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Review

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Molecular Phylogenetics, Phylogenomics, and Phylogeography

Odonata systematics: past, present, and future: a review of the phylogenetic works in Anisoptera (dragonflies)

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Odonata is an insect order that comprises ~6420 described species distributed among three suborders. Here we review the dragonflies, or Anisoptera, a suborder which has 10 described families, and forms a sister group relationship with the 'Anisozygoptera' [Epiprocta: Anisoptera + 'Anisozygoptera'], a paraphyletic grouping containing just one extant family and many extinct taxa. Dragonflies are charismatic, ancient, fast flying, predatory insects whose natural history is woven into the fabric of human culture. As objects of systematic study, their relative position in the insect tree of life relates to the origin of flight, of freshwater juvenile lifestyles, and the evolution of color and vision. In this paper, we will review the past, present, and future of Odonatology, highlighting the work being done all across the globe to revise and define the suborder Anisoptera. In particular, we focus on 'problematic' areas in the tree, the Gomphidae and Libellulidae, with an emphasis on how taxon and data sampling are solving these problems in the current global work.

Keywords: morphology, genomics, nymph, ecology, phylogeny, biogeography.

Odonata: life cycle, natural history, and a brief overview of their study

Dragonflies in freshwater

Dragonflies are ubiquitous insects that require freshwater for part of their life cycle, but they are found globally in forests, urban settings, and deserts, in tropical climates, and in the arctic. Dragonfly nymphs develop in freshwater from eggs laid either in plant or substrate material (endophytically) or directly into the water (exophytically). Unlike in Zygoptera, a majority of Anisoptera species (those found in Gomphidae and Libelluloidea) oviposit into water or mud directly, exophytically; both Gomphidae and Libelluloidea have reduced or vestigial ovipositors. Dragonfly eggs are often surrounded by jelly-like substances, especially in exophytically laid eggs (e.g., Sahlén 1995). The development time of dragonfly nymphs varies dramatically among taxa, with *Pantala flavescens* (Fabricius 1798) developing over a couple of weeks (Suhling et al. 2004) while some species of *Tanypteryx* Kennedy 1917, *Cordulegaster* Leach 1815, *Epiophlebia* Tillyard 1917, or *Somatochlora* Selys 1871 may take > 8 years (eg Asahina 1982, Baird 2012). Dragonfly nymphs breathe underwater using a so-called rectal chamber (Mill and Pickard 1972) which can double in its function to be used for jet propulsion mainly as an escape behavior (eg Corbet 1999). As in all Odonata, dragonfly nymphs climb from the water and cling to the substrate or vegetation while the adult emerges from the exuvia (Corbet 1962, 1999, Smallshire and Swash 2014, Büsse et al. 2019).

Dragonflies and humans

Across cultures, dragonflies feature commonly in human storytelling, art and culture. Examples include 10,000 year old paintings by the San people of migratory swarms of dragonflies in South Africa (Green et al. 2007) and 17th century Japanese Samurai military helmets with dragonfly adornments (eg Su 2022); see Sarot (1958) and Corbet (1991) for a review of other cultural references to dragonflies. Anisoptera have been named in several early writings; the word 'dragonfly' or its local translation is a word believed to be in the 5000 year old 'Epic of Gilgamesh', and is featured in ~3000 year old Sumerian texts of the Hubulla (Harpaz 1973). There are several names for dragonflies in global languages, suggesting a human history distinguishing these animals from other insects before more formal taxonomy of Anisoptera was underway: for example, gwaell y neidr (Welsh for 'Adder's knitting needle'; Montgomery 1972), Kapokapowai (Māori for 'Water Snatcher': Grant 2014).

A history of dragonfly description

The scientific study of dragonflies began with Linnaeus in 1757, who described the genus *Libellula* Selys 1840, in which he recognized 18 species (eg Abbott and Sandall 2023) that he considered to be in the order Neuroptera (Table 1 reviews the chronology of Anisoptera workers from around the globe who have been describing dragonflies using scientific names). The Danish zoologist Fabricius proposed new genera such as *Aeshna*, *Agrion* and later erected the order Odonata (1775, 1793). Many taxonomic and classification changes were proposed through the 1700 and 1800s (eg Leach 1815, Burmeister 1839, Say 1839, Selys de Longchamps 1840, Rambur 1842, Kirby 1890), and common names used by indigenous and local people were largely not associated with proposed scientific names so many were forgotten over time.

In the 20th century, the classification of Odonata began to take shape. While the fossil literature is rich, we focus here on extant taxa. Traditionally, odonatology workers used morphological data for taxonomic and systematic analyses. The earliest works were by Tillyard (1917) and Fraser (1957), who predominantly used wing venation to reconstruct inter-familial relationships—these early works form the basis of most morphological characters presently in use. Further morphological studies of odonate phylogeny also relied heavily on wing vein characters (eg Kirby 1890, Needham 1903, Martin 1907, Tillyard 1910, Ris 1919, Fraser 1957, Gloyd 1959, Geijskes 1970, Lieftinck 1971, Theischinger and Watson 1978, Jarzembowski and Nel 1996, Rehn 2003, Bybee et al. 2008, Pilgrim and Von Dohlen 2008). Foundational papers later established modern wing venation terminology (eg Riek and Kukalová-Peck 1984, Nel et al. 1993, Bechly 1996, Trueman and Rowe 2019); of these, Riek and Kukoalova-Peck is the most commonly used. Some studies incorporated, or focused on, specific traits of the egg, nymph, genitalia, head internal morphology, flight musculature, and color (eg St. Quentin 1939, Gloyd 1959, Theischinger and Watson 1978, Pfau 1991, 2005, May 1995, Lohmann 1996a, b, Blanke et al. 2012). Primarily these studies focused on the adult stage, and to a lesser extent on the nymph stage, while morphological studies assessing eggs were even rarer. When only morphological data were used for systematic analyses, there was considerable debate about the relative positions of the families of Anisoptera (ie, Aeshnidae, Petaluridae, Gomphidae, Cordulegastridae, Chlorogomphidae and the superfamily Libelluloidea (comprising Synthemistidae, Corduliidae, Macromiidae and Libellulidae). Head characters supported Petaluridae + Aeshnidae as sister to the remaining groups (Blanke, et al. 2013), while wing characters often placed Aeshnidae as sister to the remaining families (see Ware et al.

