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Review

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Molecular phylogenetics, phylogenomics, and phylogeography

Zygoptera systematics: past, present, and future

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Odonata is a midsized insect order (~6420 species) containing 3 suborders: Anisoptera (dragonflies, 3,120 species), Zygoptera (damselflies, ~3,297 species), and the intermediate Anisozygoptera (~3 species). In this review of the suborder Zygoptera, we provide a brief overview of their biology, ecology, and natural history. We also review the current state of their systematics and phylogenetics, highlighting remaining higher-level classification (eg family, superfamily) issues to address. Lastly, we will emphasize areas that are still in need of exploration which would greatly improve our understanding of the group.

Keywords: Odonata, phylogenetics, biogeography, natural history, ecology.

Scope of Review

Odonata is a midsized insect order (~6,420 species) comprised of 3 suborders: Anisoptera (dragonflies), Zygoptera (damselflies), and the monogeneric Anisozygoptera (*Epiophlebia* Calvert, 1903), which have the features of both Anisoptera and Zygoptera. Zygoptera currently consists of 4 superfamilies: Calopterygoidea (26 families, 112 genera, 892 species), Coenagrionoidea (3 families, 176 genera, 1921 species), Lestoidea (4 families, 21 genera, 201 species) and Platystictoidea (1 family, 10 genera, 283 species) (Paulson et al. 2024). Each of these superfamilies is characterized by a unique set of morphological characters and behaviors (Fig. 1). When compared to dragonflies, damselflies are relatively slender, often small, have a transversely elongate head, large compound eyes on the side of their head which do not touch (ie separated by more than the width of an eye), a pterothorax with wings shifted back and legs positioned forward, and fore- and hind wings often similar in appearance that are most often held over their thorax when at rest (Büsse 2023, Figure 4.1; Garrison et al. 2010).

Early classification schemes of Zygoptera based solely on morphology recovered varying relationships (eg Tillyard 1917; Fraser and Tillyard 1957; Carle 1982; Bechly 1996). More recent phylogenetic efforts based on morphological data (Rehn 2003), Sanger molecular data (Dijkstra et al. 2014a), molecular data plus morphology (Bybee et al. 2008), and high throughput molecular efforts (Bybee et al. 2021; Kohli et al. 2021; Suvorov et al. 2021) recover Zygoptera and its superfamilies as monophyletic, except for Calopterygoidea. Odonates have one of the most extensive fossil records within insects, mainly due to wing preservation and their accompanying diagnostic features. The combination of advanced phylogenetic techniques and data availability has resulted in several damselfly families being either erected or reestablished, resulting in some stability within higher-level relationships (Bybee et al. 2021), though there is still work to do to clarify these relationships. There is also little resolution in relationships below family level.

Damselflies are a charismatic group found worldwide, inhabit a variety of habitats (eg lentic, lotic, terrestrial), and are often known for their bright coloration. Damselflies have become a model system for many ecological and evolutionary topics such as flight, vision, sexual selection (including sperm competition) (Waage 1986), polychromatism (e.g. Fincke et al. 2005; Sánchez-Guillén et al. 2011), and complex life history strategies (Bybee et al. 2016). There is extensive natural history documentation that has greatly supported such studies (for a review see Corbet 1999).

In this review of the suborder Zygoptera, we will provide an overview of the history of systematics in this group, provide a brief synopsis of their biology, assess the current state of their systematics and phylogenetics, and discuss some current barriers to global efforts to the study of Odonata.

Concise Review of Biology and Natural History

Life Cycle

Odonates are hemimetabolous and amphibiotic predators with 3 life stages: egg, nymph (sometimes referred to as naiad or larva), and adult (Bybee et al. 2015; Corbet 1999, 2002; Rédei and Štys 2016; Tennessen 2003). The nymphs of Zygoptera are differentiated from the Anisoptera by a slender body, elongated and flattened caudal lamellae, and reduced cerci (Büsse 2023, Figure 4.2; Suhling et al. 2015). In contrast to Anisoptera that use an internal rectal chamber for respiration (anal breathers), the gills in Zygoptera nymphs are external and serve multiple functions (eg gas exchanges, swimming) (Eriksen 1986; MacNeill 1965; Mill and Pickard 1972; Suhling et al. 2015; Tillyard 1917). For locomotion, Zygoptera nymphs generally swim or walk on the substrate but show no escape behavior using jet propulsion, which is demonstrated in most of Anisoptera (Corbet 1999; Mill and Pickard 1975). Females lay their eggs in water, mud, or on specific substrates (plants, rocks, dead wood) for exophytic species or in plant tissues for endophytic species (Fig. 2) (Bota-Sierra and Sandoval 2017; McPeek 2008). For the latter, the female uses her sharp ovipositor to insert the egg by puncturing the plant tissue (Matushkina and Gorb 2007; Suhling et al. 2015). The eggs of some species, especially those in temperate or dry climates, may go into diapause to survive adverse weather conditions (eg winter or drought) and continue their development when environmental conditions improve (Corbet 1999). The egg stages are highly variable, lasting anywhere from a week to several months depending on the species and if embryonic development is continuous or delayed, mainly due to temperature. The hatchling, known as the pronymph or prolarva, is the first instar. In appearance, it does not resemble subsequent instars in that the labium and legs are held tight to the body. It is a very brief stage, usually lasting less than a minute or 2 before it molts. After the pronymph molts, its exuvia usually remains attached to the egg chorion. However, exceptions occur in the family Lestidae, especially in species that oviposit in woody tissue above the ground. In some instances, the pronymph drops onto ground where water is not present, and it can flip until it reaches water. Duration of the pronymph can last for up to several hours depending on environmental conditions. The emerging nymph is the second instar; the labium covers the other mouthparts and the legs are extended and functional, and the nymph generally resembles later instars in appearance.

Nymphal development ranges from 8 to 17 instars depending on the species, and the duration of the nymph stage can be as little as a few weeks (eg *Palpoleura lucia* (Drury, 1773)) (Suhling et al. 2004) but usually is over a year (ie *Lestes*, *Pyrrhosoma nymphula* (Sulzer, 1776)) (Davis 1963; Bennett and Mill 1993; Hilsenhoff 2001; McPeek 2008). The duration is influenced by the availability of food resources and fluctuations in ambient temperature (Krishnaraj and Pritchard 1995). At the termination of the last instar, the nymph leaves the water and climbs onto a stable support (eg plants, rocks, roots, or riverbanks) to reach the open air, where emergence occurs (Grand and Boudot 2006).

After emergence, the cuticle of the adult exoskeleton is soft, often referred to as teneral. The newly emerged teneral adult is capable of flight but does not have strong wing strokes or flight control. The cuticle gradually hardens, occurring first in the legs, wings, and mouthparts (Preuss et al. 2024). Adults that are no longer teneral but have a hardened cuticle often lack adult coloration. These sexually immature adults will often spend time away from the water hunting for food, where they undergo sexual maturation and acquire mature colors (Grand and Boudot 2006; Testard 1981). This is followed by the reproductive period, during which mating and egg-laying take place (Gillott 2005). While nearly all species of odonates are

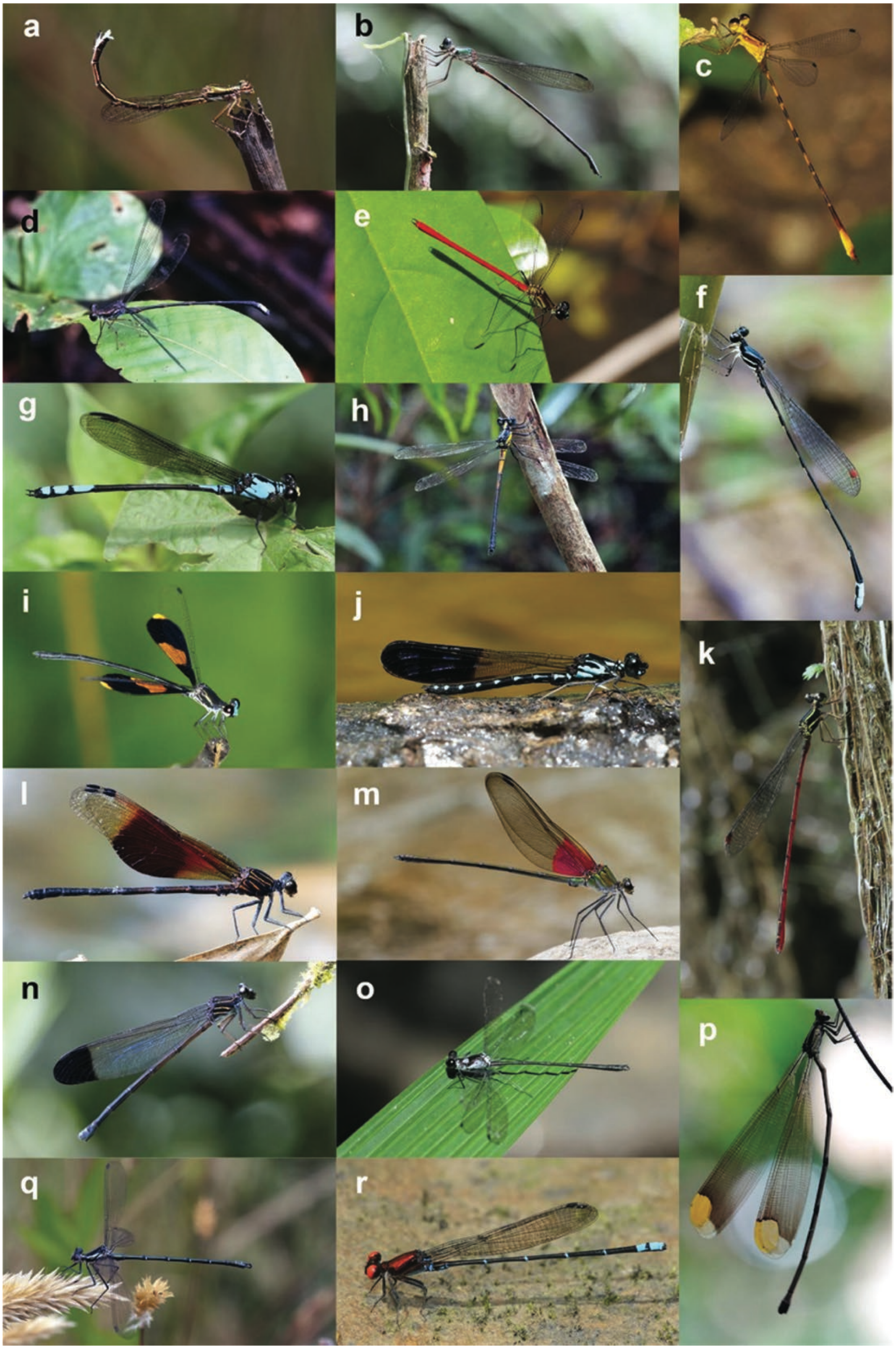


Fig. 1. Habitus diversity: A) *Hemiphlebia mirabilis* Selys, 1868 (Hemiphlebiidae, Australia), B) *Phylolestes ethelae* Christiansen, 1947 (Synlestidae, Dominican Republic), C) *Heteragrion bickorum* Daigle, 2005 (Heteragrionidae, Ecuador), D) *Philogenia gaiae* Vilela and Cordero-Rivera, 2019 (Philogeniidae, Ecuador), E) *Dicterias atrosanguinea* Selys, 1853 (Dicteriadidae, Brazil), F) *Drepanosticta zhoui* Wilson and Reels, 2001 (Platystictidae, China), G) *Cora xanthostoma* Ris 1918 (Polythoridae, Colombia), H) *Philoganga vetusta* Ris, 1912 (Philogangidae, China), I) *Pseudolestes mirabilis* Kirby, 1900 (Pseudolestidae, China), J) *Heliocypha perforata* (Percheron in Guérin-Méneville and Percheron, 1835) (Chlorocyphidae, China), K) *Mesagrion leucorrhinum* Selys, 1885 (Mesagrionidae, Colombia), L) *Euphaea ornata* (Campion, 1924) (Euphaeidae, China), M) *Archineura incarnata* (Karsch, 1891) (Calopterygidae, China), N) *Thaumatoneura inopinata* McLachlan, 1897 (Thaumatoneuridae, Costa Rica), O) *Teinopodagrion epidrium* De Marmels, 2001 (Megapodagrionidae, Colombia), P) *Mecistogaster ornata* Rambur, 1842 (Coenagrionidae, Pseudostigmatinae, Ecuador), Q) *Austroargiolestes icteromelas* (Selys, 1862) (Argiolestidae, Australia), R) *Argia dives* Förster, 1914 (Coenagrionidae, Colombia). Pictures by Adolfo Cordero-Rivera.

