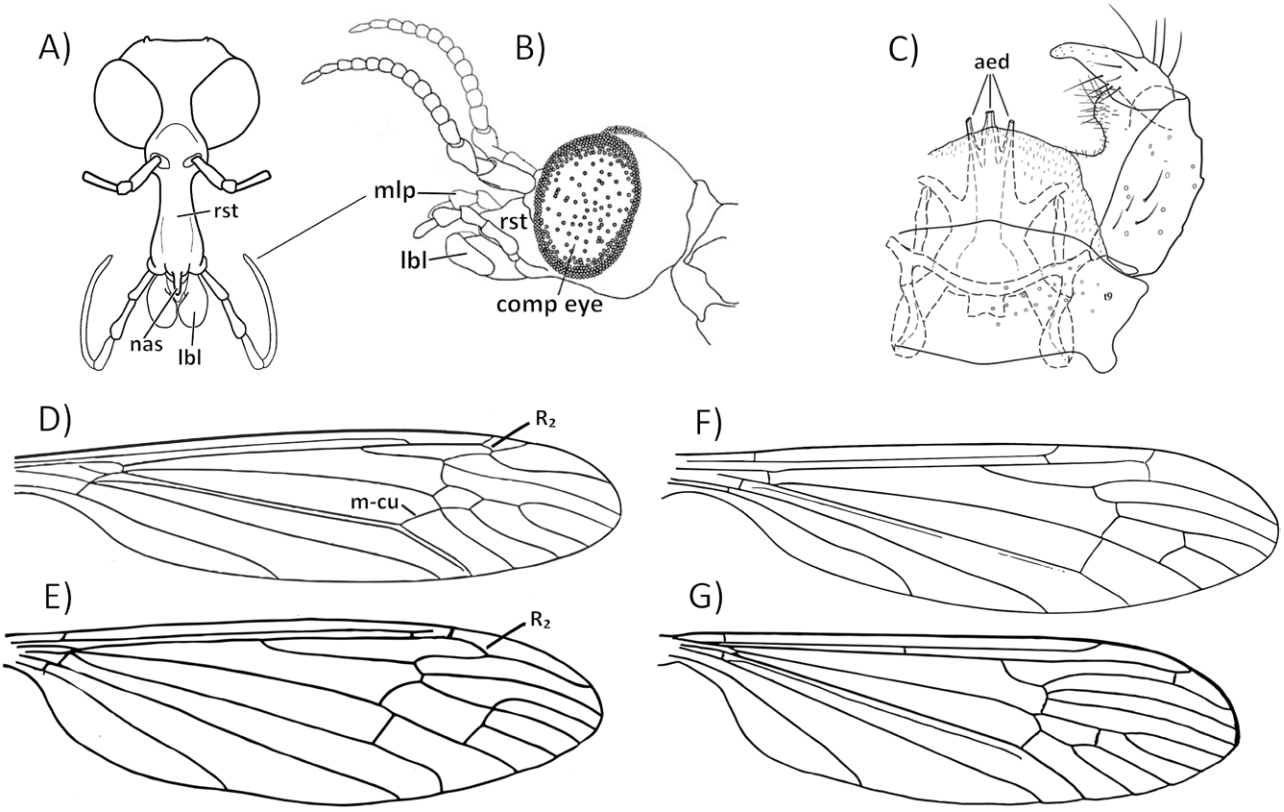

Fig. 4. Morphological synapomorphies of Tipuloidea clades. A) Head of *Holorusia* sp., dorsal view, antennae omitted (redrawn from Jong 2017); B) Head of *Dicranomyia* sp., lateral view; C) Hypopygium of *Stibadocerina chilensis* (Ribeiro 2009); D) Wing of *Holorusia sp.* (redrawn from Jong 2017); E) Wing of *Cylindrotoma distinctissima* (redrawn from Peus 1952); F) Wing of *Dicranomyia* sp.; G) Wing of *Dicranota* (*Ludicia*) *iranensis* (redrawn from Mendl 1988). Abbreviations: comp eye, compound eye; lbl, labial palpus; m-cu, medial cubital vein; mlp, maxillary palps; nas, nasus; R_2, second radial vein; rst, rostrum.