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Table 1: Chronology Table of species authors of Anisoptera with number of species that the author described and the years they were actively describing species, sorted by region of author origin, country, and author name

Author	Number of species described	Time period of activity	Home region	
Mens	1	2016	Ghana	Africa
Luke	1	2015	Kenya	Africa
Couteyen	1	2009	Mauritius	Africa
Desjardins	2	1832–1835	Mauritius	Africa
Diedericks	1	2015	South Africa	Africa
Marais	1	2010	South Africa	Africa
Samways	2	2007	South Africa	Africa
Kisakye	1	2004	Uganda	Africa
Bao	1	2002	China	Asia
Cai	17	2013–2016	China	Asia
Cao	2	1988–1989	China	Asia
Chao	55	1953–1999	China	Asia
Chen, C.	2	1950	China	Asia
Chen, J.	6	2005–2020	China	Asia
Guan	1	2017	China	Asia
Han	2	1997	China	Asia
Hong	2	1999–2001	China	Asia
Hu	1	2023	China	Asia
Lee	1	2015	China	Asia
Li	7	1988–2022	China	Asia
Liao	3	2013	China	Asia
Liu	14	1985–-994	China	Asia
Lu	2	2005	China	Asia
Luo	1	1993	China	Asia
Mao	2	2006–2010	China	Asia
Qiu	1	2009	China	Asia
Shuai	3	1994	China	Asia
Tang	1	2013	China	Asia
Tong	3	2009–2010	China	Asia
Wang	5	1990–2017	China	Asia
Wei	2	1979–1980	China	Asia
Wong	1	2015	China	Asia
Wu	7	1985–2007	China	Asia
Xu	9	1987–2012	China	Asia
Yan	2	1988	China	Asia
Yang	11	1993–2019	China	Asia
Yu	1	2022	China	Asia
Zhang	26	1999–2017	China	Asia
Zheng	2	1988–1989	China	Asia
Zhou	22	1979–2005	China	Asia
Zhu	12	1985–2007	China	Asia
Babu	2	2019–2020	India	Asia
Chandran	1	2023	India	Asia
Chhotani	2	1983	India	Asia
Dalvi	1	2024	India	Asia
Dawn	2	2021–2024	India	Asia

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Table 1. Continued

Author	Number of species described	Time period of activity	Home region	
Dharwadkar	1	2019	India	Asia
Joshi	5	2017–2020	India	Asia
Kambli	1	2023	India	Asia
Khan	1	2021	India	Asia
Koli	1	2024	India	Asia
Kunte	2	2017	India	Asia
Lahiri	6	1975–2007	India	Asia
Mital	1	2022	India	Asia
Mitra	4	1975–1994	India	Asia
Naik	1	2013	India	Asia
Ram	2	1985	India	Asia
Rangnekar	2	2013–2019	India	Asia
Sadasivan	1	2019	India	Asia
Sandhu	1	2007	India	Asia
Sawant	3	2020–2023	India	Asia
Subramanian	5	2013–2020	India	Asia
Thakur	1	2024	India	Asia
Veenakumari	1	2000	India	Asia
Walia	1	2007	India	Asia
Yousuf	4	1976–1977	India	Asia
Asahina	58	1940–1997	Japan	Asia
Doi	2	1937–1945	Japan	Asia
Futahashi	3	2021	Japan	Asia
Inoue	1	2001	Japan	Asia
Karube	59	1994–2022	Japan	Asia
Katatani	5	2012–2019	Japan	Asia
Matsuki	1	1995	Japan	Asia
Matsumura	6	1926–1935	Japan	Asia
Mitamura	1	2002	Japan	Asia
Oguma	13	1913–1926	Japan	Asia
Okumura	4	1949	Japan	Asia
Sasamoto	7	2001–2021	Japan	Asia
Teramoto	2	2011–2015	Japan	Asia
Toko	2	2017	Japan	Asia
Yokoi	7	2002–2020	Japan	Asia
Yokota	1	2001	Japan	Asia
Ishida	4	1964–1996	Japan	Asia
Kiyoshi	4	2015–2018	Japan	Asia
Saito	1	1995	Japan	Asia
Ri	1	2001	Korea	Asia
Souphanthong	2	2019–2020	Laos	Asia
Choong	3	2007–2017	Malaysia	Asia
Dow	9	2007–2020	Malaysia	Asia
Yunus	4	1976–1977	Malaysia	Asia

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Table 1. Continued

Author	Number of species described	Time period of activity	Home region	
Limbu	1	2018	Nepal	Asia
Gyger	8	1937–1941	Philippines	Asia
Villanueva	4	2012–2022	Philippines	Asia
Bartenev	9	1909–1929	Russia	Asia
Borisov	1	1983	Russia	Asia
Djakonov	1	1926	Russia	Asia
Eversmann	1	1836	Russia	Asia
Kosterin	9	2012–2023	Russia	Asia
Snegovaya	2	2021	Russia	Asia
Ngiam	4	2011–2017	Singapore	Asia
Simaika	2	2007	South Africa	Asia
Bae	1	2020	South Korea	Asia
Conniff	1	2018	Sri Lanka	Asia
Sumanapala	1	2021	Sri Lanka	Asia
Hwang	1	1999	Taiwan	Asia
Yeh	11	1999–2016	Taiwan	Asia
Boonsoong	1	2020	Thailand	Asia
Chainthong	1	2020	Thailand	Asia
Dawwrueng	1	2012	Thailand	Asia
Keetapithchayakul	1	2022	Thailand	Asia
Makbun	8	2012–2023	Thailand	Asia
Wongkamhaeng	1	2022	Thailand	Asia
Anh	1	2021	Viet Nam	Asia
Do	3	2005–2011	VietNam	Asia
Hung	1	2021	VietNam	Asia
Ngo	1	2020	VietNam	Asia
Nguyen	1	2021	VietNam	Asia
Phan	7	2020–2022	VietNam	Asia
Tam	1	2003	Vietnam	Asia
Vu	3	2018–2021	VietNam	Asia
Arthington	1	1978	Australia	Australia/NZ
Brown	1	1998	Australia	Australia/NZ
Davies	5	1993–2002	Australia	Australia/NZ
Ferguson	1	1950	Australia	Australia/NZ
Harvey	1	1898	Australia	Australia/NZ
Moulds	1	1985	Australia	Australia/NZ
Orr	4	2007–2015	Australia	Australia/NZ
Reels	3	2001	Australia	Australia/NZ
Theischinger	63	1973–2020	Australia	Australia/NZ
Tillyard	51	1906–1926	Australia	Australia/NZ
Tough	1	1900	Australia	Australia/NZ
Watson	31	1958–1995	Australia	Australia/NZ
White	2	1843–1846	Australia	Australia/NZ
Rowe	1	2019	New Zealand	Australia/NZ
Winstanley	1	1984	New Zealand	Australia/NZ
Haber	6	2015–2022	Costa Rica	Central America