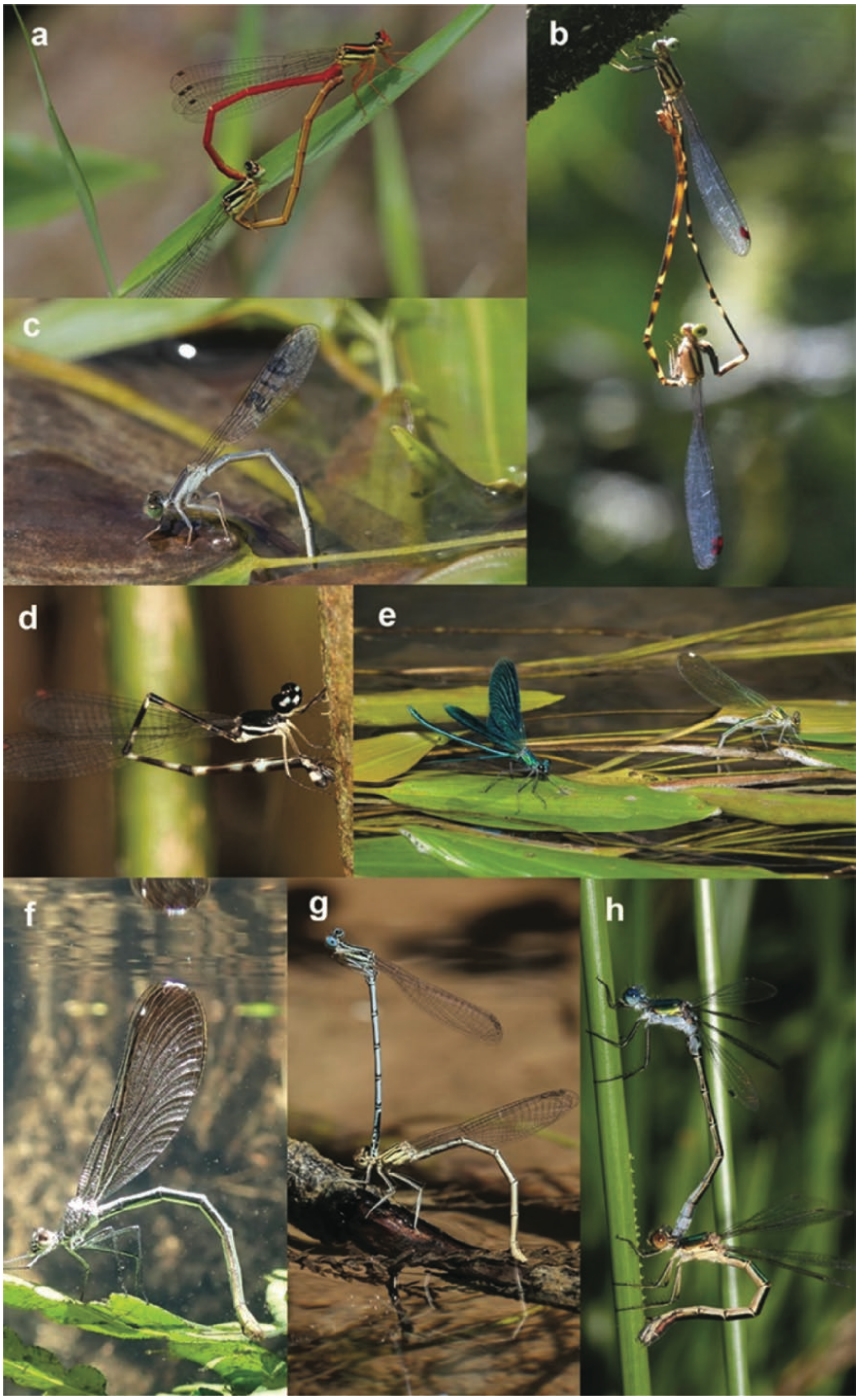


Fig. 2. Behavior diversity: A) Stage I of copulation (sperm removal) in *Calicnemia eximia* (Selys, 1863) (Platycnemididae, China), B) Stage II of copulation (insemination) in *Perissolestes* (Perilestidae, Ecuador), C) oviposition by unmated parthenogenetic *Ischnura hastata* (Say, 1840) (Coenagrionidae, Azores, Portugal), D) oviposition alone in tree roots by *Drepanosticta zhoui* Wilson and Reels, 2001 (Platystictidae, China), E) oviposition with noncontact guarding in *Calopteryx splendens* (Harris, 1780) (Calopterygidae, Italy), F) oviposition alone underwater by *Calopteryx virgo* (Linnaeus, 1758) (Calopterygidae, Spain), G) oviposition in tandem by *Platycnemis pennipes* (Pallas, 1771) (Platycnemididae, Italy), H) oviposition in tandem far from the water by *Lestes sponsa* (Hansemann, 1823) (Lestidae, Spain). Pictures by Adolfo Cordero-Rivera.

obligatory sexual organisms, parthenogenesis is known in one species of Zygoptera, *Ischnura hastata* (Say, 1840) from the Azores Islands (Cordero Rivera et al. 2005; Lorenzo-Carballa et al. 2009). Adults can survive for several days to months, particularly in species that endure the dry season in tropical climates (McPeek 2008). Daily survival is about 0.90, with no difference between the sexes, but immature individuals have slightly lower survival compared to mature adults (Sanmartín-Villar and Cordero-Rivera 2023).

Damselflies are particularly adapted to their role as generalist visual predators. Like dragonflies, the combination of their visual and flight systems are highly attuned to detect and efficiently capture prey (Olberg et al. 2000). Damselflies commonly capture and consume prey while in flight (Ingley et al. 2012; Suhling et al. 2015). While most damselflies consume any available prey, some are more specialized. For example, the giant Pseudostigmatinae target spiders and insects caught in spider webs (Fincke 1984; Ingley et al. 2012; Toussaint et al. 2019). Nymphs also have remarkable vision, at least in the final instars, but generally ambush prey using a highly sophisticated modified labium that rests just underneath the head and/or thorax to be thrust forward in a high-speed movement (Büsse et al. 2021). The shape and size of this modified labium varies between groups. Damselfly species with large nymphs may feed on vertebrates, such as fish and tadpoles. Damselfly adults and nymphs, in turn, serve as prey for fish, birds, reptiles, amphibians, invertebrates (including spiders), and even Anisoptera, and are able to export significant freshwater secondary production to terrestrial systems (Rivas-Torres and Cordero-Rivera 2024).

Courtship, Mating, and Sexual Conflict

Zygoptera have a unique mating system that can be broken into 6 stages (male competition, courtship display, tandem linkage, copulation, oviposition, and mate guarding), although not all stages are present in every species (Battin 1993). Male reproductive behavior is related to aggression and site attachment (Galicia-Mendoza et al. 2021). When males are territorial, they may actively attempt to corral females while also defending an area where preferred oviposition substrates are present (eg water, mud, rocks, dead wood). They try to prevent other males from encroaching on their space through threat displays or flight chases. Males may also gather in close proximity and perform confrontational flights. Male territoriality and other male–male competition (eg lekking) often consists of noncontact threats where males will fly frons to frons in order to determine who is the fitter male (Grether 2019). Females will observe these male displays from perches around the lek, with the most impressive displays to our eyes performed by species with pigmented wings, such as *Pseudolestes mirabilis* Kirby, 1900, from Hainan (China) (Cordero-Rivera and Zhang 2018). Alternatively, nonterritorial males actively search for females, and upon discovery of a female, will attempt to signal the female directly (eg wing spot, courtship arc, wing clapping). The female will respond with a refusal (eg all 4 wings spread, downward flex of the abdomen) or acceptance to create a tandem (Battin 1993; Guillermo-Ferreira 2021). To form a tandem, males clasp the female by the pronotum with their anal appendages, which is different from Anisoptera where the female is held by the head (Suhling et al. 2015). Although, in Polythoridae, this link is made by grasping the mesothorax, a fact that might explain the reduction of paraprocts in that family (Sanmartín-Villar and Cordero-Rivera 2016).

This tandem link is necessary as the male's reproductive organs are separated into 2 locations. The primary genitalia where sperm production occurs is internally located in the ninth abdominal segment near the anal appendages. Before copulation occurs, the male must transfer sperm to the secondary genitalia, which is located on the ventral portion of the second and third abdominal segments (Rivas-Torres et al. 2019). The female will then complete the "mating wheel" or "copulatory wheel" by raising the end of her abdomen to the male secondary genitalia, which signals the start of copulation. The tandem lasts from a few minutes to several hours depending on species [eg *Heteragrion consors* Hagen in Selys, 1862: 5.2±5.45 min (Loiola and De Marco 2011), *Ischnura fluviatilis* Selys, 1876: 65.2±6.9 min (Almeida et al. 2018), *Phylolestes ethelae* Christiansen, 1947: 166.2±62 min (Cordero-Rivera et al. 2024), *Ischnura senegalensis* (Rambur, 1842): 395.3±11.6 min (Sawada 1995)]. Intra-specific variation of tandem duration can be driven by mating history of the female, time of day, male density, and male age (Cordero 1990; Cordero et al. 1995; Andrés and Cordero Rivera 2000; Uhía and Cordero Rivera 2005; Rivas-Torres et al. 2023; Brozzi et al. 2024).

Within Zygoptera, copulation is broken into 2 distinct processes: sperm removal and insemination, since females tend to store and keep the sperm of multiple males, which is common within polyandrous species (Córdoba-Aguilar et al. 2003). The ability to remove the sperm from other males sets the stage for sperm competition (eg plugs, structural adaptations, toxic fluids) seen throughout sexual individuals in the animal kingdom. The 2 most documented methods of sperm competition among Zygoptera males are using highly evolved penile structures to assist with removal or to reposition the sperm packages within the spermatheca itself pushing them farther into the cavity (Córdoba-Aguilar et al. 2003; Cordero-Rivera and Córdoba-Aguilar 2010). Repositioning the sperm is highly effective as the sperm closest to the egg during oviposition will fertilize the egg. Oviposition occurs relatively quickly after copulation, often with the male guarding the female. The male will either remain in tandem with the female by clasping the prothorax, perch, or hover close to the female until oviposition is complete, ensuring the reproductive success of his sperm (Fig. 2).

Zygoptera courtship and mating behavior is an ideal system to study sexual conflict. As demonstrated above, common male strategies stem from harassment, physical harm, and mating duration (Andrés and Cordero Rivera 2000; Gosden and Svensson 2009). Females have evolved strategies and adaptations in an attempt to avoid or minimize these negative effects. For example, the females of some genera (eg *Enallagma* Charpentier, 1840) possess a specialized genital spine which allows them to reduce sexual conflict over mating duration, by causing pain and discomfort on the male's abdomen thereby significantly reducing the mating duration (Rivas-Torres et al. 2023; Brozzi et al. 2024). A commonly hypothesized phenomenon to avoid male harassment is female polychromatism (multiple color patterns within a population), including one that mimics male coloration. Females that mimic male coloration also tend to mimic their behavior (ie aggression) (Sirot et al. 2003). While it is often suggested that sexual conflict is the main driving force for polychromatism, there is evidence that ecological drivers (eg temperature, parasitism, UV protection) can also influence polychromatism (Cooper et al. 2016; Cook et al. 2018). Polychromatism is observed in 4 families (Calopterygidae, Lestidae, Coenagrionidae, and Platycnemididae) but unevenly distributed among the genera (Cordero and Andrés 1996; Fincke et al. 2005).

Recent evidence suggests that nonadaptive mechanisms have played a predominant role in the radiation of damselflies, driving species divergence through sexual selection linked to male–female mating interactions. Studies on 3 genera (*Calopteryx* Leach in Brewster, 1815, *Enallagma*, and *Ischnura* Charpentier, 1840) highlight the extent of adaptive ecological divergence in niche use and nonadaptive differentiation in reproductive traits, such as sexual morphology and behavior (Wellenreuther and Sánchez-Guillén 2015). In *Calopteryx*, species diversification is largely attributed to nonadaptive divergence in coloration and behavior, which influences premating isolation, as well as structural differentiation in reproductive morphology, affecting postmating isolation (Lorenzo-Carballa et al. 2014). Similarly, in the sister genera *Enallagma* and *Ischnura*, most diversification events are driven by differences in genital structures that play a key role in species recognition during copulation (Wellenreuther and Sánchez-Guillén 2015). These findings suggest that closely related species can exhibit minimal ecological differences while remaining reproductively isolated. This uncoupling of reproductive isolation from niche-based divergent natural selection challenges traditional niche models of species coexistence, emphasizing the significant role of sexual selection and nonadaptive processes in damselfly speciation.

Habitat Requirements

Damselflies are highly effective generalist predators in both aquatic and terrestrial habitats surrounding freshwater ecosystems (Wesner 2012). The diversity of freshwater habitats worldwide has facilitated the adaptation of damselflies to a variety of lentic and lotic environments, including rivers, waterfalls, ponds, lakes, ephemeral pools, bogs, seeps, damp leaf litter, phytotelmata, and brackish water. Nymphs are especially dependent on specific microhabitats and are generally associated with their preferred substrate (eg gravel, stone, mud, detritus, vegetation) (Corbet 1999; Suhling et al. 2015). Consequently, the spatial and temporal distribution of damselflies is generally influenced by the availability of suitable breeding habitats (Pulliam 1988). Damselflies are diurnal heliophiles (sun lovers), whose activity is mainly influenced by the fluctuations of ambient temperature and sunlight throughout the day (Corbet 1962), though at least one species (*Phylolestes ethelae* Christiansen, 1947) shows nocturnal copulation (Cordero-Rivera et al. 2024). Usually, Zygoptera are active earlier than Anisoptera as their smaller body size does not require high ambient temperatures to warm muscles to fly (Corbet and May 2008). Damselflies are also thermoconformers (May 1976; Castillo-Pérez et al. 2022) and usually have narrower thermal tolerances than dragonflies, leading to smaller distributions and a higher rate of endemism compared to dragonflies (Bota-Sierra et al. 2022).

For damselflies, survival and maintenance depend on local abiotic (eg temperature, physicochemical parameters of the water) and biotic (eg food availability, parasites, inter-, and intraspecific competition) requirements (McPeek 2008; Wellenreuther et al. 2011; 2012). Due to these requirements, most species have a narrow tolerance to anthropic disturbance, more so than Anisoptera (Silva et al. 2022). Therefore, damselflies are good indicators of the health of freshwater ecosystems and can provide unique and valuable insights on the drivers of global insect decline (habitat degradation, pollution, climate change) (Arce-Valdés and Sánchez-Guillén 2022 ; Oliveira-Junior et al. 2015; Samways and Simaika 2016; Oliveira-Junior and Juen 2019), especially in the context of freshwater ecosystems, which are the most threatened ecosystems in the world (Dudgeon et al. 2006; Dijkstra et al. 2014b; Piczak et al. 2024).