longer than the combined length of the previous 2 segments (Fig. 4A). This character is likely a synapomorphy for the group; however, it is absent in several genera, suggesting one or more losses. It is also present in some Pediciidae (eg *Pedicia*) and Cylindrotomidae. Lukashevich and Ribeiro (2019) identified the long and more inclined wing vein m-cu (Fig. 4D), as compared to Limoniidae (Fig. 4F) and Pediciidae (Fig. 4G), as a synapomorphy based on the analysis of extinct and extant taxa. The nasus found at the end of the rostrum is also unique to Tipulidae (Fig. 4A) but not found universally across the group (absent in *Leptotarsus*, for example) and might be a synapomorphy within the family.

Cylindrotomidae

Cylindrotomidae is consistently recovered as monophyletic and is divided into 2 subfamilies: Cylindrotominae and Stibadorcerinae. The subfamilies are differentiated based on the elongate nature of the adult flagellomeres, which are 3 times longer than wide (Ribeiro 2008b) found in Stibadocerinae. These subfamilies are united by the presence of a trifid aedeagus (Ribeiro 2008b, Lukashevich and Ribeiro 2019, Fig. 4B) and the loss of wing vein R_3 (Lukashevich and Ribeiro 2019) (Fig. 4E). A trifid aedeagus is also present in *Neophylidorea* (Limnophilinae) (Petersen et al. 2012) and could suggest this as a potential plesiomorphy, or an instance of convergent evolution. Starý (1992) additionally suggested an elongate rostrum with extended and open genal areas, a reduced meron, and the overall shape and phytophagous nature of the larvae as other potential synapomorphies, though these have not been thoroughly investigated.

Tipulidae ± Cylindrotomidae

The sister group relationship between Cylindrotomidae and Tipulidae has been consistently supported (Oosterbroek and Theowald 1991, Starý 1992, Ribeiro 2008a, Petersen et al. 2010, Zhang et al. 2016, Lukashevich and Ribeiro 2019), although morphological synapomorphies uniting these 2 clades are not clearly evident. The strongest support for this relationship comes from an interpretation of adult wing venation, specifically the capture of R_2 into a transverse connection with R_1 (Alexander 1927) (Fig. 4D and E). This interpretation, supported by Lukashevich and Ribeiro (2019), represents the best morphological evidence for this relationship.

Limoniidae

The monophyly of Limoniidae remains problematic, with repeated studies using different data sets all showing a paraphyletic family group (Oosterbroek and Theowald 1991, Ribeiro 2008a, Petersen et al. 2010). Despite this, the subfamilies Chioneinae, Limnophilinae, Dactylolabinae, and Limoniinae are still recognized. Currently, no study has included a broad sampling to fully address the scope of this issue. It is highly likely that these taxonomic groups, in some revised nature, can be supported by synapomorphies with further analysis and broader taxon sampling. For example, both Oosterbroek and Theowald (1991) and Petersen et al. (2010) support multiple clades that largely correspond to the Limnophilinae and Chioninae. However, several genera, such as *Epiphragma* and *Cladura* Osten Sacken, that have been traditionally maintained in these subfamilies will need to be removed and may represent new taxonomic groups (*see* Petersen et al. 2010).