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Table 1. Continued

Author	Number of species described	Time period of activity	Home region	
Gundlach	2	1888–1889	Cuba	Central America
Brauer	44	1864–1900	Austria	Europe
Aguesse	1	1966	Belgium	Europe
Cammaerts	11	1967–2004	Belgium	Europe
Dumont	4	1977–2023	Belgium	Europe
Hellebuyck	1	2002	Belgium	Europe
Schouteden	17	1917–1934	Belgium	Europe
Selys	303	1839–1900	Belgium	Europe
Vander Linden	6	1820–1825	Belgium	Europe
Vierstraete	4	2015–2023	Belgium	Europe
Marinov	8	2001–2020	Bulgaria, New Zealand	Europe
Kolenati	1	1846	Czech Republic	Europe
Fabricius	20	1775–1798	Denmark	Europe
Müller, O.F.	6	1764–1767	Denmark	Europe
Nielsen	1	1935	Denmark	Europe
St. Quentin	5	1936–1973	England	Europe
Barona	1	2020	Europe	Europe
Hämäläinen	9	1985–2002	Finland	Europe
Blanchard	1	1843	France	Europe
Boisduval	1	1835	France	Europe
Brullé	1	1832	France	Europe
Fleck	11	2009–2024	France	Europe
Fonscolombe	2	1837–1838	France	Europe
Gaschignard	1	2017	France	Europe
Gauthier	4	1987–1988	France	Europe
Geoffroy	1	1785	France	Europe
Lachaise	1	2001	France	Europe
Lacroix	6	1920–1921	France	Europe
Latreille	1	1805	France	Europe
Legrand	24	1975–2003	France	Europe
Machet	2	1990	France	Europe
Martin	83	1895–1921	France	Europe
Mézière	13	2015	France	Europe
Minot	1	2017	France	Europe
Nicolas	1	2022	France	Europe
Palisot de Beauvois	5	1807–1817	France	Europe
Paulian	1	1960	France	Europe
Rambur	87	1842–	France	Europe
Robert	1	1954	France	Europe
Buchholz	3	1950–1953	Germany	Europe
Charpentier	6	1825–1840	Germany	Europe
Clausnitzer	3	2005–2015	Germany	Europe
Damm	2	2009	Germany	Europe
Erichson	6	1848	Germany	Europe
Förster	43	1898–1914	Germany	Europe
Grünberg	4	1902	Germany	Europe

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Table 1. Continued

Author	Number of species described	Time period of activity	Home region	
Hadrys	2	2009	Germany	Europe
Ikemeyer	2	2021	Germany	Europe
Jödicke	1	1994	Germany	Europe
Jurzitza	1	1979	Germany	Europe
Karsch	59	1889–1903	Germany	Europe
Kaup	2	1866	Germany	Europe
Kipping	10	2010–2015	Germany	Europe
Knopf	2	1980	Germany	Europe
Krüger	11	1898–1902	Germany	Europe
Lempert	2	1999–2015	Germany	Europe
Lohmann	10	1981–1993	Germany	Europe
Müller, O.	3	1993–2021	Germany	Europe
Oppel	1	2012	Germany	Europe
Peters	2	1991–2011	Germany	Europe
Schmidt	11	1934–1961	Germany	Europe
Schneider, E.	2	1984–2015	Germany	Europe
Schneider, J.	1	2015	Germany	Europe
Schneider, T.	3	2015–2021	Germany	Europe
Schneider, W.	5	1845	Germany	Europe
Schütte	1	2016	German	Europe
Seehausen	2	2016–2024	Germany	Europe
Ström	1	1783	Germany	Europe
Suhling	1	2020	Germany	Europe
Wagner	1	2015	Germany	Europe
Hagen	127	1854–1890	Germany, United States	Europe
Burmeister	50	1839	Germany/ Argentina	Europe
Kovács	2	2015–2016	Hungary	Europe
Donovan	1	1807	Ireland	Europe
Carfi	1	1997	Italy	Europe
Carletti	1	2001	Italy	Europe
Consiglio	1	1978	Italy	Europe
D'Andrea	1	1997	Italy	Europe
Marconi	1	2001	Italy	Europe
Terzani	1	2001	Italy	Europe
Albarda	1	1881	Netherlands	Europe
Belle	115	1964–1995	Netherlands	Europe
Caspers	2	2021	Netherlands	Europe
Dijkstra	51	2004–2015	Netherlands	Europe
Geijskes	10	1931–1984	Netherlands	Europe
Kalkman	4	2008–2015	Netherlands	Europe
Kompier	20	2015–2021	Netherlands	Europe
Lieftinck	189	1926–1977	Netherlands	Europe
Pinhey	47	1950–1981	Netherlands	Europe
Stokvis	3	2016–2017	Netherlands	Europe
Van Beijnen	1	2022	Netherlands	Europe
van Tol	8	1987–1997	Netherlands	Europe