For example, in the Owabi wetland sanctuary in Ghana, Manu et al. (2022) found that the damselfly species *Africallagma vaginale* (Sjostedt, 1917) is a good indicator of habitats with moderate anthropogenic disturbance while they found and *Chlorocypha curta* (Hagen in Selys, 1853), *Chlorocypha luminosa* (Karsch, 1893), *Chlorocypha radix* Longfield, 1959 and *Agriocnemis zerafica* Le Roi, 1915 to be indicators of low anthropogenic disturbance. In Badu et al. (2024), *A. zerafica* and *Ceriagrion glabrum* (Burmeister, 1839) were recorded only in highly disturbed habitats, while *Allocnemis elongata* (Hagen in Selys, 1863) was only recorded in the least disturbed habitats. Damselfly species uniquely adapted for inhabiting moderately disturbed habitats included *A. elongata* and *C. curta*. *Phaon camerunensis* Sjöstedt, 1900 was present in both the least disturbed and moderately disturbed habitats, though higher abundance was recorded in the least disturbed habitats.

Flight

Although still among the best flyers in the animal kingdom, Zygoptera have lesser flight ability compared to Anisoptera, in part due to their smaller average body size, less developed flight muscles, and proportionally smaller homonomous fore- and hind wings (Büsse et al. 2013; Dijkstra et al. 2013; Bomphrey et al. 2016). Damselfly wings are driven by direct flight muscles (Bäumler et al. 2018), allowing them to control each wing pair independently. For example, males of *P. mirabilis* and *Chalcopteryx scintillans* McLachlan, 1870 only use their forewings for elaborate flight maneuvers during threat displays (Cordero-Rivera and Zhang 2018; Guillermo-Ferreira et al. 2019). Damselflies ability to hover is unmatched, and some species are even able to fly backward (Grimaldi and Engel 2005; Rüppell and Hilfert-Rüppell 2013; Bomphrey et al. 2016).

Damselflies are generally found closer to the water surface than Anisoptera and referred to as “perchers” because they spend most of their time resting instead of flying (Corbet 1962). However, there is nuance within Zygoptera where some groups spend more time perched (eg Lestoidea) than other more active groups (eg Calopterygoidea). There can also be intraspecific variation in these behaviors (Vilela et al. 2017). Their comparably limited flight abilities may translate to limited dispersal abilities, which may contribute to their small ranges and high levels of endemism (Dijkstra and Clausnitzer 2004). However, some Zygoptera, like the genus *Ischnura* and *Agriocnemis exsudans* Selys, 1877, are among the best colonizers of oceanic Pacific islands, likely thanks to the help of wind currents.

Vision

Odonates are highly visual insects and appear to have reduced the other senses or lack them altogether (Futahashi et al. 2015; Suvorov et al. 2016; but see Rebora et al. 2022). This highly evolved visual system is critical to both communication (eg inter- and intraspecies recognition) and predation. Odonates have both ocelli and compound eyes which are some of the largest in relation to body and head size among insects (Corbet 1999; Bybee et al. 2012; Suárez-Tovar et al. 2022). The compound eyes of nymphs possess dark banding, which is lost over time and might be an adaptation to the dark aquatic environment (Corbet 1999; Bybee et al. 2008). Both adults and nymphs can detect color ranging from ultraviolet (UV) to long wavelength (LW) (~300 nm to ~700 nm) (Yang and Osorio 1996; Bybee et al. 2012; Futahashi et al. 2015). In the transition from nymph to adult, the number of ommatidia (individual facets of the compound eye) greatly expands from ~340 to ~7,000 (Lew 1934; Sherk 1977). With this expanded eye size, adults are able to see in greater detail, and sections of the eye are specialized for acuity and light detection (Suárez-Tovar et al. 2022). For example, the dorsal ommatidia are usually quite small and sensitive to UV wavelengths, which allows them to detect movement against high contrast and bright backgrounds (eg sky). In comparison, the ventral ommatidia are larger, resulting in less acuity but an ability to sense the full light spectrum, allowing them to distinguish movement against a constantly changing background environment (Bybee et al. 2012; Futahashi et al. 2015). The size of the ommatidia also varies by section. For example, species that hunt at dusk have patches of larger ommatidia, which allows more light to enter the ommatidia for them to see better in darker environments while still maintaining good vision throughout the day (Bybee et al. 2012).

Most vision research has centered on opsins, which are the genes located in photoreceptor cells that control color vision. When combined with a chromophore, they form a photopigment specifically attuned to UV, short wavelength (SW), or LW light. Odonata documented thus far have as many as 33 opsin genes with varying levels of duplication, gains, and losses. The majority of these gains and losses are found within the LW opsins, with the SW being mildly duplicated (Futahashi et al. 2015; Suvorov et al. 2016). All Odonata examined thus far have only a single UV opsin copy expressed in the eye. Zygoptera opsin numbers range from 9 to 22, again with the greatest expansion occurring within the LW. Currently, the estimated opsin composition of ancestral Zygoptera was 1 UV, 2 SW, and 7 (Futahashi et al. 2015) or 10 (Suvorov et al. 2016) LW copies. Understanding opsin evolution allows greater insight into some of the most highly evolved visual systems among arthropods.

Other Sensory Systems

In light of their incredibly developed vision system, the other senses of odonates have received relatively little attention. Odonata, along with their sister Order Ephemeroptera, lack structures common to arthropod olfaction such as mushroom body calices (Farris 2005), which is likely a derived trait (Strausfeld et al. 2020). Nevertheless, there is a growing body of research to support the chemical perceptive abilities (olfaction) of Odonata. Ultrastructural investigations of odonate antennae have revealed features similar to other insect chemoreceptors (Rebora et al. 2008), and some chemical classes have been shown to elicit an electrophysical response in odonate antennae (Rebora et al. 2012). Behavioral studies have further confirmed the biological role of odonate olfaction. For example, while vision likely provides the first cue in mate recognition, smell may also be utilized by polychromic coenagrionids with males preferring the scent of females (both gyno- and andromorphs) when compared to males or a control (Frati et al. 2015). Olfaction doesn't appear to be very specialized between the odonate suborders: when presented with a panel of 48 chemical compounds, the olfactory neurons of both Anisoptera and Zygoptera species responded to the same 22 compounds, with only one compound provoking a unique response in each species (Piersanti et al. 2014).

Odonate flight is aided by mechanoreceptors in the pedicel of the antenna. The stiff flagellum, which is connected to the pedicel via a ball-and-socket joint, moves in all directions during flight. These movements are perceived by Johnston's organ in the pedicel, which provides feedback about flight direction and relative wind speed (Gewecke and Odendahl 2005). Zygoptera also use olfaction cues to detect flight conditions (eg humidity, temperature, air currents) (Piersanti et al. 2014). Mechanical and chemical receptors have been found on mouthparts (Rebora et al. 2014) and the ovipositor (Frati et al. 2016), which may help damselflies evaluate the suitability of food and prevent egg damage during oviposition.

As they mature, damselfly nymphs transition from their aquatic habitat to the terrestrial habitat of adults. Because they are ectotherms, adults regulate body temperature by modulating the amount of sunlight hitting their bodies, such as changing perching posture and location (Corbet 1962). These strategies would require structures to sense temperature and humidity. Structures similar to other insect thermo/hygroreceptors have been described on the odonate antenna (see Rebora et al. 2008). These receptors have been shown to be sensitive to dry, moist, and cold stimuli (Piersanti et al. 2011).

Taxonomists: Past and Present

The basis of systematics relies on taxonomy, and there have been numerous experts that have expanded our understanding of the diversity within Zygoptera. In terms of the number of species described, the top 50 authors have described 3,163 of the 3,709 taxa (Table 1). Below are a few of the taxonomists that have significantly contributed to this group and where the majority of their type material is stored.

Rambur, Jules Pierre (1801–1870)

Most type material deposited at: Royal Belgian Institute of Natural Sciences (RBINS), Muséum national d'histoire naturelle (MNHN), and zoological collection of the University of Sevillia.

Rambur studied medicine, but retained passion for the natural world, especially Lepidoptera and Coleoptera. Regarding Odonata, he is most recognized for his chapter on worldwide Neuroptera within *Nouvelles suites à Buffon* (1842), in which he cataloged 233 odonate species. His descriptions are notable for their novel attention to genitalia and other sexual characters (Endersby and Fliedner 2015).

de Selys-Longchamps, Edmond (1813–1900)

Most type material deposited at: RBINS.

Widely regarded as the "father of odonatology," Selys-Longchamps (usually "Selys" in literature) remains the most prolific taxonomist of the order Odonata. Born into aristocracy, his professional career culminated in the appointment as president of the Belgian senate. Though a politician by trade, Selys was fervently interested in the natural world. In 1885, his expansive personal collection of odonates contained 1,530 of the about 1,800 then described species. His 2 monographs with Hagen and 26 synoptic publications cover the majority of odonate diversity (Wasscher and Dumont 2013). Approximately 400 species were originally described by Selys, as well as assisting in the description of 500 currently accepted species. Selys also described approximately 370 nymphs.

Hagen, Hermann August (1817–1893)

Most type material deposited at: Museum of Comparative Zoology (MCZ).

For his thesis as a medical student at the University of Königsberg, Hagen studied European dragonflies and synonymized many problematic taxa. Together with Selys, Hagen produced reviews and monographs of European odonates, such as *Revue des Odonates de Europe* (1850), for which he provided many of the illustrations (Endersby and Fliedner 2015). He also described approximately 147 nymphs. He was the first odonate researcher settled in America.

Martin, René (1846–1925)

Most type material deposited at: Muséum national d'histoire naturelle (MNHN).

The French lawyer Martin was asked to catalog the Cordulinae (1906) and Aeschninae (1908) of Selys' collection, for which he published a monograph for each. He and his daughter moved to Chile later in life, where he formed the entomological society in Santiago (Endersby and Fliedner 2015).

Förster, Johann Friedrich Nepomuk (1865–1918)

Most type material deposited at: University of Michigan's Museum of Zoology (UMMZ).

Förster was a frequent collaborator in Selys' later years, mostly regarding the Indo-Australian odonates. His first species description honored Selys (*Caconeura selysi* Förster, 1896), and he was invited to catalog the Agriónines of the Selys collection (Endersby and Fliedner 2015).

Ris, Friedrich (1867–1931)

Most type material deposited at: Senckenberg Museum.

Before his matriculation as a medical student at the University of Zurich, Ris published the first comprehensive work on Swiss

Table 1. The top 50 most active taxonomists for Zygoptera, limited to first-author descriptions

Surname	Given names	No. of species	Nationality	Description years
Selys	Baron Edmond de	383	Belgium	1831–1898
Burmeister	Hermann	24	Germany	1839–1839
Rambur	Jules Pierre	43	France	1842–1842
Hagen	Hermann August	142	Germany	1853–1889
Brauer	Friedrich Moritz	24	Austria	1865–1877
McLachlan	Robert John	40	England	1869–1903
Karsch	Ferdinand	19	Germany	1891–1899
Calvert	Philip Powell	133	USA	1891–1961
Förster	Johann Friedrich Nepomuk	42	Germany	1896–1916
Martin	René	31	France	1896–1921
Williamson	Edward Bruce	39	USA	1898–1930
Ris	Friedrich	99	Switzerland	1898–1936
Sjöstedt	Yngve	24	Sweden	1900–1933
Laidlaw	Frank Fortescue	69	Scotland	1902–1950
Needham	James George	35	USA	1903–1941
Tillyard	Robert John	47	England	1906–1926
Navás	Longinos	20	Spain	1907–1936
Kennedy	Clarence Hamilton	30	USA	1916–1946
Fraser	Frederic Charles	175	England	1919–1960
Kimmins	Douglas Eric	26	England	1929–1958
Lieftinck	Maurits Anne	324	Netherlands	1929–1987
Longfield	Cynthia Evelyn	17	Ireland	1931–1959
Schmidt	Erich	49	Germany	1931–1964
Asahina	Syoziro	45	Japan	1949–1997
Pinhey	Elliot Charles Gordon	49	England	1950–1981
Rácenis	Jorge	19	Venezuela	1955–1968
Machado	Ângelo Barbosa Monteiro	70	Brazil	1956–2019
Santos	Newton Dias dos Santos.	27	Brazil	1956–1979
Aguesse	Pierre	20	France	1958–1968
Donnelly	Thomas W.	34	USA	1961–2013
Watson	John Anthony Linthorne	20	Australian	1967–1991
Legrand	Jean	16	France	1980–1992
De Marmels	Jürg	57	Venezuela	1982–2008
Garrison	Rosser William	63	USA	1982–2023
Theischinger	Günther	74	Austria	1983–2024
Bick	Gordon and Joan	17	USA	1985–1996
Hämäläinen	Matti	57	Finland	1985–2020
Daigle	Jerrell J.	14	USA	1990–2014
van Tol	Jan	59	Netherlands	1995–2018
Wilson	Keith	25	England	1997–2007
Tennessen	Kenneth J.	15	USA	1997–2024
Gassmann	Dieter	15	Germany	1999–2019
Lencioni	Frederico A.A. Lencioni.	19	Brazil	1999–2023
Orr	Albert	21	Australian	1999–2024
Villanueva	Reagan Joseph T.	29	Philippines	2005–2020
von Ellenrieder	Natalia	86	Argentina	2006–2022
Dijkstra	Klaas-Douwe B.	27	Netherlands	2007–2015
Kalkman	Vincent	21	Netherlands	2007–2023
Dow	Rory A.	52	England	2008–2020
Phan	Quoc Toan	26	Vietnam	2011–2023

odonates, *Die Schweizerischen Libellen* (1885). During his post as a ship surgeon, his travels (eg the Americas and Southeast Asia) allowed him to study the worldwide biodiversity of Odonata. After Selys' death in 1900, Ris studied his extensive collection, eventually using it to produce the first monographs on Libellulinae (1909) (Endersby and Fliedner 2015) and some accurate regional inventories filled with illustrations and descriptions of new species (eg Ris 1918).

Calvert, Philip Powell (1871–1961)

Most type material deposited at: Academy of Natural Sciences (ANSP), Carnegie Museum of Natural History (CM), British Museum Natural History (BMNH), MCZ.