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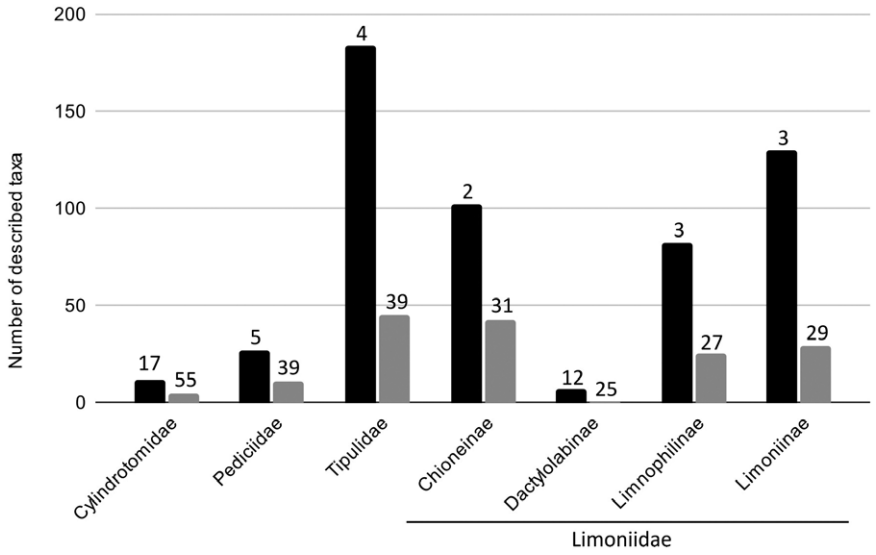

Fig. 5. Status of crane fly larval taxonomy. The number of species (black) and the number of genera/subgenera with at least one larval description (gray) per family/subfamily. The percentage of descriptions (species and genus) relative to the richness of each family/subfamily is indicated above each bar.

Tipuloidea Database—Catalogue of the Craneflies of the World

The Catalogue of the Craneflies of the World (CCW; ccw.naturalis.nl) is the primary online reference database for crane flies, going online on 13 March 2005 (Oosterbroek 2017). It is continuously updated and maintained by Pjotr Oosterbroek and is hosted by the Naturalis Biodiversity Center in Leiden. This database includes updated taxonomic information (genus, subgenus, author, publication, synonyms, etc.) for all described taxa. Individual taxon pages provide information on regional distributions (by country, and in larger countries by state, province, or island), citations, descriptions of biology and phenology, and published images of habitats and morphological traits, when available. Users can search the database using either a basic keyword search or an advanced search that allows filtering by criteria such as islands, biogeographical realms, and authors. All records can additionally be exported to Excel via a provided link.

The catalog was developed by digitizing the printed catalogs for the Nearctic, Neotropic, Afrotropic, and Indo-Malayan realms. Then, along with the available Australian/Oceanian and Palearctic catalogs, they were merged into a single FileMaker database. Thereafter, the database was updated by Oosterbroek to include all taxonomic, distributional, and relevant other data that had become available since the print catalogs were first published. The original intent of the database was not for public use, but rather to the benefit of crane fly workers at the Entomology Department of the Zoological Museum of Amsterdam. Subsequent support, and requests from outside, allowed the catalog to be more widely distributed through the development of an online portal. The website was developed by the Expertcenter for Taxonomic Information (ETI, based at the University of Amsterdam, now integrated in the Naturalis Biodiversity Center) as made possible by a grant from the Global Biodiversity Information Facility (gbif.org). Both Tinde van Andel (NLBIF) and Ruud Altenburg (ETI) greatly contributed to this process. At its start, the 2005 version included (without synonyms) records of 204 genera, 321 subgenera, and 15,268 (sub)species; presently (20 August 2024) these numbers are 216, 325, and 15,831. Apart from the increase in the number of species, many new distributional information has become available. Among the 51,313 literature citations, there are 3,620 first-country records, 19,879 images are available for 3,807 taxa, as well as over 5,300 downloadable pdfs, including the complete set of 1,055 crane fly papers published by Charles P. Alexander. Citations are searchable through a search function and are also linked to the taxon pages, where they are displayed in sections such as biology, taxonomy, distribution, flight period, and altitude.

The continued maintenance of the catalog is due to the efforts of Pjotr Oosterbroek. However, the long-term support and sustainability of the catalog are uncertain, and plans are needed to ensure its growth and continued availability as an essential tool for crane fly research.

Areas of Taxonomic Impediments and Challenges in Advancing Systematic Research

All biogeographic realms have been examined, and no realm appears to have been overly neglected. However, 3 apparent trends limit our understanding of worldwide crane fly biodiversity: limited information for the larval stage, resampling of currently described species, and an under sampling in the Afrotropical realms.