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Table 1. Continued

Author	Number of species described	Time period of activity	Home region	
Waterston	2	1976–1985	Scotland	Europe
Bedjanič	2	2013–2020	Slovenia	Europe
Díaz	1	2020	Spain	Europe
Navás	15	1916–1936	Spain	Europe
de Geer	1	1773	Sweden	Europe
Linnaeus	16	1758–1763	Sweden	Europe
Sjöstedt	15	1900–1933	Sweden	Europe
Trybom	1	1889	Sweden	Europe
Zetterstedt	1	1840	Sweden	Europe
De Marmels	28	1981–2017	Switzerland	Europe
Juillerat	1	2019	Switzerland	Europe
Perty	2	1834	Switzerland	Europe
Pictet	1	1843	Switzerland	Europe
Ris	144	1897–1931	Switzerland	Europe
Sartori	1	2020	Switzerland	Europe
Sulzer	2	1776	Switzerland	Europe
Balinsky	3	1961–1965	Ukraine	Europe
Barnard	2	1933–1937	United Kingdom	Europe
Brooks	3	1989	United Kingdom	Europe
Campion	10	1915–1928	United Kingdom	Europe
Dale	1	1834	United Kingdom	Europe
Davis	2	1921–1927	United Kingdom	Europe
Drury	12	1773	United Kingdom	Europe
Kimmins	11	1929–1958	United Kingdom	Europe
Kirby	55	1889–1909	United Kingdom	Europe
Laidlaw	37	1902–1936	United Kingdom	Europe
Leach	2	1815	United Kingdom	Europe
Lindley	3	1970–1980	United Kingdom	Europe
Longfield	9	1932–1955	United Kingdom	Europe
McLachlan	28	1870–1898	United Kingdom	Europe
Nunney	1	1895	United Kingdom	Europe
Price	1	2020	United Kingdom	Europe
Pritchard	2	1935	United Kingdom	Europe
Richards	14	2011–2020	United Kingdom	Europe
Vick	7	1988–2006	United Kingdom	Europe
Waterhouse	1	1877	United Kingdom	Europe
Westwood	1	1837	United Kingdom	Europe
Wilson	18	1993–2008	United Kingdom	Europe
Gambles	7	1956–1979	United Kingdom	Europe
Fraser	184	1918–1962	United Kingdom and India	Europe
Morton	7	1916–1929	United Kingdom, Scotland	Europe
Brunelle	1	2000	Canada	North America
Cannings	1	1991	Canada	North America
Currie	2	1901–1917	Canada	North America
Provancher	1	1875	Canada	North America
van der Poorten	1	2009	Canada	North America
Walker	11	1907–1940	Canada	North America

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Table 1. Continued

Author	Number of species described	Time period of activity	Home region	
De La Rosa	1	2015	Mexico	North America
González–Soriano	12	1986–2020	Mexico	North America
Novelo–Gutiérrez	13	1990–2020	Mexico	North America
Ogale	1	2022	Mexico	North America
Ortega–Salas	2	2015–2018	Mexico	North America
Villeda–Callejas	1	2000	Mexico	North America
Walsh	9	1862–1863	United Kingdom, United States	North America
Cook	6	1984–2004	United States	North America
Fisher	1	1939	United States	North America
Westfall	9	1943–2000	United States	North America
Abbott	1	2011	United States	North America
Bailowitz	1	2013	United States	North America
Banks	1	1896	United States	North America
Bird	1	1933	United States	North America
Borror	25	1931–1957	United States	North America
Bromley	1	1924	United States	North America
Bybee	1	2020	United States	North America
Byers	2	1934–1939	United States	North America
Calvert	88	1890–1958	United States	North America
Carle	11	1979–1987	United States	North America
Carpenter	1	1897	United States	North America
Daigle	2	1985–1996	United States	North America
Danforth	1	2013	United States	North America
Donnelly	14	1961–1992	United States	North America
Dunkle	6	1982–1992	United States	North America
Garrison	13	1982–2008	United States	North America
Gloyd	7	1933–1944	United States	North America
Hibbitts	1	2011	United States	North America
Hodges	1	1955	United States	North America
Holden	2	2017–2021	United States	North America
Kennedy	9	191–1946	United States	North America
Klots	4	1944–1947	United States	North America
Laudermilk	1	2004	United States	North America
May	4	1987–2000	United States	North America
Michalski	1	2012	United States	North America
Montgomery	6	1940–1943	United States	North America
Morse	1	1895	United States	North America
Muttkowski	1	1911	United States	North America
Needham	72	1897–1937	United States	North America
Packard	1	1863	United States	North America
Paulson	4	1983–2005	United States	North America
Rehn	1	2003	United States	North America
Say	18	1840	United States	North America
Scudder	6	1866	United States	North America
Smith	1	1993	United States	North America
Tennessen	9	1983–2024	United States	North America
Uhler	5	1857–1858	United States	North America