Calvert was associated with the American Entomological Society for 74 years, 60 of which he served in a leadership or administrative position. As a youth, he served as curator for the Agassiz Association, a society intending to promote the study of natural science among young people. His first publication of Odonata, *Catalogue of the Odonata (dragonflies) of the Vicinity of Philadelphia* (1893), inventoried the species of his local Pennsylvania. Throughout his career, he published over 300 works on Odonata (White 1984). Probably his most influential work was the revision of the odonate fauna from Central America, published as a chapter in the *Biologia Centrali-Americana* (1908). His descriptive illustrations and dichotomous keys were central to the systematic treatment of odonates (Garrison et al. 2010). Additionally, he described approximately 135 nymphs.

Laidlaw, Frank Fortescue (1876–1963)

Most type material deposited at: BMNH.

The Scottish Dr. Laidlaw studied zoology and medicine. His work on Odonata stems from participation in the Cambridge University Expedition to Malaya from 1899 to 1900. He maintained an interest in Odonata from the region the rest of his life, describing 106 species in total (Dance 1964).

Fraser, Frederic Charles (1880–1963)

Most type material deposited at: British Museum of Natural History (BMNH), Australian National Insect Collection (ANIC), Zoological Survey of India.

Fraser, a British surgeon who served in the Indian Medical Service, published over 300 documents on Odonata, most concerning the species of India and Africa. He also described approximately 176 nymphs. He completed R. J. Tillyard's reclassification of Odonata (1957), which was informed by wing venation of fossil taxa (Endersby and Fliedner 2015).

Lieftinck, Maurits Anne (1904–1985)

Most type material deposited at: Naturalis Biodiversity Center Leiden (RMNH).

Lieftinck was a Dutch entomologist. As a university student, he collected and published on Odonata in his native country, The Netherlands. He then moved to Dutch Java in 1929 to accept a zoologist position at the Buitenzorg Museum. He was a productive describer of South Asian and Pacific odonates: 60% of New Guinean species are attributed to Lieftinck (Kalkman and Orr 2013). He additionally described approximately 320 nymphs. Even as a prisoner of war in the Japanese-occupied Dutch East Indies, Lieftinck observed helodid beetle larvae in phytotelmata and reared libellulid eggs to maturity (Geijskes 1984).

Pinhey, Elliot Charles Gordon (1910–1999)

Most type material deposited at: Natural History Museum of Zimbabwe.

After employment as a science educator in England, Pinhey accepted a teaching position in Rhodesia, which fostered his interest in African odonates. His major work *A Descriptive Catalogue of the Odonata of the African Continent* (1962) represents a comprehensive treatment of the African species. Also notable is his almost 100 descriptions of African odonate nymphs (Vick et al. 2001).

Newton Dias, dos Santos (1916–1989)

Most type material deposited at: Nacional do Rio de Janeiro (MNRJ); however, most were lost when the museum burned down in 2018.

Santos, regarded as the father of Brazilian Odonatology (Garrison et al. 2010), obtained his medical degree in 1940. In 1944, he was admitted to the Museu Nacional as a Naturalist, where he conducted his studies on Odonata, founding the collection of dragonflies (which were lost in a devastating 2018 fire) (Loaiza and Anjos-Santos 2019). During his first 15 years as an odonatologist, he concentrated on libellulids, but later shifted his focus to coenagrionids, describing many new species, females and nymphs. He visited the most important collections in Europe and the United States, with a special emphasis on studying the types of Brazilian species, which enabled him to clarify many taxonomic controversies (Machado and Costa 1990).

Martins Costa, Janira (1941–2018)

Costa, the first female specialist in Odonata in Central and South America, began her academic career in 1964 as an intern at the National Museum da Universidade Nacional de Rio de Janeiro, Brazil, under the mentorship of Dr. Newton Dias dos Santos. She was a Professor of Zoology and director of the Museu Nacional do Río de Janeiro, where she curated the institution's extensive Odonata collection. Costa hosted many Brazilian and international researchers, fostering collaborative research networks that advanced the study of Neotropical dragonflies (Anjos-Santos and Almeida 2018). Over her career, she published over 90 taxonomic papers on Odonata.

Machado, Ângelo Barbosa Monteiro (1934–2020)

Most type material deposited at: Departamento de Zoologia, Universidade Federal de Minas Gerais, Belo Horizonte, Brasil (UFMG)

Although Machado's main accomplishments were in neurology, he established himself as a leading odonatologist in Brazil. Machado started his passion for dragonflies in his early years, guided by Santos Newton Dias (Anjos-Santos 2020). He accumulated over 35,250 odonate specimens from 1,050 species, including 105 holotypes, which were donated to the Universidade Federal de Minas Gerais in 2014. Besides Selys, Machado has described more species of Odonata in Brazil than any other taxonomist (Pinto 2016).

Theischinger, Günther (Current)

Most type material deposited at: Collection of the Australian Museum (AM), ANIC, South Australian Museum (SAMA).

Theischinger was born in Austria, where he curated invertebrates at Oberösterreisches Land museum in Linz before moving to Australia. He worked in environmental consulting and biological assessments for 2 decades, after which he served as curator of aquatic insects for the CSIRO Division of Entomology and identified aquatic macroinvertebrates for the New South Wales Environmental Protection Authority. He has contributed significantly to our understanding of the taxonomy, morphology, and nymphal biology of Australian Odonata and their potential as biological indicators. Much of this knowledge is published in the second edition of The Complete Field Guide to Australian Odonata (2021). Theischinger is currently a Research Associate for the Australian Museum and a Visiting Fellow of the Smithsonian Institution, Washington DC.

Garrison, Rosser W. (Current)

Most type material deposited at: Florida State Collection of Arthropods (FSCA), US National Museum (USNM), University of Michigan, Museum of Zoology (UMMZ).

Garrison's contributions to the study of the Neotropical odonates allow the accurate identification of most species in this region. Some of his most significant contributions are the illustrated and annotated keys to New World Anisoptera (Garrison et al. 2006) and Zygoptera (Garrison et al. 2010). In 2017, he retired from his position as senior insect biosystematist for the California Department of Food and Agriculture and remains active in odonate taxonomy.

von Ellenrieder, Natalia (Current)

Most type material deposited at: FSCA, University of Michigan, Museum of Zoology (UMMZ), US National Museum (USNM).

von Ellenrieder earned her Ph.D. from La Plata University, Argentina, under the supervision of Dr. J. Muzón. She dedicated her career to the study of Neotropical Odonata, making significant contributions through comprehensive revisions of genera within Aeshnidae, Coenagrionidae, and the former "Protoneuridae." Throughout her still-active career, she has described five new genera and 85 new species.

van Tol, Jan (Current)

Most type material deposited at: Naturalis Biodiversity Center Leiden (RMNH)

van Tol is currently affiliated with the Naturalis Biodiversity Center. He specializes in the Odonata of Southeast Asia, particularly Indonesia (van Tol 2007; van Tol and Günther 2018) and the Philippines (van Tol and Müller 2003).

de Marmels, Jürg (Current)

Most type material deposited at: Museo del Instituto de Zoología Agrícola (MIZA)

de Marmels is currently affiliated with the Museo del Instituto de Zoología Agrícola Francisco Fernández Yépez. He is a prolific describer of Odonata species from Venezuela and other South American countries, including larval descriptions (eg de Marmels 2001, de Marmels 2012; de Marmels 2024).

Hämäläinen, Matti (Current)

Most type material deposited at: Naturalis Biodiversity Center Leiden (RMNH)

Hämäläinen is currently affiliated with the Naturalis Biodiversity Center. Through his vignettes and biographies, he has memorialized many notable odonate researchers and their influences (Hämäläinen and Orr 2016; Hämäläinen and Orr 2017; Hämäläinen, Verspui, and Orr 2020; Hämäläinen et al. 2022). His monograph with Orr of *Neurobasis* and *Matronoides* is notable for its comprehensive descriptions, illustrations, and histories of the genera (Orr and Hämäläinen 2007). He has described many Odonata species from China (Hämäläinen, Yu, and Zhang 2011; Yu and Hämäläinen 2012; Zhang and Hämäläinen 2012) and other Southeast Asian countries (Hämäläinen and Orr 2024).

Dow, Rory A (Current)

Most type material deposited at: Naturalis Biodiversity Center Leiden (RMNH)

Dow has provided many species descriptions (eg Dow and Orr 2012; Kompier, Dow, and Steinhoff 2020) and checklists (Dow et al. 2024) for the Odonata of southeast Asia. He has also contributed to conservation efforts as a member of the IUCN SSC Dragonfly Specialist Group. He is currently affiliated with the Naturalis Biodiversity Center.

Marinov, Milen (Current)

Most type material deposited at: New Zealand Arthropod Collection, Lincoln University Entomology Research Museum (LUNZ), FSCA.

Marinov attended the Institute of Zoology at the Bulgarian Academy of Sciences, from which he obtained his PhD in 2003. Specializing in the Pacific islands, he has published guides to the Odonata of Viti Levu, Fiji (Marinov and Waqa-Sakiti 2013) and New Zealand (Marinov and Ashbee 2013). His species descriptions, taxonomic reviews, and studies of island biogeography have greatly expanded the understanding of Pacific Odonata. He is currently employed as entomologist for the biosecurity and surveillance team of New Zealand's Ministry for Primary Industries. He also serves as editor for the Odonata section of the journal *Zootaxa*.

Phylogenetic History

Linnaeus (1758) described the first odonate species and placed them all into a single genus, *Libellula*, which at the time was within Neuroptera. This genus was eventually split by Fabricius (1775) into 3 groups (*Libellula*, *Aeshna*, and *Agrion*) to account for morphological and behavioral differences (Trueman 2007). The ordinal name Odonata was introduced by Fabricius (1793) and was eventually split from Neuroptera by Martynov (1923). Selys (1889), while the order was still included within Neuroptera, was the first to attempt a classification system for what is now Odonata and introduced the 2 suborders, Anisoptera and Zygoptera, as well as later describing the seemingly intermediate Anisozygoptera species, *Epiophlebia superstes* (Selys, 1889) (Trueman 2007).

Morphological Classification

Early odonatologists relied on morphological characters for taxonomy and relationships (Fig. 3A), with the most utilized characters being wing venation (Rehn 2003; Bybee et al. 2008; Kohli and Ware 2023). Over time, several wing venation nomenclatures were proposed (eg Comstock and Needham 1898; Lameere 1923; Tillyard and Fraser 1938; Hamilton 1972; Carle 1982; Riek and Kukalová-Peck 1984; Nel and Piney 2023) and provided the basis for the first ordinal and familial classification attempts (Trueman 2007).

Numerous catalogs and evolutionary classification attempts were based heavily on wing venation (eg Kirby 1890; Needham 1908; Ris 1918; Tillyard and Fraser 1938; Geijskes 1970; Carle 1982; Davies and Tobin 1985; Bechly 1996; Rehn 2003). Authors took different approaches which resulted in classification hypotheses that in some cases were strongly opposed to one another (ie Lieftinck 1971 vs Fraser and Tillyard 1957) (Hennig 1966). For example, Tillyard (1917) and Munz (1919) were able to separate the suborders and proposed elevating many groups to family status. Fraser and Tillyard (1957) presented new ordinal and superfamily relationships (eg paraphyletic Lestoidea by Calopterygoidea). While this classification was widely accepted, it grouped species from a "primitive" to "advanced" state, which has been proven to be an inaccurate interpretation since the beginning of computational phylogenetics (Rehn 2003; Trueman 2007; Bybee et al. 2008; 2021; Kohli et al. 2021; Suvorov et al. 2021; Kohli and Ware 2023).

In the late 20th and early 21st century, morphological cladistic attempts (ie parsimony) were common. Bechly (1996) added numerous new species and families using a Hennigian "hand and brain" approach. Rehn (2003) greatly increased the number of morphological characters for cladistic analysis, mostly wing venation but with emphasis on wing articulation, and recovered a well-supported monophyletic Zygoptera for the first time. Other morphological characters beyond wing venation have also been used in phylogenetic research (eg Kennedy 1920; Gloyd 1959; Lieftinck 1971; Pfau 1971; Lohmann 1996) relating to sexual characters (eg genital ligula), egg characters, nymph characters, physiological characters (eg flight muscle, head morphology), colors, and more (Kohli and Ware 2023). While exclusively morphological phylogenetic studies are becoming less common, morphological cladistic analyses have yielded important and relevant findings in both fossil and extant odonate classifications (eg Rehn 2003; Pessacq 2008). By implementing various character sources, synapomorphies can become more apparent, but remain absent for many tropical genera (Garrison et al. 2006, 2010) and rarely provided in molecular phylogenetic studies.

Early Molecular Classification

In the late 20th and early 21st century, molecular techniques (ie Sanger sequencing) and analytic methods (eg Bayesian and maximum likelihood) were developed and quickly gained traction in phylogenetics (Fig. 3B). Most studies (eg Artiss et al. 2001; Misof et al. 2001; Dumont et al. 2005; Carle et al. 2008), focused on 1 or 2 mitochondrial genes (ie COI, 12S) as it was costly and time consuming to generate these data. Saux et al. (2003) published the first ordinal level molecular phylogeny, but only suborder relationships could be tested because of the limited taxon sampling. There were several other molecular phylogenies that quickly followed with larger sampling schemes (eg Ogden and Whiting 2003; Kjer 2004; Hasegawa and Kasuya 2006; Kjer et al. 2006), in an attempt to parse out the higher-level (eg family, superfamily) relationships, but all disagreed on points such as the monophyly of Zygoptera and the family level relationships. Bybee et al. (2008) took a combined morphological and molecular approach with a significantly expanded taxon sampling to try to clarify the higher-level relationships within the order, finding Zygoptera consistently monophyletic. Dijkstra et al. (2014a) made several classification changes based on a molecular reconstruction, which were supported with morphological synapomorphies (eg restructuring Coenagrionoidea from five families to 3) (Fig. 3B). Neither were able to recover consistent relationships within the superfamilies (eg Calopterygoidea as a large polytomy, and Isostictidae as a member of Coenagrionoidea).