Crane fly systematics is largely based on adult characteristics, often overlooking larval and pupal features. It is well established that larval head capsules (Limoniidae and Pediciidae) and spiracular fields (in all families) are typically confined to a single genus. However, the discovery and characterization of larvae sometimes reveal unexpected features. For instance, the discovery of larvae from the genus *Phyllolabis* Osten Sacken showed characteristics more closely aligned with the subfamily Limnophilinae rather than Chioneinae, prompting the reclassification of the genus (Podėnienė and Gelhaus 2017). Conversely, larvae from different genera (*Gonomyia* Meigen, *Idiocera* Dale, and *Ellipteroides* Becker) can exhibit strikingly similar characteristics, further complicating classification (Gelhaus and Podeniene 2019). This issue is exacerbated by the fact that larvae are known for only a small number of crane flies species (Fig. 5) and very problematic in large genera such as *Dicranomyia* and *Hexatoma* Latreille. Studies combining

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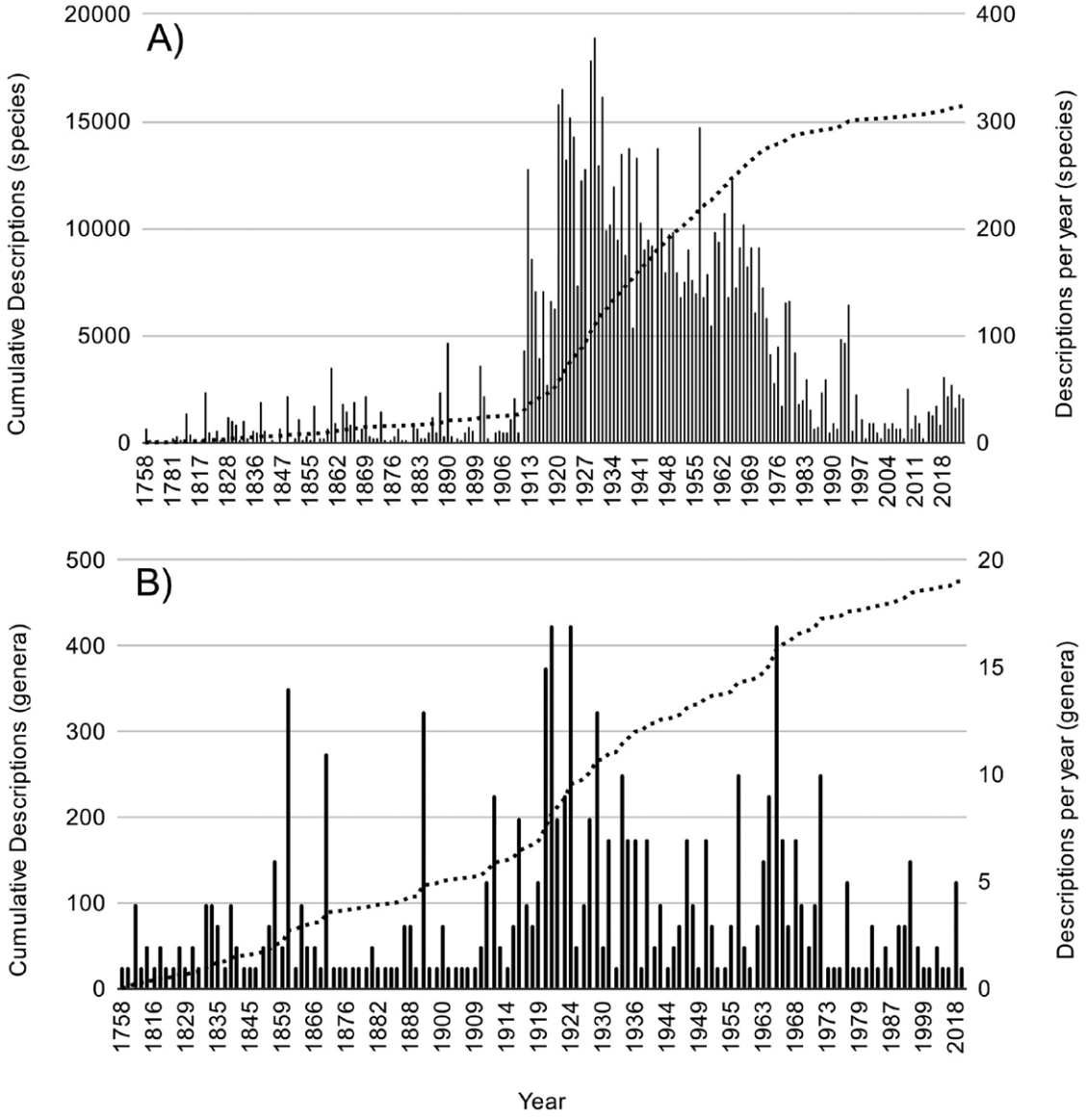