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Table 1. Continued

Author	Number of species described	Time period of activity	Home region	
Upson	1	2013	United States	North America
van Pelt	2	2021	United States	North America
Vogt	3	1993–2004	United States	North America
Williamson	38	1902–1933	United States	North America
Hine	1	1901	United States	North America
Cardo	1	2020	Argentina	South America
Del Palacio	1	2020	Argentina	South America
Etcheverry	1	1956	Argentina	South America
Muzón	5	2001–2020	Argentina	South America
von Ellenrieder	21	2000–2014	Argentina	South America
Papazian	6	2009–2015	Armenia	South America
Ávila Júnior	2	2017–2021	Brazil	South America
Batista	1	2020	Brazil	South America
Bispo	2	2016–2023	Brazil	South America
Carriço	2	2010	Brazil	South America
Carvalho	7	1992–2010	Brazil	South America
Costa	19	1990–2010	Brazil	South America
Datto–Liberato	1	2022	Brazil	South America
De Almeida	1	2016	Brazil	South America
De Souza	1	2006	Brazil	South America
Del–Claro	1	2016	Brazil	South America
Ferreira	4	2009–2022	Brazil	South America
Hamada	2	2009–2012	Brazil	South America
Juen	1	2019	Brazil	South America
Lamas	2	2010–2011	Brazil	South America
Lourenço	1	2002	Brazil	South America
Machado	18	1984–2012	Brazil	South America
Neiss	2	2012–2017	Brazil	South America
Penalva	1	2007	Brazil	South America
Pinto	5	2009–2016	Brazil	South America
Pujol–Luz	1	1993	Brazil	South America
Ravanello	1	2008	Brazil	South America
Rodrigues	3	1985–1992	Brazil	South America
Salgado	3	2004	Brazil	South America
Santos	6	1992–2000	Brazil	South America
Santos (Dias dos Santos)	20	1941–1981	Brazil	South America
Souza	1	2022	Brazil	South America
Souza–Franco	1	2008	Brazil	South America
Stefani–Santos	1	2021	Brazil	South America
Viera	1	2002	Brazil	South America
Vilela	3	2016–2022	Brazil	South America
Werneck–De– Carvalho	1	2004	Brazil	South America
Hoffmann	1	1991	Chile	South America
Amaya–Vallejo	2	2012–2017	Colombia	South America
Bota–Sierra	4	2014–2020	Colombia	South America
Torres–Pachón	1	2017	Colombia	South America
Rácenis	11	1953–1982	Venezuela	South America

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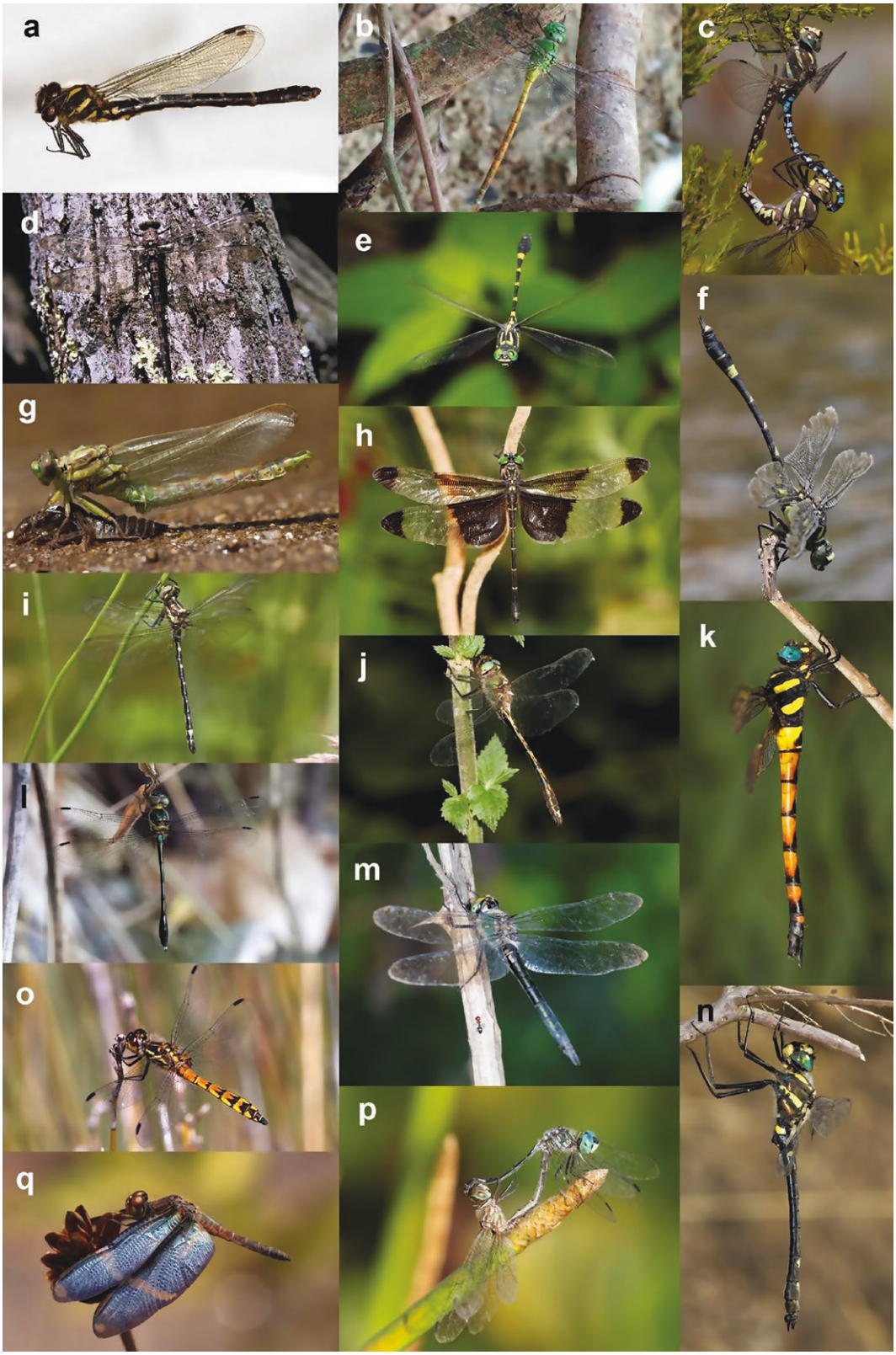


Fig. 1. Habitus and behavior of Anisozygoptera and Anisoptera. (a) Epiophlebia superstes (Selys 1889) (Epiophlebiidae, Japan), (b) Staurophlebia reticulata (Burmeister 1839) (Aeshnidae, Brazil), (c) Aeshna juncea (Linnaeus 1758) in copula (Aeshnidae, Spain), (d) Tachopteryx thoreyi (Hagen in Selys 1858) (Petaluridae, USA), (e) Lamelligomphus camelus (Martin 1904) in patrol flight (Gomphidae, China), (f) Gomphidia kruegeri Martin 1904 in obelisk position (Gomphidae, China), (g) emergence of Onychogomphus uncatus (Charpentier 1840) (Gomphidae, Spain), (h) Chlorogomphus usudai Ishida 1996 (Chlorogomphidae, China), (i) Eusynthemis sp. (Synthemistidae, Australia), (j) Oxygastra curtisii (Dale 1834) (Synthemistidae, Italy), (k) Anotogaster sp. (Cordulegastridae, China), (l) Macromidia rapida Martin 1907 (Synthemistidae, China), (m) Somatochlora meridionalis Nielsen 1935 (Corduliidae, Italy), (n) Macromia splendens (Pictet 1843) (Macromiidae, Portugal), (o) Austrothemis nigrescens (Martin 1901) (Libellulidae, Australia), (p) Micrathyria ocellata Martin 1897 in copula (Libellulidae, Colombia), (q) a thermoregulating male of Zenithoptera lanei Santos 1941 (Libellulidae, Brazil). Photos by Adolfo Cordero-Rivera.