Next Generation Sequencing and Genomics

The development of new "-omic" tools has revolutionized our ability to explore the "natural history" of life within Arthropoda, exemplified by initiatives like i5K, which aims to sequence 5,000 arthropod genomes (i5k Consortium 2013). As whole genome comparative functional tools expand, they offer fresh insights into the origins and maintenance of key traits, driving radiations, and significant evolutionary transitions. However, despite concerted efforts to develop "-omic" resources across the Tree of Life, substantial gaps persist, particularly concerning aquatic insects (Hotaling et al. 2020) and particularly damselflies. With the increasing availability of both genomic resources and analysis of genomic data, research on damselfly population processes, local adaptation, and speciation is poised to significantly advance our understanding of evolutionary dynamics (eg Swaegers et al. 2021, 2022). Opportunities exist to investigate parallel evolutionary processes within and across species, explore spatially varying selection across multiple loci, and corroborate findings from gene expression and whole genome sequencing with experimental data across different life stages (eg Swaegers et al. 2023). This approach can yield a deeper understanding of how damselflies and other odonates adapt to changing environments, shedding light on broader evolutionary patterns and processes.

With the cost of sequencing continuing to decrease, a shift to more genome studies is a possibility in the future (eg Lancaster et al. 2016). Such studies will provide deep insight into all aspects of odonate ecology and evolution (Bybee et al. 2016). Nine genome assemblies are currently available on GenBank from 7 genera (*Ischnura*, *Platycnemis* Burmeister, 1839, *Pyrrhosoma* Charpentier, 1840, *Ceriagrion* Selys, 1876, *Hetaerina* Hagen in Selys, 1853, *Calopteryx*, *Rhinocypha* Rambur, 1842) all varying in completeness and quality (Clark et al. 2015; Newton et al. 2023). There are international collaborations and long-term plans afoot to significantly increase the amount of publicly available genomes, particularly at the family level, within the next few years. Odonata genomics, particularly within Zygoptera, is a growing field with exceptional opportunities in comparative and conservation biology, as well as population genomics. As more genomic resources, such as multispecies genotyping platforms, become available, researchers will gain the tools needed to explore the genetic foundations of species boundaries, identify cryptic species, and understand the evolutionary processes driving speciation (eg coloration). This will lead to a deeper and more precise understanding of damselfly biodiversity and evolution. Large-scale ordinal level transcriptomic phylogenies (Fig. 3C) focusing on the evolution of certain traits (eg introgression, color vision, color, etc.) provided evidence and support for our phylogenetic understanding of the group (Kohli and Ware 2023).

Current Classification Status

Limited data sets (eg taxon, genetic, and morphological data) left many odonate phylogenetic efforts with low support, particularly along the backbone and discordant results between studies. The advent of high throughput sequencing and targeted enrichment techniques have enabled more efficient ways to generate large amounts of molecular data. For example, Bybee et al. (2021) is the most recent ordinal level phylogeny for Odonata that specifically focuses on large diversity of Zygoptera and classification (Fig. 4; Supplementary Table 1) (but see Kohli et al. 2021 and Suvorov et al. 2021). In comparison to the single-digit gene sampling of earlier Sanger-based phylogenies, this study utilized up to 478 genes with an anchored hybrid enrichment approach. This comprehensive sampling allowed Bybee et al. (2021) to erect five new families (Amanipodagrionidae, Mesagrionidae, Mesopodagrionidae, Priscagrionidae, Protolestidae) and reinstate 2 (Rhipidolestidae, Tatocnemididae). This current hypothesis proposes a monophyletic Zygoptera containing 4 superfamilies: 3 monophyletic (Lestoidea, Platystictoidea, and Coenagrionoidea) and 1 paraphyletic (Calopterygoidea).

Lestoidea

Lestoidea contains 4 families (Hemiphlebiidae, Perilestidae, Synlestidae, and Lestidae). The monophyly of this superfamily was

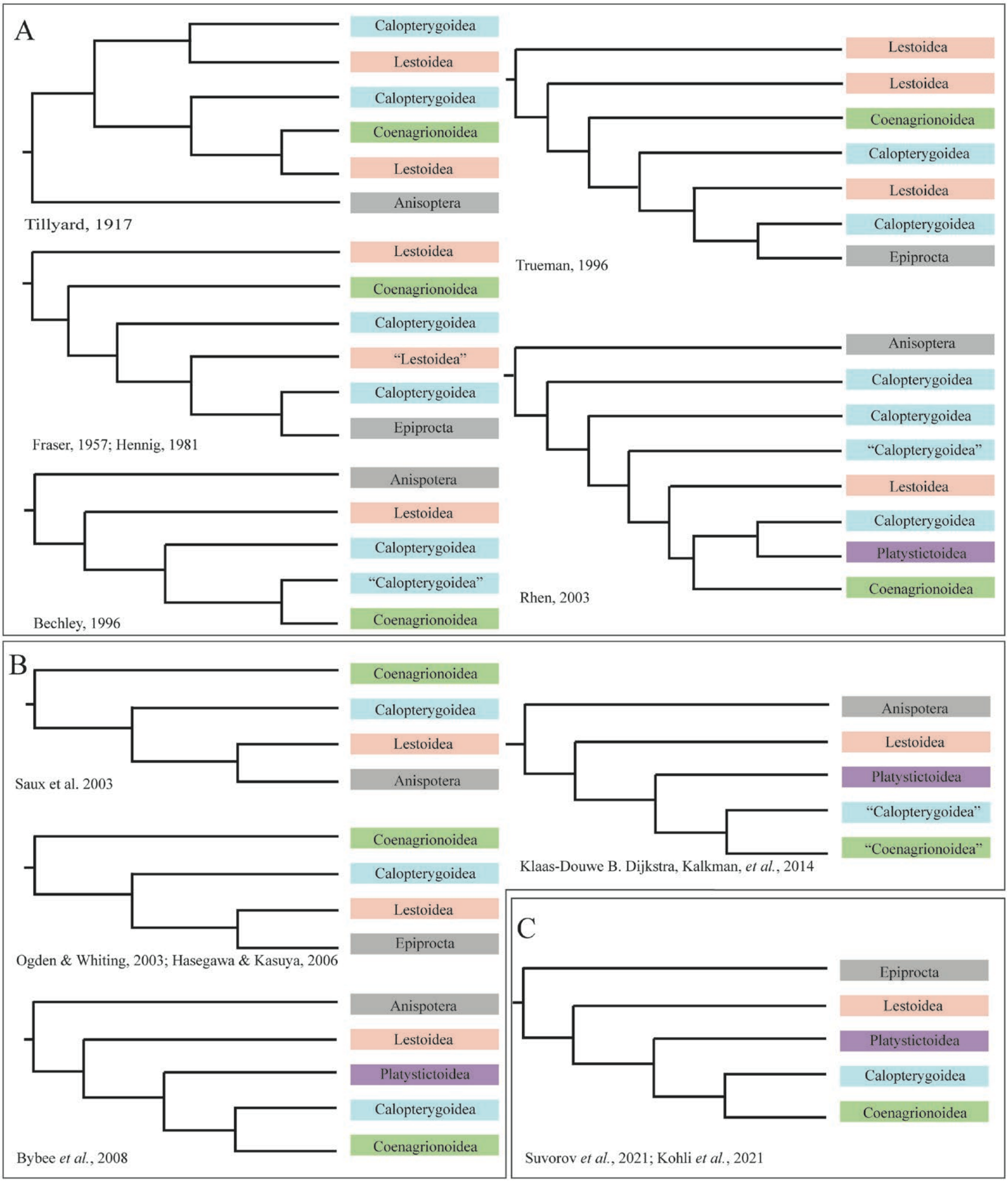


Fig. 3. Summary of superfamily relationships over time based on A) strictly morphology data B) molecular (Sanger) data, expect Bybee et al. (2008) which combined molecular and morphological data C) transcriptomic data. A nonmonophyletic grade is indicated by "". While the composition of each superfamily differed between authors, there is variation between the relationships regardless. The main relationships were summarized, adapted, and reconstructed by hand from Bybee et al. (2008), Bechly (1996), Dijkstra et al. (2013), Kohli et al. (2021), Suvorov et al. (2021), and Trueman (2007).

heavily debated prior to 2008. It was often authoritatively placed or recovered by Sanger phylogenetics as sister to Anisoptera. Since 2008, it has been consistently recovered as sister to all Zygoptera with high support. This relationship has been tested by phylogenetic studies based on high throughput sequencing and continues to be recovered with high support (Bybee et al. 2021; Kohli et al. 2021; Suvorov et al. 2021). There is, however, uncertainty in the monophyly of Perilestidae and Synlestidae, but better taxa coverage is needed to clarify the relationship between these 2 families (Dijkstra et al. 2014a, Bybee et al. 2021).

Platystictoidea

Platystictoidea contains only Platystictidae. It is currently hypothesized, with substantial data across several independent phylogenetic studies, to be sister to all remaining Zygoptera, except Lestoidea (Bybee et al. 2008; Bybee et al. 2021). This family has both strong molecular and morphological support (Dijkstra et al. 2014a, Bybee et al. 2021).

Calopterygoidea

Calopterygoidea is a diverse group that contains 25 of the 38 families within Zygoptera, but inter-familial relationships are not well supported. The nonmonophyly of the superfamily is a well-known issue due to several families and previously hypothesized superfamilies now being placed within the current superfamily. Based on Bybee et al. (2021), Calopterygoidea is paraphyletic and is composed of 4 clades. Clade 4 is sister to Coenagrionoidea with Clade 1 (composed entirely of the family Priscagrionidae and likely to become its own superfamily) as sister to remaining Calopterygoidea + Coenagrionoidea. While Bybee et al. (2008), Suvorov et al. (2021), and Kohli et al. (2021) recovered Calopterygoidea as monophyletic, all used a more limited taxon or data sampling (Fig. 3B and C). The differences in the taxon sampling and reconstruction methods between the 3 studies could potentially explain the differences in the results (Newton et al. 2023).

Coenagrionoidea

Coenagrionoidea has 3 families (Coenagrionidae, Platycnemididae, and Isostictidae) and contains the most species diversity (~1,900 species). The behavioral and morphological uniqueness of the former Protoneuridae and Pseudostigmatidae must be analyzed in detail with more taxon sampling to test whether these should be included in the family Coenagrionidae or re-stated. The position of Isostictidae has been consistently debated due to low nodal support. It is currently sister to Platycnemididae + Coenagrionidae (Dijkstra et al. 2014a, Bybee et al. 2021). Coenagrionoidea is also known to have numerous generic classification issues. Willink et al. (2024) produced the most recent and extensive phylogeny highlighting 20 paraphyletic genera. However, Isostictidae was not included, indicating that this is most likely an underestimate.

Nymph History and Status

The nymphs of Zygoptera are less known taxonomically than their adult counterparts, and the discovery and description of damselfly nymphs also lags behind adults. In the 18th century, several entomologists in western Europe were the first to become interested in the microscopic examination of insects while also discovering nymphs (ie Charles DeGeer (1720–1778, Sweden) and Jean-Marie Léon Dufour (1780–1865, France)). Their interest in insects predates entomology as a recognized field of study. In the mid-1850s, Hermann Hagen in Germany became interested in odonate nymphs, encouraging a student Louis Cabot to study them, which resulted in the description of Anisoptera nymphs, whereas in Britain, W. J. Lucas described numerous Zygoptera nymphs. The study of odonate nymphs was continued by others in several western European countries.

While there has been an effort to associate Zygoptera nymphs with adults, either through rearing (Tennessen and Tennessen 2019) or molecular studies (Yeo et al. 2018), there is a lot of work remaining. For instance, there has been more effort to rear and associate Zygoptera from temperate regions than tropical regions, which is the same pattern in Anisoptera (Ware et al. 2025). For example, nearly all species of the temperate genera *Enallagma* and *Ischnura* are known in the nymph stage whereas about 30% of the Neotropical genus *Acanthagrion* Selys, 1876 and about 20% of *Telebasis* Selys, 1865 are known. Fortunately, contributions to nymph descriptions and associations have been made increasingly in the last 2 decades by students in Argentina, Brazil, and Colombia. Much work is left to be done in Africa and Southeast Asia.

Currently, very little is known about which morphological nymph characters reveal phylogenetic affinities. For example, Coenagrionidae, the largest family still has major hurdles to overcome including (i) in the subfamily Coenagrioninae, nymphs of only 60% of the 50 Western Hemisphere genera have been described and less than 30% of the species are known; (ii) within the 2 largest genera of Coenagrioninae, nymphs of less than 30% of the *Argia* species and about 20% of the *Pseudagrion* species are known; (iii) in the family Protoneuridae, only five of the 15 genera have been discovered with only about 15% of the species known. Worldwide, a rough estimate of nymph descriptions is probably around 30% of the ~6,420 species, offering huge opportunities for taxonomic, evolutionary, and ecological studies. It is likely that nymph morphology, when better known, will contribute greatly to the phylogeny of the suborder. Examples of traditional nymph morphology to support phylogenetic inferences is demonstrated in Amphipterygidae (Novelo-Gutiérrez 1995) and Synlestidae (Simaika et al. 2020). However, it is unclear whether mouthparts (eg mandibular structure) (Büsse et al. 2017), thoracic structures and patterns (Tennessen 2020), and lateral abdominal and anal gills are homoplasious.

In the future, as comparative morphological studies that incorporate microtomography (µCT—a 3D imaging technique utilizing X-rays) (Büsse et al. 2017), become more common, there is the potential for them to greatly expand our knowledge of odonate phylogeny for both adults and nymphs. The capabilities of µCT allow researchers to examine and compare internal structures, including musculature and their attachments, in a biomechanical framework. These characters can be coded in large numbers for phylogenetic analysis and offer an untapped data set for phylogenetic systematics.