Fig. 6. Trends in descriptive taxonomy. Figures illustrate trends in A) new species descriptions and B) new genus and subgenus descriptions over time. The number of descriptions is presented by year (solid bar) and as cumulative descriptions over time (dotted line).

Table 3. Trends in new crane fly species descriptions

	Newly described species per period						Total
Realm	1758–1979	1980–1989	1990–1999	2000–2009	2010–2019	2020–2024	1980–2024
Nearctic	1,604	21	3	21	8	0	53
West Palearctic	1,246	133	54	67	54	16	324
East Palearctic	1,913	89	49	13	94	75	320
Neotropical	3,678	4	2	14	22	21	63
Afrotropical	1,368	10	1	6	9	21	47
Indo-Malayan	3,433	18	21	19	40	35	133
Austral/Oceanian	2,111	53	335	26	48	10	472

Time frames are through the career of C.P. Alexander (1758–1979) and then divided into 10 yr increments. The proportion of species described per biogeographic realm is presented through and after the career of Alexander.

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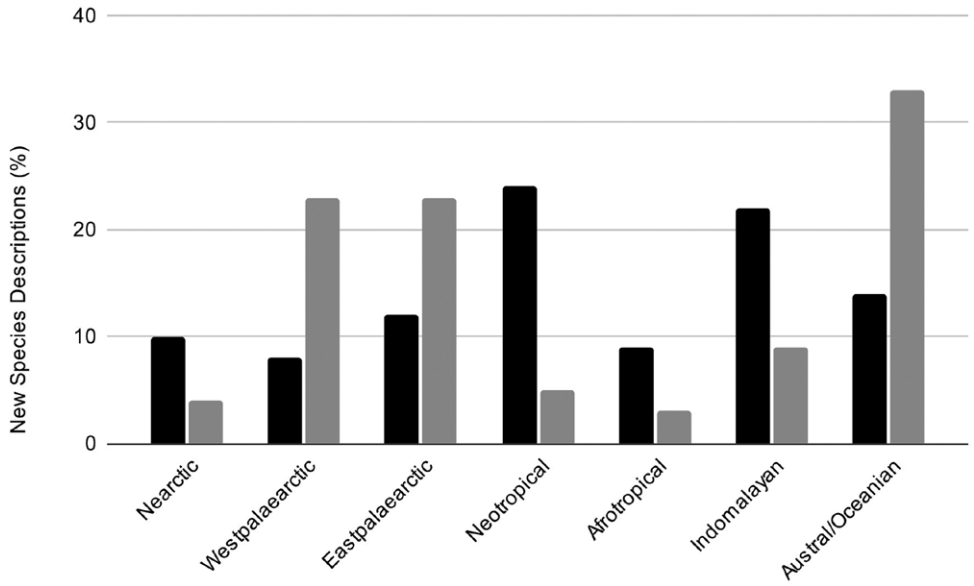

Fig. 7. Proportions of new crane fly descriptions by biogeographic realm. The percentage (%) of new species descriptions are given per realm occurring between 1758 to 1979 (gray) and 1980 to 2024 (black).