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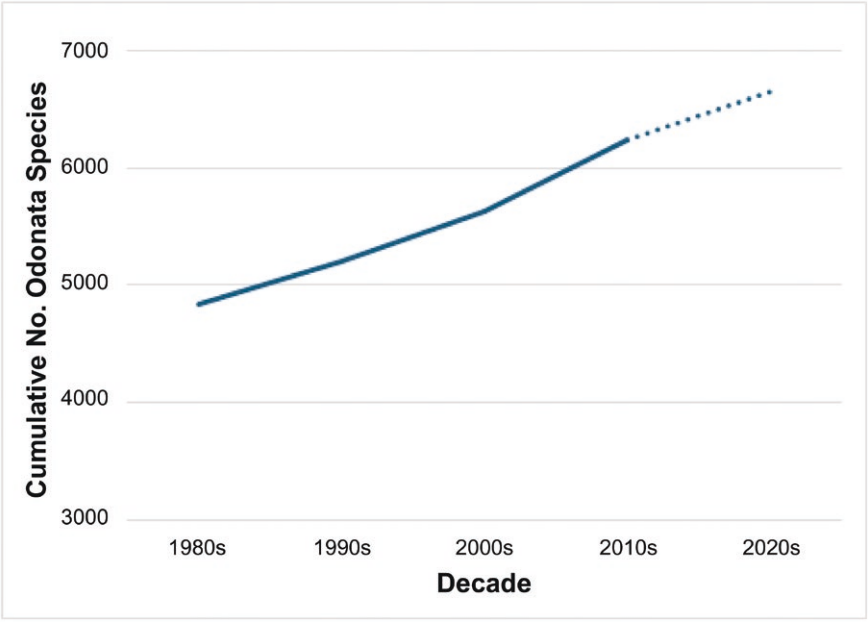


Fig. 2. Cumulative number of new Odonata species described during the last 5 decades; dotted line for the decade 2020–2029 is a projection based on the number for each of the first 4 years from 2020 to 2023.

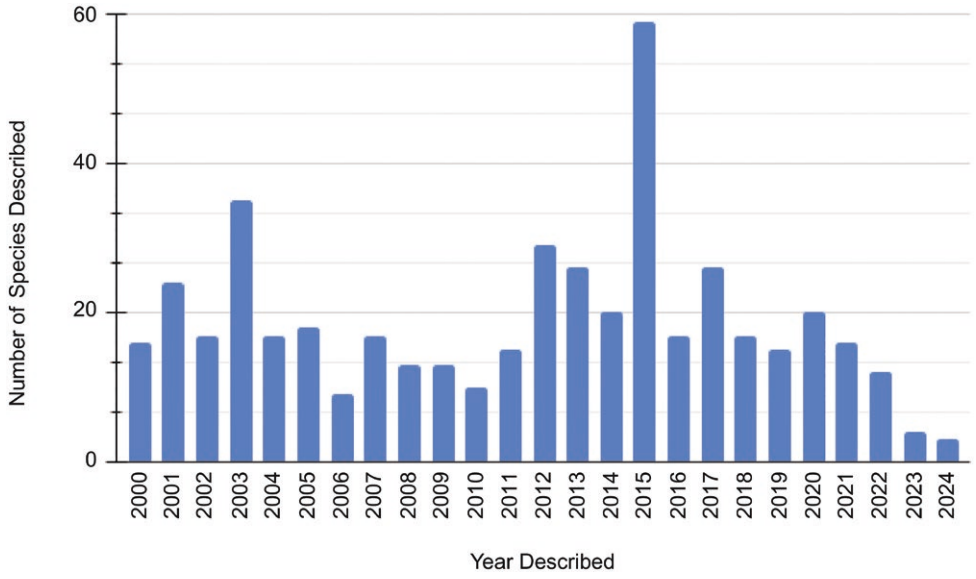


Fig. 3. Number of Anisoptera species described since the year 2000.

2007 for a review of relationships supported by specific character sets). Within Libelluloidea, egg, nymph, and wing characters supported Corduliidae + Libellulidae (eg Needham et al. 2000), but the internal relationships within each family were considered taxonomically chaotic. Bechly (2007) proposed upward of 13 families within Libelluloidea while others (eg May et al. 2000) proposed 1 to 3 families within the superfamily (Fig. 1).

Species descriptions in Anisoptera continue at a rate (averaged over the last 10 years) of roughly 20 dragonfly species per year (see Figs. 2–4, and Table 1). A summary of the early pioneering odonatologists is provided by Abbott and Sandall (2023). Baron Michael Edmond de Selys Longchamps (1813–1900), a Belgian nobleman and politician described the most dragonfly species by far, describing over 300 species. The second most prolific describer of dragonfly species was Maurits Anne Lieftinck (1904–1985), a Dutch entomologist who worked as a curator at the Rijksmuseum van Natuurlijke Historie (National Museum of Natural History) in Leiden, the Netherlands, and described 189 species. Several researchers described over one hundred species, including Frederick Charles Fraser (1880–1963), a medical doctor who lived and worked in India, who described 184 species of dragonflies, and Friedrich Ris (1867–1931), a Swiss physician, who described 144 species of dragonflies. Outside of the western colonial era, notable contributors include Tadamasa Karube (1953–2020; researcher at the Kanagawa Prefectural Museum of Natural History) and Syoziro Asahina (1913–2010; a researcher at the National Science Museum in Tokyo (now the National Museum of Nature and Science)) who each described almost 60 species of largely Japanese Anisoptera. Günther Theischinger, formerly of the New South Wales Department of Environment and Conservation described 63 Australasian dragonflies and Chao Hung-Chang described 55 species of mostly Chinese Anisoptera during the 20th century.