Paleontological Record

Odonata has one of the best paleontological records within insects. Extant Odonata are modern day representatives of one of the most ancient lineages of winged insects. They occupy aquatic habitats conducive to fossilization (wetlands with fine sediments), and their large, sclerotized wings lead to well-preserved wing venation. Odonate fossils are primarily compression fossils, but many are known from amber as well, especially within Zygoptera. Fossil wing venation offers informative characters for identification and provides insight into the evolution of the group as well as insect flight. With such a rich fossil record, classification and taxonomy of the group has been given significant attention. Additionally, analyses of wing venation in living species are also common and well-documented (Trueman 1996). However, the classifications of the fossil taxa and the extant taxa have been siloed and are not currently integrated using modern methods.

Odonatoptera Classification

Extant Odonata represent a clade within the ancient superorder of winged insects, Odonatoptera. There exist at least 16 extinct clades, many of which have clear synapomorphies that relate to extant

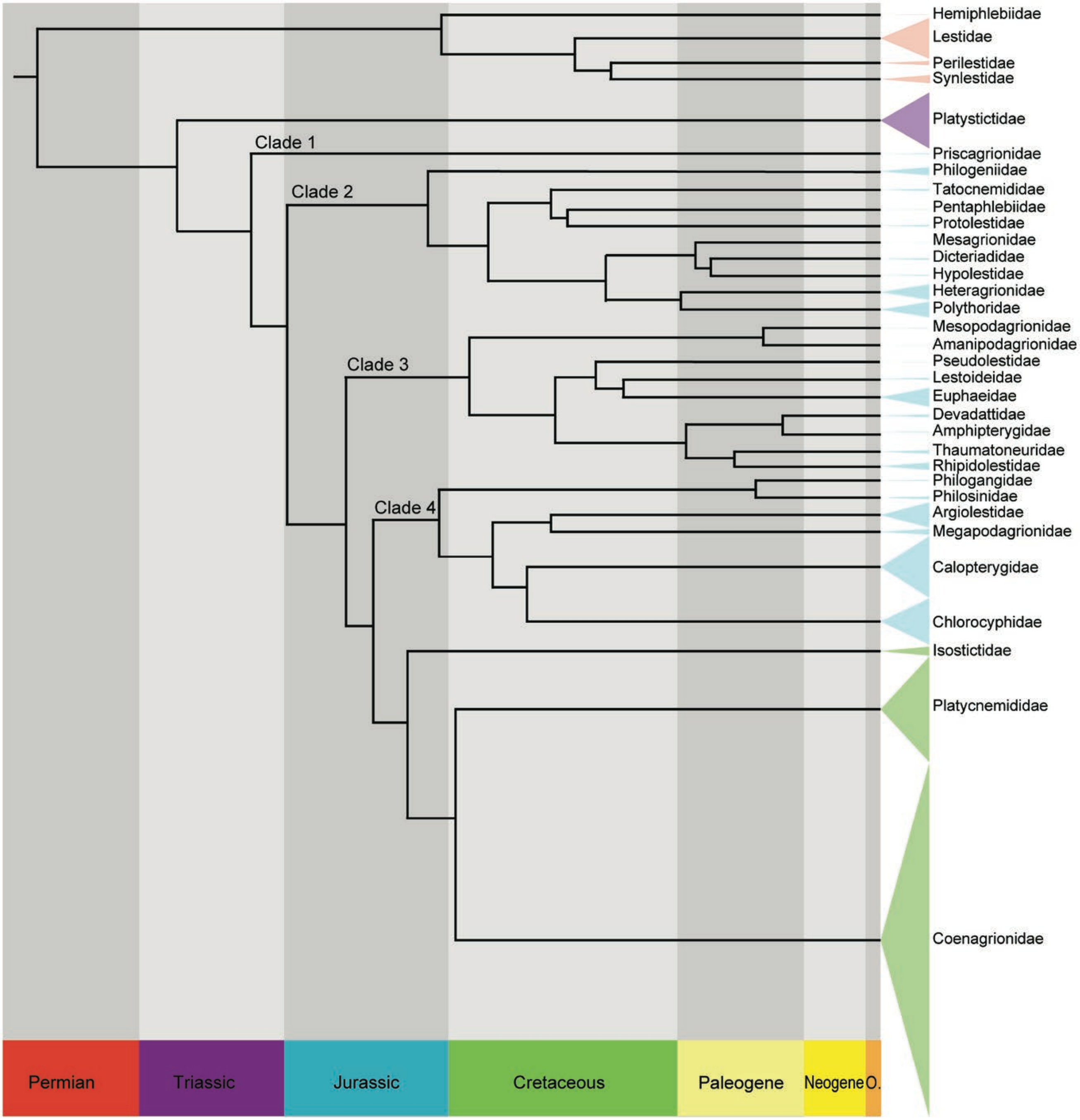


Fig. 4. Current superfamily and family relationships within Zygoptera reconstructed from Bybee et al. (2021) with general divergence times based on unpublished data.

Odonata based on wing venation (Fig. 5) (Nel and Piney 2023). There are 4 main wing innovations, known as smart mechanisms—nodus, pterostigma, discoidal cell, discoidal triangle—which arose in a stepwise pattern throughout the Odonatoptera that assisted in the evolution of extant Odonata, where these mechanisms appear to evolve together (Wootton 1991, 1992, 1998, 2002, 2003; Bybee et al. 2008; Nel and Piney 2023). The oldest Odonatoptera fossils date to the Serpukhovian age of the Early Carboniferous period (325–324 Mya), which also represent some of the oldest known winged insect fossils (Petrulevičius and Gutiérrez 2016). The most recognizable stem group at this time was Meganisoptera (griffenflies or giant dragonflies) with a wingspan up to 70 cm (Nel and Piney 2023). During the Mesozoic era, modern Odonata arose in the Triassic period with extant Zygoptera diversifying in the late Jurassic period (Kohli et al. 2016; Suvorov et al. 2021; Nel and Piney 2023). There are ~1,000 fossil records for odonates between several databases (eg ENDA Fossil Insect Database fossilworks, Paleobiology Database), with new ones continuing to be discovered and described (eg Zheng et al. 2016, Huang et al. 2017, 2018). These databases catalog fossil holotypes, taxonomy, and geology with an extensive bibliography.

Dated Phylogenies

Molecular data in conjunction with the fossil calibrations suggest Zygoptera diverged from Anisoptera in the Triassic (~226 Mya), although this story is complex and may not have been a clean split (Fig. 4) (Suvorov et al. 2021). Zygoptera began to diversify in the Jurassic with estimates for the origins of the extant superfamilies as follows: Platystictoidea arising in the late Jurassic, Lestoidea arising in the early Cretaceous, Coenagrionoidea arising in the Mid-Cretaceous, and Calopterygoidea arising in the late Cretaceous (Kohli et al. 2021; Suvorov et al. 2021). With such an extensive fossil record to select from, careful consideration needs to be taken when selecting fossils to use as calibration points. Previous work has been done to select crown fossils for Odonata (*Triassolestodes asiaticus* Pritykina, 198), Anisoptera (*Sinacymatophlebia mongolica* Nel and Huang, 2009) and Zygoptera (*Mersituria ludmilae* [Vasilenko, 2005]) but more work is needed to select optimal fossils for additional groups within Zygoptera (Kohli et al. 2016).

Discussion on Taxonomic Databases

The taxonomy for Odonata is published and maintained in the World Odonata List (Paulson et al. 2024), which is hosted on TaxonWorks through Odonata Central (Paulson et al. 2024). Regularly updated by a worldwide community of odonatologists, the list includes all known species, subspecies, and synonyms. Planned expansions will integrate additional taxonomic information, such as notes and country distributions.

Collections

Abbott and Sandall (2023) conducted a survey of the physical odonate collections at 13 institutions that possess at least 100 type specimens. Notable among these are the FSCA (~1.1 million specimens representing ~1,800 species and 178 types), the Naturalis Biodiversity Center (RMNH) (~200,000 samples and 964 types), and the Natural History Museum at London (NHMUK) (~110,000 samples and 1,289 types).

Citizen Science

In addition to physical collections, digital repositories play an important role in modern Odonatology. Numerous platforms exist (ie Odonata Central, African Dragonflies and Damselflies Online, Dragonflies and damselflies of Vietnam, Odonata of China, Dragonflies of India, iNaturalist) which allow community scientists to upload observations and photos, which can then be vetted by expert identifiers. These databases, along with museum collections and academic datasets, are aggregated by services like the Global Biodiversity Information Facility (GBIF) to provide a wealth of data for the odonate researcher. GBIF currently utilizes 581 datasets with entries for Zygoptera, which represent 38,981 preserved specimens and 49,409 observations.

Community databases, such as those mentioned above, offer substantial advantages, particularly in data quantity and geographic coverage, thanks to contributions from professional and citizen scientists (Bried et al. 2020). However, limitations exist regarding data quality control, species identification accuracy, and taxonomic resolution. While expert vetting helps mitigate these issues, there is an ongoing need for continuous curation and validation of entries to ensure scientific reliability. Such platforms are invaluable for large-scale biodiversity studies, species distribution mapping, and conservation efforts despite these challenges.

Genetic Resources

The genetic dimension of taxonomic research is supported by repositories like the National Center for Biotechnology Information (NCBI) GenBank, which hosts public genetic resources, such as 9 Zygoptera genome assemblies and 76,817 nucleotide sequences (Clark et al. 2015; Newton et al. 2023). Many journals require that genetic data used in published analyses be deposited in public repositories like NCBI to enhance transparency, reproducibility, and collaborative opportunities. Combining existing genetic data with new datasets, as demonstrated in a recent study (Willink et al. 2023), expands taxon sampling and minimizes duplicated efforts.

Conservation

For conservation assessments, the International Union for Conservation of Nature (IUCN) Red List evaluates Odonata species extensively. Of the 6,224 odonate species currently assessed for the Red List, 1,830 are classified as Data Deficient. In addition to its conservation assessments, the Red List also provides occurrence and trait data (IUCN 2024). Further trait data can also be found from resources such as the Odonate Phenotypic Database.

Regions in Need of Biodiversity Exploration and Documentation

Biodiversity exploration and survey coverage has historically been biased, for varying reasons, and numerous publications have highlighted potential causes and note regions where there are still gaps in biodiversity knowledge today (Dijkstra and Clausnitzer 2004; Paulson 2004; Wijesekara 2006, Kalkman et al. 2007, 2020, Dijkstra et al. 2011, 2013; Bota-Sierra et al. 2016; Brasil et al. 2021, Dow et al. 2024; Pires et al. 2024; Sumanapala 2024). The IUCN Red List assessment (2024) found that 16% of odonates are threatened with extinction, primarily due to the rapid decline and degradation of freshwater habitats. Many of these areas suffer from insufficient sampling efforts, leaving critical knowledge gaps in species distribution, taxonomy, and conservation status. Expanding survey coverage in these regions is important to better understand their biodiversity and develop effective conservation strategies before more species face extinction. Therefore, we aim to address the regions that urgently require biodiversity exploration and documentation. We focus on the gaps that occur in the Afrotropics, Australasia, Indomalaya, the Neotropics, and Oceania (Fig. 6).

Afrotropics

Currently, 760 species are described from mainland Africa and 227 from the Malagasy region (~80% endemic), but many areas are underinvestigated. Specifically, there is a need for exploration in areas where relict species are found (Dijkstra 2003). This includes areas such as the Western Highlands of Cameroon (*Pentaphlebia* Förster, 1909, *Neurolestes* Selys, 1882, *Nesolestes* Selys, 1891, *Nubiolestes* Fraser, 1945), eastern forests of Madagascar (*Libellulosoma* Martin, 1907, *Nesocordulia* McLachlan, 1882), South Africa (*Syncordulia* Selys, 1882), and Tanzania (*Amanipodagrion* Pinhey, 1962) (Dijkstra and Clausnitzer 2006). For example, the Cameroon Dragonfly Project expedition in 1995–1997 was the last major survey in the Western Highlands of Cameroon. However, a smaller recent expedition in the mountains of Nigeria recorded *Pentaphlebia stahli* Förster, 1909 and *Neurolestes trinervis* Selys, 1885 (Vries et al. 2024), but failed to record *Pentaphlebia gamblesi* Parr, 1977, which is only known from the holotype.

On a continental scale, Central Africa as a whole is the least explored region but also the most diverse and threatened. The highest proportion of IUCN Red List Data Deficient species in Africa (41.8%) are found within this region (Dijkstra et al. 2011, Bemah 2019).

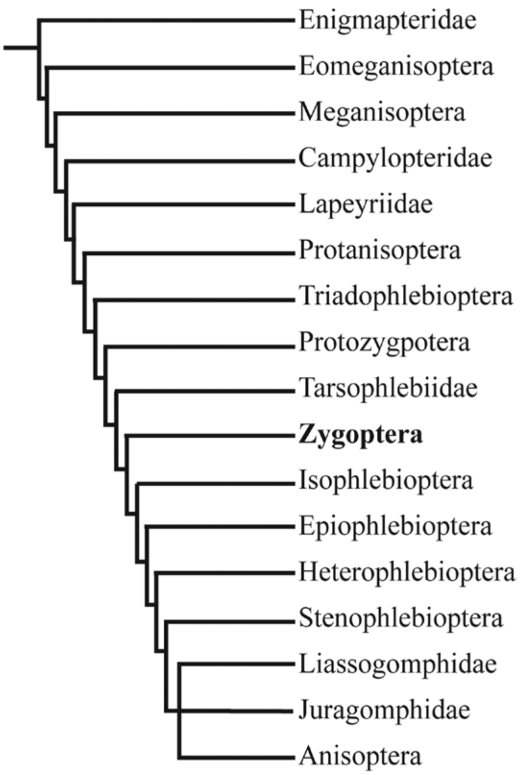


Fig. 5. Current hypothesis of Odonatoptera with focus on Paneodonatoptera reconstructed by hand from Nel and Bertrand (2023).