larval morphology with molecular phylogeny indicate that genetically distinct clades are often supported by morphological differences in larvae (Podėnienė et al. 2023). In the genus *Tipula*, larvae from a single subgenus sometimes show as much variation as is typically seen between different subgenera or genera (Podėnienė et al. 2006). This underscores the many unresolved taxonomic and phylogenetic issues within Tipuloidea. Therefore, additional molecular and morphological data from both larval and adult stages are essential for a clearer understanding of the taxonomy of this diverse group. A better understanding of larval stages is crucial for addressing these phylogenetic challenges, as the selection of appropriate groups for molecular and morphological studies cannot proceed without taking into account the unique characters of the larvae.

The majority of currently described crane fly species are known only from the adult type series designated at the time of description (Oosterbroek 2024). This trend is less pronounced in the Holarctic, and in fact some areas are extensively cataloged due to years of structured sampling (Stubbs 2021). However, a lack of documented collection is still evident for the majority of non-Holarctic species. This lack of distributional knowledge created by nonexistent recollections hampers our ability to accurately diagnose regional trends. Few studies have systematically quantified diversity relative to sampling effort (*but see* Petersen and Courtney 2010, Kolcsár et al. 2023), but such studies are needed to more fully understand regional trends in biodiversity.

Beyond trends in the resampling of currently described species, patterns in new species descriptions indicate that further work is needed to accurately catalog yet-to-be-discovered species. Trends for both new species (Fig. 6A) and of genera/subgenera (Fig. 6B) descriptions continue to suggest the needs for basic taxonomic work. When considering biogeographic realms requiring additional attention, it is helpful to analyze these trends across 2 distinct time periods relative to the work of C.P. Alexander, either before and during his lifetime (1758 to 1980) or after his work (1980 to 2024). Alexander's immense contributions spanned the globe, and while it is difficult to directly link collection efforts to species description rates, examining how these rates have changed since his time can help guide future research (Table 3). Based on these criteria, the Afrotropical realm appears less diverse than other equatorial realms (Neotropical, Austral/Oceanian, and Indo-Malayan) and temperate areas. Additionally, trends in new species descriptions in the Afrotropics lag all other realms (Fig. 7). A recent study in Cameroon (Boardman 2020), which involved a year of Malaise trap sampling, resulted in the discovery of 21 new species and 40 new country records. This study supports the idea that with increased effort, many new species could still be found in this understudied biogeographic realm.

Recent work in Neotropics also outlines the challenges and opportunities in documenting the diversity of Tipuloidea. Although this realm had the highest diversity and showed reduced new descriptions in subsequent years, a multiyear intensive sampling project at Zurqui Costa Rica (ZADBI project, Borkent et al. 2018) yielded 225 species of Tipuloidea from a 4-hectare patch of cloud forest. Of the species collected, the genus *Geranomyia*, which already had 167 species recorded from the Neotropics, was represented by 23 species, 15 (65% of collected species) of which were new to science. Extrapolating this high level of unknown diversity to many sites in the realm with the implications for total biodiversity is astounding. These attempts at quantifying sampling needs are merely estimates of what is likely to be a still understudied group. Regions with long histories of study still maintain steady rates of species descriptions, and intensive studies, such as Zurqui Costa Rica, hold high levels of undescribed diversity. Added to this are areas where in situ researchers are currently not housed, including sub-Saharan and southern Africa, India, Southeast Asia, and Central America.

In many ways, the challenges facing crane fly systematics are those shared by other taxonomic groups, a shortage of trained taxonomists and insufficient support for basic taxonomic work (Engel et al. 2021). The current rates and trends (Figs. 5 and 6) suggest additional descriptive work is needed to effectively document, describe, and catalog all species. Furthermore, C.P. Alexander's monumental work greatly expanded our knowledge of crane fly diversity but also provided a framework that has never been thoroughly assessed. Many, if not most, described species are still known only from type material and many taxa lack adequate illustrations, complete descriptions, and taxonomic keys for their identification. There is also

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a lack of associations for conspecific life stages that must be completed to formalize our understanding of the group.