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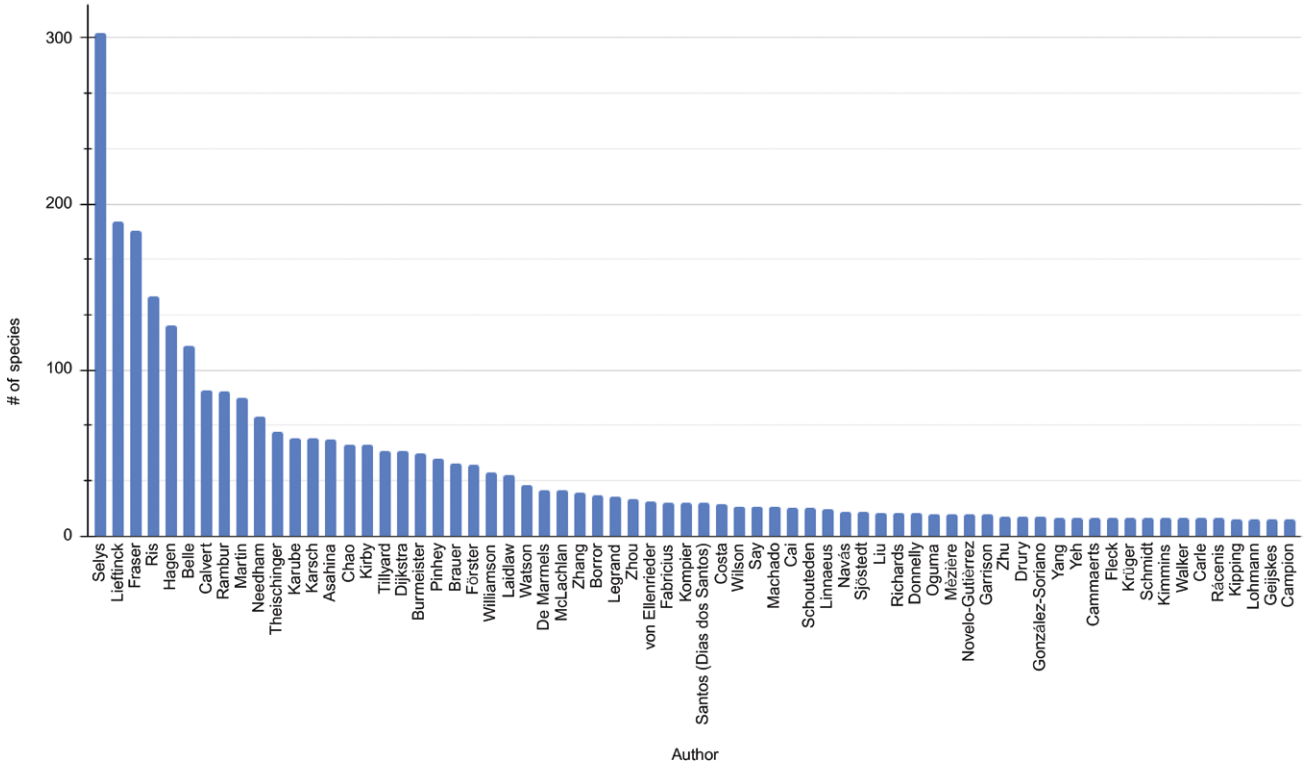


Fig. 4. A histogram showing the number of species described by authors who have described at least 10 species each.

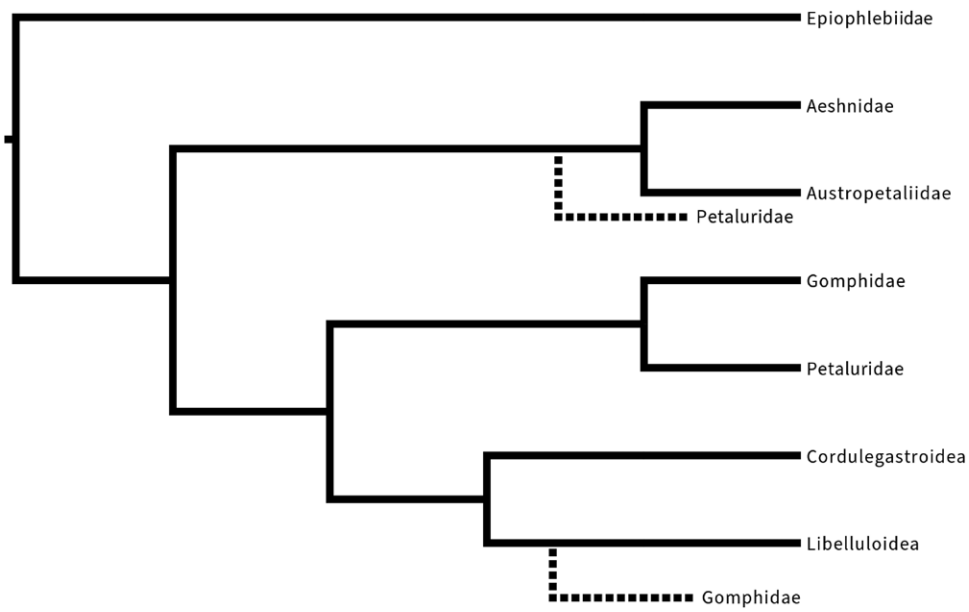


Fig. 5. A summary phylogeny based on past hypotheses.