Additional areas with several listed Data Deficient species include Madagascar and islands in the Indian Ocean (Clausnitzer and Martens 2004; Suhling et al. 2015). More fieldwork in these areas will help provide more distribution records, establish an updated species range, and reassess their conservation status (Kalkman et al. 2007; Dijkstra et al. 2011). Other areas of priority include the Upper and Lower Guineas, West and South Congo Basin and Angolan Escarpments and Highlands, and the Albertine Rift (Dijkstra et al. 2011).

Recently, efforts have been made to publish data on the islands surrounding Africa, notably in the Malagasy region (Dijkstra and Cohen 2022); Príncipe, São Tomé, Annobón, and Cape Verde (Aistleitner et al. 2008, Martens 2010, 2013, Dijkstra et al. 2022). While this effort has increased our understanding of these islands, they are still underexplored in general.

Australasia

Wallacea, belonging to the Australasia realm, is one of the world's biodiversity hotspots and has high levels of endemism (Struebig et al. 2022). There are 270 odonate species in Wallacea (not including Papua and Papua New Guinea) (Dow et al. 2024). However, the number of odonate species in New Guinea alone has been estimated to be as high as 500 (Kalkman and Orr 2013; Orr and Kalkman 2015). The last new species from Sulawesi was described 6 years ago, and the types were from museum collections in the 1940s to late 1990s (Tol and Günther 2018). Sulawesi, Moluccas, Lesser Sunda Islands, and the Indonesian portion of Papua are still relatively poorly explored. Hence, biodiversity surveys that describe the patterns and ecology are valuable for these areas (Dow et al. 2024). Including taxa from Wallacea in phylogenetic studies of the broader odonates, especially for the complex biogeographical history of Sulawesi, will likely yield highly interesting results regarding their colonization of the region.

Indomalaya

The Indomalaya region ranges from the Indian subcontinent to South China, Mainland Southeast Asia up to the Philippines, and Sundaland in Indonesia. This area represents one-fifth of the world's diversity of flora and fauna. There are no exact numbers of described species of Odonates in Indomalaya, but according to Sánchez-Herrera and Ware (2012), the odonate diversity in the Oriental region (now called Indomalaya) is about 1,665 species. Sandall et al. (2022) compiled country level checklists of odonates that are depicted on the Map of Life (Jetz et al. 2012). The recent number of odonate species reported from the Indian subcontinent and adjacent countries is 559 species (Kalkman et al. 2020) and with Sundaland having 549 species (Dow et al. 2024), while the Philippines have 224 species (Hämäläinen and Müller 1997).

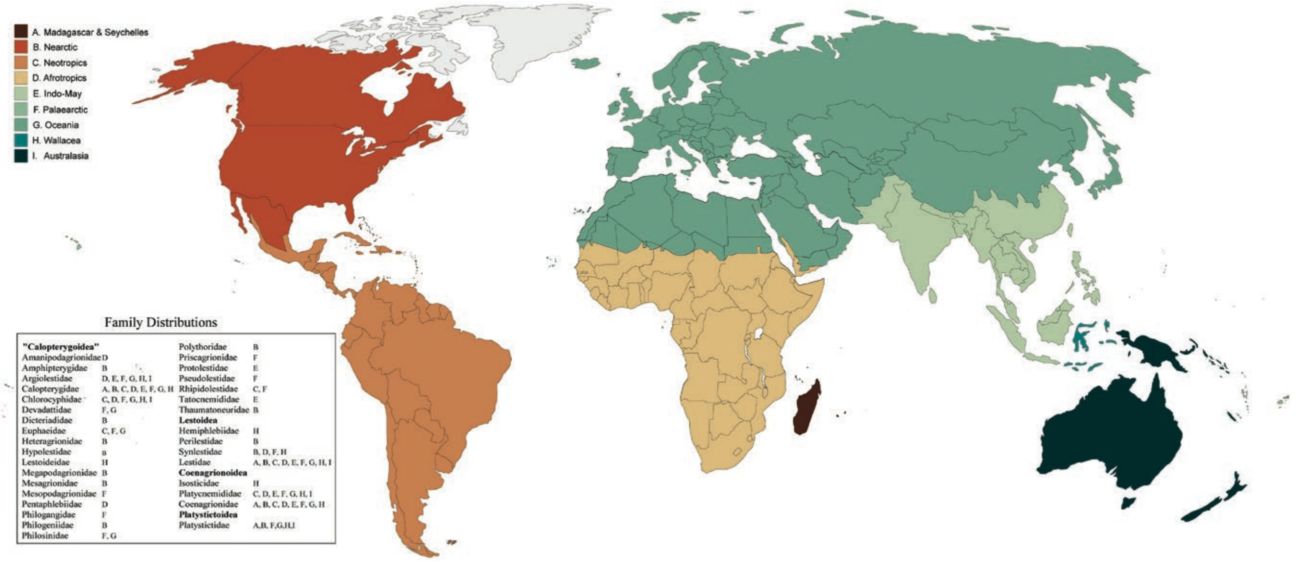
The Himalayas and China are regions that need expanded exploration. The Himalayas are formed by well-defined geographical barriers between the Afrotropical and Indomalaya regions (Kalkman et al. 2022). The border between the Palearctic and the Indomalaya region in China is located on the line between the Qin Mountains of southern Saanxi to the mouth of the Yangtze River, so this demarcation can test whether there is a clear disparity between the Palaeartic and Oriental fauna (Huang et al. 2020; Kalkman et al. 2022). In addition, Northeast India and the Himalayan area have the highest number of poorly known species and noted taxonomic issues. The adjacent Myanmar is likely the least studied country in Asia (Kalkman et al. 2020).

Sri Lanka, the Western Ghats, Pakistan, and northeast India still need more exploration. Many genera are difficult to identify due to a lack of taxonomic work (Kalkman et al. 2020). Moreover, a large issue for this region is the accessibility of type material. Type material is often unavailable for loan, under documented, and sometimes lost (Kalkman et al. 2020).

Both nymphs and adults of odonates in Sundaland also deserve more taxonomic work in species description, identification keys, and generic revisions (Kalkman et al. 2008; Dow et al. 2024). Lack of local expertise, lack of education in systematic entomology, expensive technology, accessibility to online depositories, accessibility to comprehensive literature collections (Wijesekara 2006; Sumanapala 2024), challenges in legislation for research and export of scientific material permits, security issues (some protected areas are inside conflict areas), and access to remote areas and islands create a gap of knowledge that are challenging to resolve.

Neotropics

The Neotropics contains 1,888 (29.5%) of all described odonate species (Neiss and Hamada 2014; Pessacq et al. 2018; Beatty et al. 2022; Paulson et al. 2024). All Zygoptera superfamilies occur in the Neotropics, with high endemism in the region (Neiss and Hamada 2014; Pessacq et al. 2018). Multiple families (ie Amphipteryridae, Dicteriadidae, Heteragrionidae, Hypolestidae, Megapodagrionidae, Mesagrioniidae, Neopetaliidae, Philogeniidae, Perilestidae, Polythoridae, Rimanellidae, and Thaumatoneuridae) are exclusively Neotropical, and families with broad distributions (eg Calopterygidae, Coenagrionidae, Lestidae, and Platystictidae) have exclusively Neotropical genera and species (Kalkman et al. 2008, Bybee et al. 2022). This region includes diverse geography, including mountain ranges, tropical rainforests, active volcanoes, large rivers, and complex drainage systems, providing heterogeneous habitat conditions that can contribute to diversification. Areas such as the Andes, the Atlantic forests, the Mexican Altiplano, the Amazon rainforest, and the Guyanese tepuis are known for extensive odonate diversification (Kalkman et al. 2008).



Family Distributions

"Calopterygoidea"		Polythoridae	B
Amanipodagrionidae	D	Priscagrionidae	F
Amphipterygidae	B	Protolestidae	E
Argiolestidae	D, E, F, G, H, I	Pseudolestidae	F
Calopterygidae	A, B, C, D, E, F, G, H	Rhipidolestidae	C, F
Chlorocyphidae	C, D, F, G, H, I	Tatocnemididae	E
Devadattidae	F, G	Thaumatoneuridae	B
Dicteriadidae	B	**Lestoidea**	
Euphaeidae	C, F, G	Hemiphlebiidae	H
Heteragrionidae	B	Perilestidae	B
Hypolestidae	B	Synlestidae	B, D, F, H
Lestoideidae	H	Lestidae	A, B, C, D, E, F, G, H, I
Megapodagrionidae	B	**Coenagrionoidea**	
Mesagrionidae	B	Isosticidae	H
Mesopodagrionidae	F	Platycnemididae	C, D, E, F, G, H, I
Pentaphlebiidae	D	Coenagrionidae	A, B, C, D, E, F, G, H
Philogangidae	F	**Platystictoidea**	
Philogeniidae	B	Platystictidae	A,B, F,G,H,I
Philosinidae	F, G		

Fig. 6. Biogeographic regions based on Newton et al. (in prep) and family-level distribution data.

Although the number of well-sampled locations has increased 15-fold over the past 5 decades, our understanding of Neotropical Zygoptera diversity, distribution, and biology is lacking (Juen and De Marco 2012; Beatty et al. 2022; Ferreira et al. 2023; Alves-Martins et al. 2024; Pires et al. 2024). Reliable information on species richness exists for only about 1% of the region, with notable knowledge gaps particularly evident in the Caribbean, Central America, northeastern Brazil, and northern Chile (Alves-Martins et al. 2024). For example, a recently published update of the Colombian Odonata checklist showed an increase of 233 new country species records in the 13 years since the last checklist publication, highlighting the historical gaps in Odonata records in the region (Bota-Sierra et al. 2024). Other specific regions in need of attention are the Pampas and the Amazon basin (Kalkman et al. 2008; Brasil et al. 2021; Renner et al. 2022; Ferreira et al. 2023; Pires et al. 2024). An assessment of the occurrence records for the Pampas showed that odonates were recorded in only 1.7% of grasslands (Pires et al. 2024). In addition to the study gaps, multiple species in the Neotropics are listed by the IUCN Red List as endangered or critically endangered, most of which are mountain forest specialist damselflies with narrow distributions (Bota-Sierra et al. 2021, 2016, IUCN 2024, Pires et al. 2024).

It is important to note that despite the knowledge gaps in the Neotropics, there have been recent local advancements in expertise and research. Recently, multiple new records have been documented for the Amazon region, shedding light on both the progress being made and the current gaps in knowledge (Garcia Junior et al. 2020; Koroiva et al. 2020; Stand-Pérez et al. 2021; Miranda Filho et al. 2022; Cano-Cobos et al. 2023; Gonçalves et al. 2023; Medina-Espinoza et al. 2024). New molecular data for Neotropical taxa not previously included in analyses have driven updated phylogenies (eg Polythoridae (Sánchez-Herrera et al. 2020) and Pseudostigmatidae (Ingley et al. 2012)). Completing the species lists and performing comprehensive studies of odonates in Neotropical countries remains vital to more fully characterize odonate diversity and monitor the status of populations and at risk species across the region (Bota-Sierra et al. 2016).

The creation of the Latin American Odonatology Society (SOL) represents a pivotal milestone for advancing Odonata studies in the Neotropics. Through its efforts, SOL has promoted the integration of researchers from various Latin American countries, fostering scientific collaborations and knowledge exchange. Additionally, society plays a crucial role in building cooperative networks and partnerships, providing opportunities for student and early career researcher exchanges, thereby strengthening regional research. As a result, SOL has been a key player in developing collaborative projects and expanding our knowledge of the biodiversity and conservation of Odonata, especially in underexplored areas with significant gaps in taxonomic and ecological studies.

Oceania

Oceania includes over 4,500 islands across the Pacific, with a total land area of 47,150 km². The isolation of these islands has resulted in highly endemic flora and fauna, including Zygoptera. Recent taxonomic work on Zygoptera in Oceania has led to the description of several new species (eg Englund and Polhemus 2010; Rivas-Torres et al. 2021; Saxton 2021; Beatty et al. 2023) and one new genus endemic to Fiji (Ferguson et al. 2023). Additional specimens collected from archipelagos such as the Marquesas, the Austral Islands, and the Society Islands need description (pers. comm. Jordan). These specimens may represent new species and/or genera endemic to their respective islands or archipelagos.

The Zygoptera of Oceania often have extraordinary ecology, morphology, behavior, and/or evolutionary and biogeographic histories (eg Polhemus and Asquith 1996; Polhemus 1997; Jordan et al. 2003; Lorenzo-Carballa et al. 2009; Saxton et al. 2023). Odonates across the Pacific, especially Zygoptera, may be more significant as bioindicators compared to Zygoptera on more biodiverse continents due to their specialized adaptations, and the lack of other traditional bioindicators, especially macroinvertebrates (Englund and Arakaki 2003). Unlike Anisoptera, oceanic species require running water making them a more informative island bioindicator.

Areas of Taxonomic Impediments and Challenges in Advancing Systematic Research

As the expertise and interest in Odonata biodiversity has grown, so has the ability to document the odonate species of the world and place them in an evolutionary context. Placing them in an evolutionary context is essential so that their taxonomy, natural history, behavior, ecology, systematics, and phylogenetics can be assessed simultaneously to test hypotheses related to systematics, as well as identify plausible drivers of their diversity. Yet as expertise in Odonata has grown, so have barriers that have thwarted what is the tantalizing possibility of all odonate species being placed in an evolutionary context.

International Laws and Regulations

Much needed laws enacted to protect biodiversity have also proven to be roadblocks to large-scale international collaboration and the overall spirit of scientific collaboration. We recognize the importance of laws and regulations, as well as the sovereignty of local scientists to have the priority of stewardship over the biodiversity of their countries (Sánchez Herrera et al. 2024). Currently there is an inability to share samples outside the researcher's country, nonexistent or difficult permit processes for both local and international researchers, and the lack of a mechanism or desire to work with local researchers, which inhibits collaboration efforts. Additionally, international travel has become more restricted. This may include scientists not being able to travel for workshops, conferences, lab exchanges, etc. where relationships are fostered and grow face-to-face. These examples, among others, offer a major challenge to the transfer of knowledge.