Our understanding of crane fly ecology, evolution, and significance remains incomplete due to several major challenges. Crane flies are a group with few obvious taxa of economic or medical importance, which can limit source funding for basic taxonomic work. However, evidence suggests that when taxon importance is clear, funding can increase. This is evident for the few crane flies that are pests and tend to be well-studied (Petersen 2012). New students of crane fly systematics are presented with high diversity, an inadequate classification, and with low specimen representation. Additionally, species-level taxonomic keys are lacking, and many species descriptions lack illustrations or are sparse. Combined this creates difficulties in examining interspecific variation in diagnostic characters for proper taxon delineation and limits the capacity for full revisionary work to be completed on taxa that are often found throughout several biogeographic realms.

Future of Tipuloidea Systematics

While a taxonomic impediment hinders progress and critical gaps in knowledge remain, recent insights and novel approaches are providing opportunities to explain why further systematic work is so critically important. Crane flies play a critical role in environmental processes and can be among the first aquatic taxa to repopulate an area after disturbance (Allen et al. 2023) and can be used to illustrate anthropogenic effects on biodiversity in natural environments (Byriel et al. 2020). Further, the phylogenetic relationships inferred from multiple taxonomic groups can be used to reconstruct paleodistributions (Ribeiro 2008b) and define areas of conservation importance (Petersen and Courtney 2010, Santos and Santos 2024). DNA metabarcoding is also helping to identify the importance of crane fly taxon identity in aquatic water monitoring (Serrana et al. 2022), in quantifying the impacts of terrestrial gradients on species diversity (Lewthwaite et al. 2024), and for provisioning other trophic levels (Bullington et al. 2021, Curran et al. 2022).

The immense taxonomic diversity of crane flies can serve to provide valuable insight into the evolution of Diptera, and their evolutionary relationship can help us to better understand historical biogeography, contribute to the use of phylogenetic diversity in conservation planning, and elucidate ecological systems. However, our capacity to fully embrace this capacity is limited unless we rectify the shortcomings present in our current systematic understanding of this group. Critically, new crane fly species continue to be described at a high pace, and we would expect this trend to continue with additional investigation. We must work to better understand the boundaries and validity of currently described taxa, embrace newer technologies that can be used to further delineate taxa (Petersen 2010, Podėnienė et al. 2021), and produce novel phylogenetic information that will challenge our existing hypotheses of character homology and validate a revised and stable higher-level taxonomy.

The future of crane fly systematics will rely on (i) developing new taxonomists trained in morphology who can work to examine, validate and revise existing taxa, particularly through new collections of specimens that can be compared to existing type series to illustrate existing intraspecific variation, (ii) expanding our view of systematics through integrated taxonomy that can draw from ecological data, molecular data, larval characteristics, phylogeography, and comparative morphology, (iii) expanding efforts to associate conspecific life stages, (iv) expanding training in molecular approaches that can distinguish cryptic species, facilitate the creation of sequence data that will enhance the utility of barcoding initiatives, help create multimarker phylogenetic information that will validate a revised and stable higher-level taxonomy, and explore diversification rates to identify areas in need of additional taxonomic effort, and (v) continuing to support the maintenance of the Catalogue of the Craneflies of the World, with an expansion to include digitization of type material, well-illustrated taxonomic resources including interactive keys and integrating artificial intelligence applications.

Author contributions

Matthew Petersen (Conceptualization [lead], Project administration [lead], Writing—original draft [lead], Writing—review & editing [lead]), Jon Gelhaus (Conceptualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Pjotr Oosterbroek (Writing—original draft [equal], Writing—review & editing [equal]), Sigitas Podėnas (Writing—original draft [supporting], Writing—review & editing [equal]), Virginija Podėnienė (Writing—original draft [equal], Writing—review & editing [equal]), Guilherme Ribeiro (Writing—original draft [equal], Writing—review & editing [equal]), Daubian Santos (Writing—original draft [supporting], Writing—review & editing [equal]), and Xiao Zhang (Writing—original draft [supporting], Writing—review & editing [equal])

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