Natural History Collections

In consequence of dwindling administrative support, funding cuts, and the debates over the ethics of collecting, growth rate of natural history collections has sharply declined in recent years (Rohwer et al. 2022). Based on GBIF Odonata occurrence data for five northern institutions with prominent odonate collections (Naturalis Biodiversity Center; Smithsonian Institution, National Museum of Natural History; FSCA, The Museum of Entomology; Natural History Museum, London; Harvard University, MCZ), the number of Zygoptera specimens collected increased each decade from 1840 (excepting the decade after 1940), reaching a peak in the decade after 1960 (12,000 specimens) (Fig 7). The following decades have only attained one to two-thirds of that peak, but collection efforts have remained fairly consistent. However, only 55 Zygoptera samples collected from 2020 until July 2024 have so far been added to GBIF (*Occurrence Download* 2024). While there may be a time delay from the date of collection to digitization and submission to GBIF, this notable low count could be an effect of the COVID-19 pandemic, which surely impeded both sampling and archival efforts. Nonetheless, the lack of increase in natural history collections for Odonata species, and insects generally, is concerning.

On the other hand, although there is no such marked decline in the number of specimens collected in Latin America, there is a significant lack of funding for the proper functioning of its scientific collections. The most striking example of this is, undoubtedly, the fire in 2018 at the National Museum of Rio de Janeiro in Brazil, which destroyed thousands of odonates and approximately 450 type specimens (Loaiza and Anjos-Santos 2019), an immeasurable loss for Neotropical odonatology. Although the growth of local research groups and specialists has allowed the expansion of odonatological collections in Latin America (eg Anjos-Santos 2019; Cano-Cobos et al. 2022; Mendoza-Penagos et al. 2022; Navarro et al. 2024), the absence of clear and sustained science funding policies in each country continues to hinder the advancement of neotropical odonatology.

For taxonomists in developing countries, accessing type material is challenging, as most of it is stored in foreign institutions. Shipping valuable specimens internationally is risky and generally avoided by institutions. This creates significant barriers to conducting taxonomic work and increases the risk of taxonomic mistakes due to the lack of access to type series. Thus, type material is often not available where it is most needed. The current efforts to digitize specimens (see below) might help to overcome this problem.

Natural history collection research has historically revolved around taxonomy and systematics, but data from collections have more recently been utilized, for example, to generate genomic resources, analyze and predict the progression of climate change, and observe changes in phenotypic traits (Kharouba et al. 2018). Wing scans from museum samples are used to train machine learning models for automated classification (Sáenz Oviedo et al. 2022), while occurrence data are used to generate species distribution models and estimate odonate diversity (Abbott et al. 2022; Kalkman et al. 2022). Digitization also improves access for the scientific community and preserves data about irreplaceable type specimens against the threat of natural disasters or loss of funding (De Almeida et al. 2021). However, it is estimated that less than 5% of North American arthropod specimens have digitized records, and less than 1% have associated images (Cobb et al. 2019). Citizen science platforms like iNaturalist have demonstrated utility as free, externally funded, out-of-the-box services for managing collection associated data (eg digital photographs and geographic coordinates) (Heberling and Isaac 2018). Convolutional neural networks have also been trained on odonate images to provide a method of automated species determination (Theivaprakasham et al. 2022), which could be utilized by collections with limited financial and human capital to clear backlogs of unidentified specimens.

Future of Zygoptera Systematics

Clarifying and resolving the systematics of Zygoptera relies on 3 main areas of work: (i) descriptive work, including alpha taxonomy, biology, and distribution, (ii) phylogenetic analysis, based in both morphological and/or molecular data, and (iii) classification, including beta taxonomy and revision. Success in each of these 3 areas will require collaborative curation, databasing, and organization and will facilitate the evaluation of evolutionary hypotheses, including diversification, trait evolution, biogeography, and much more.

Descriptive Work

Zygoptera is a relatively well-described group of insects; there are currently 3,322 described species of damselflies (Paulson et al. 2024). At the current rate of description, 95% of the estimated 7,000 odonate species will be described by 2030 (Kalkman et al. 2008). Nevertheless, extensive work remains to complete species descriptions for the remaining undescribed species, especially in understudied regions mentioned above.

Most species descriptions are based on adult males, and there are, by comparison, extremely few descriptions for adult females and nymphs. For example, in the Neotropics, only the nymphs of about 75% genera and 40% of the species have been described, and many of these descriptions are overly brief and need to be updated (Pessacq et al. 2018). Nymph descriptions are especially important due to their presence in freshwater ecosystems, potential as bioindicator taxa, and their ecological roles as both predatory and prey in food webs. Characters used to define some species and genera may be unstable or not true synapomorphies in the strictest sense. In these cases, stable, distinguishing synapomorphies should be identified and described (eg Pinto et al. 2022). Sound nymph and adult female descriptions will allow the use of nymph and adult female specimens in future studies. Nymphs and females are especially important to understanding the behavior and ecology of odonates.

Aside from field work to collect undescribed specimens, there are many specimens in museums and personal collections that await description and further study. Inventory, digitization, and additional study of existing data from these collections will help complete species descriptions for Zygoptera and identify taxonomic and geographic areas that require additional exploration. Fossil collections should also be reexamined as new discoveries may highlight previously obscure synapomorphies. As species descriptions continue, identification keys must also be updated and tested to ensure consistent functionality.

Alpha taxonomy, new species descriptions, likely make up a small portion of the descriptive work remaining for Zygoptera. To complement the remaining descriptive work, the natural history, ecology, distribution, and behavior of each species should be a major focus. This information will provide the ability to test evolutionary hypotheses of animal evolution generally and odonate evolution specifically. It may also yield useful characters for keys, identification, classification, and phylogenetic analyses (Waller et al. 2019). Recent efforts (eg Abbott et al. 2022; Kalkman et al. 2022) have widely improved distribution data and provided ecological niche modeling/species distribution models for Palearctic and Nearctic odonates. Alves- Martins et al. (2024) address the study of data quality on the distribution and diversity of odonate species in the Neotropical region and examine the influence of sampling completeness on climate–richness relationships. Similar studies of Zygoptera distribution and ecology in the Neotropics, Afrotropics, Asia, Australasia, and Oceania are in progress.

Phylogenetics

In the age of genomics and high-performance computing, phylogenetic analyses that include more taxa and more data are becoming more feasible, common, and accessible. The GEODE (Genealogy & Ecology of Odonata) group is a multidisciplinary effort involving scientists worldwide, with a goal of using targeted enrichment to sequence two-thirds of Zygoptera species for ~20,000 base pairs. One representative of each genus will also have expanded sequencing of ~500,000 base pairs. These sequences will be used to reconstruct phylogenetic estimates and test evolutionary questions across Zygoptera. Determining the phylogenetic placement of the remaining species of Zygoptera will involve a continuing effort to gather specimens and use similar sequencing techniques and Sanger data with bioinformatic tools to add them to a comprehensive phylogeny of Zygoptera. As these efforts coalesce with Anisoptera, Odonata will become an insect order with one of the most complete extant species-level phylogenies. Moreover, taxonomic and evolutionary hypotheses will be testable at a resolution not previously possible across any diverse insect order. These phylogenetic efforts, as well as follow-up efforts to include the remaining species and newly described species, will lay a firm foundation for taxonomic revision.

Additional work will be needed to fully explore the validity of the taxonomy of currently described species. Species delimitation may be in need of reexamination across the suborder. Some issues are more obvious, such as paraphyly in recent phylogenetic analyses (Zhang et al. 2021), while others are more nuanced. For example, widespread species with several distinct populations may represent multiple species, or subspecies that have been described based on geography or morphology may be distinct species. These hypotheses can be tested in a phylogenetic context including multiple representatives within each species, subspecies, or population under question to determine whether to raise subspecies or populations to species status, or whether several populations or subspecies are indeed members of the same species. In addition, despite the extensive database of damselfly fossils and their use to calibrate phylogenetic analyses (Kohli et al. 2016; Suvorov et al. 2016, 2021), only a fraction of these fossils have been included as taxa in phylogenetic analysis (Bybee et al. 2008). Including fossils as taxa in phylogenetic analyses will allow us to test taxonomic hypotheses and integrate the systematics of extant and extinct Zygoptera.

Classification

Phylogenetic insights in recent decades have revealed paraphyly in some families, genera, and species (eg Dijkstra et al. 2014a; Bybee et al. 2021; Suvorov et al. 2021; Zhang et al. 2021). In many cases, these issues can be resolved by moving some species or genera to the most appropriate taxonomic group. Occasionally, describing new species, genera, or families is practical or necessary. Fossil taxa also warrant description of new genera or families and a phylogenetic test of monophyly. By testing taxonomic hypotheses in a phylogenetic framework, we can develop an evidence-based and integrated classification system for both extinct and extant Zygoptera that reflects evolutionary history and relationships.

The World Odonata List provides a comprehensive and frequently updated taxonomic list of Zygoptera worldwide (Paulson 2004). Continuing to update this list will be paramount to making progress in the 3 areas previously described. In addition, the inventory, preservation, and databasing of type specimens will be a critical endeavor to ensure the future success of zygopteran systematics. Collaboration between collections maintained by governments, individuals, and academic and private institutions will be necessary to successfully describe and classify all damselflies and to maintain efficiency in research projects testing evolutionary hypotheses. The future of Odonata systematics will involve extensive curation of existing specimens, holistic descriptions of ecology, biology, distribution, and behavior, and a strong focus on both morphological phylogenetics and phylogenomics. With this wealth of well-curated data, the unique properties of Zygoptera will provide an intriguing insect model for testing evolutionary hypotheses of flight, vision, biogeography, and early insect evolution (Bybee et al. 2016).

Author contributions

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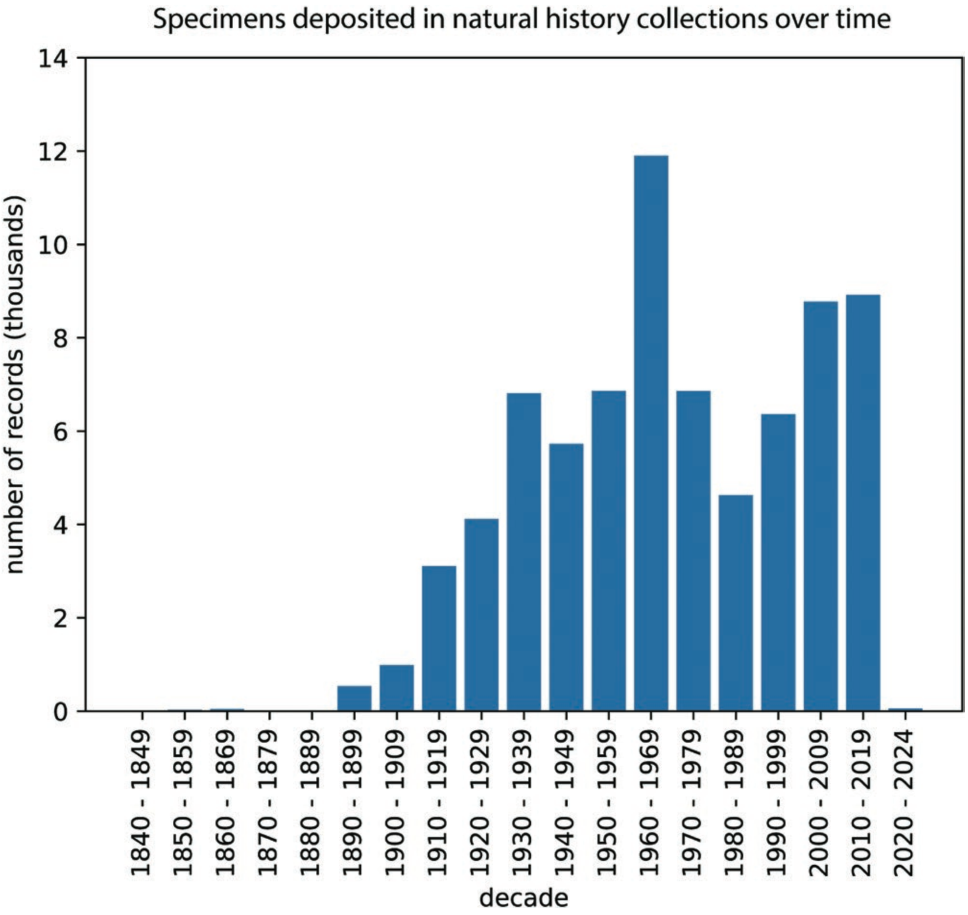

Fig. 7. Number of specimens that were added to the five major odonate collections (Naturalis Biodiversity Center; Smithsonian Institution, National Museum of Natural History; FSCA, The Museum of Entomology; Natural History Museum, London; Harvard University, MCZ) over time.

(Writing—review & editing [equal]), Ying Fei Lin (Writing—review & editing [equal]), Judicael Fomekong Lontchi (Writing—original draft [supporting], Writing—review & editing [equal]), Pungki Lupiyaningdyah (Writing—original draft [supporting], Writing—review & editing [equal]), Lacie Newton (Writing—review & editing [equal]), Violet Onsongo (Writing—review & editing [equal]), Pablo Pessacq (Writing—review & editing [equal]), Melissa Sanchez-Herrera (Writing—review & editing [equal]), Rosa Ana Sanchez Guillen (Writing—review & editing [equal]), Ken Tennessen (Writing—review & editing [equal]), Ethan Tolman (Writing—review & editing [equal]), Jessica Ware (Writing—review & editing [equal]), Maren Wellenreuther (Writing—review & editing [equal]), and Seth Bybee (Conceptualization [equal], Project administration [equal], Supervision [equal], Writing—review & editing [equal])

Supplementary material

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