Dragonflies in the molecular age

Molecular approaches to Odonata systematics began in the late 20th century, focusing on familial or generic relationships (Chippindale et al. 1999, Kambhampati and Charlton 1999, Brown et al. 2000, Misof et al. 2000). Misof et al. (2001), incorporated data from the mitochondria for Anisoptera; subsequent analyses focused either at the ordinal or interfamilial level, using mitochondrial datasets (Artiss et al. 2001, Misof and Fleck 2003, Saux et al. 2003). Several additional molecular studies were published using multi-gene sanger datasets (eg Hasegawa and Kasuya 2006, Ware et al. 2007, 2008, 2009, Bybee et al. 2008, Pilgrim and Von Dohlen 2008, Dijkstra et al. 2014, Carle et al. 2015, Letsch et al. 2016), although not all focused exclusively on the Anisoptera and others were deep-dives into the systematics of particular families. Most studies undertaken in the last 5 years have used next-generation sequencing data (incorporating several targeted regions as in Bybee et al. 2021 or using transcriptomic data as in Kohli et al. (2021) and Suvorov et al. (2021) to determine phylogenetic relationships and revise family relationships (Bybee et al. 2021).

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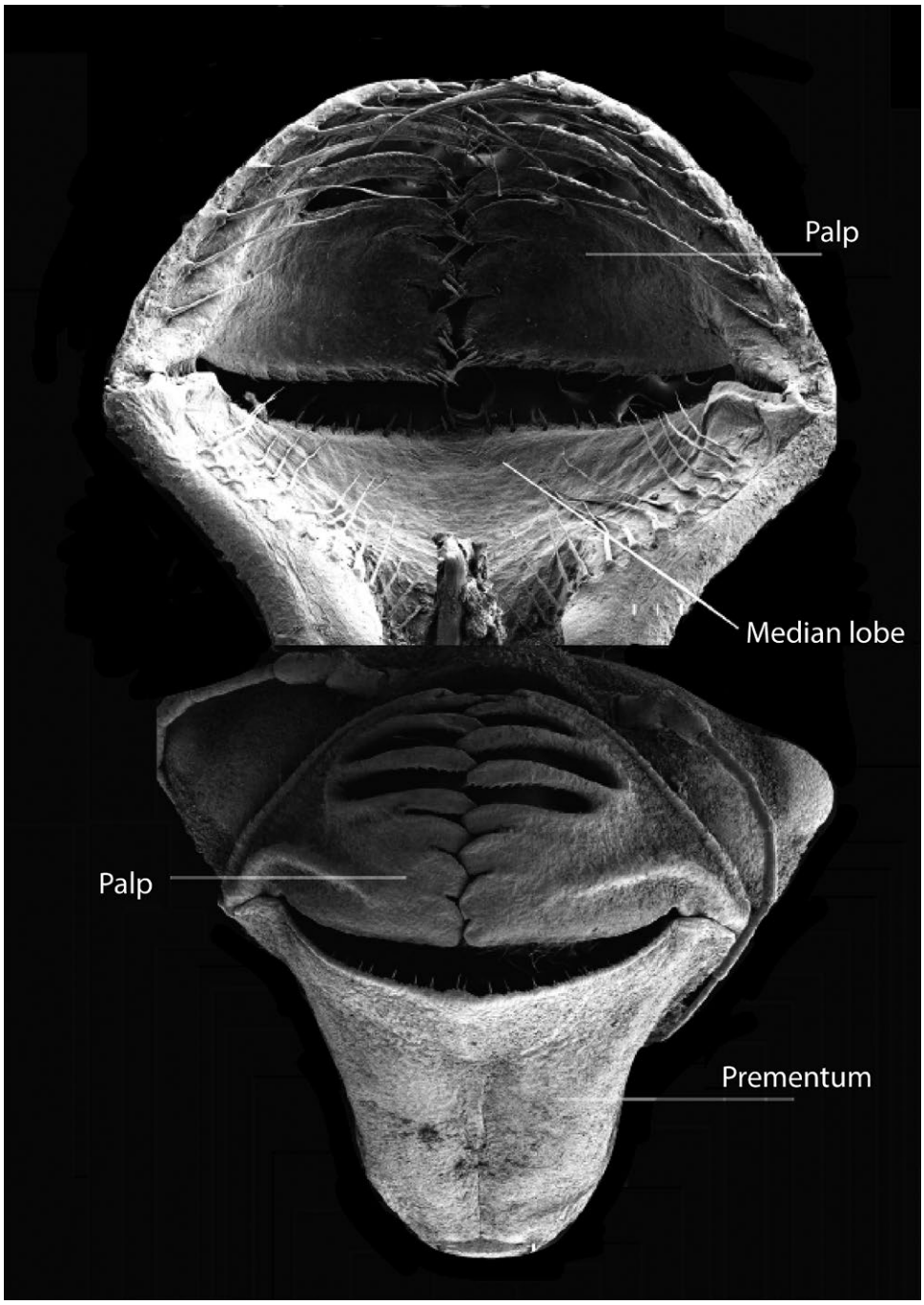


Fig. 6. Labial mask of Cordulephya sp. nymph, labeled; dorsal view in top image and ventral view in bottom image.

The National Science Foundation (NSF) supported Genealogy and Ecology Of Odonata (GEODE) project team (led by Abbott, Bybee, Frandsen, Guralnick, Kalkman, and Ware) is working with the next generation of odonatologists to use a large Anchored Hybrid Enrichment (AHE) dataset to resolve the Odonata Tree of Life; this team is working with the global dragonfly community to revise Anisoptera systematics in a way that prioritizes leadership on generic revisions by authors from the regions in which the taxa are found. Below, current phylogenetic relationships are discussed when there is strong support for clades (eg supported by bootstrap values, posterior probabilities, concordance factors).

Current taxonomy and classification

Epiprocta andand 'Anisozygoptera'

Beyond the 2 well-known groups of Odonata, the dragonflies (Anisoptera) and damselflies (Zygoptera), a third enigmatic group exists—the 'Anisozygoptera'.

The only extant family in this paraphyletic grouping contains 3 species: *Epiophlebia superstes* (Selys 1889), *E. laidlawi* Tillyard 1921 and *E. sinensis* Li and Nel 2011 (eg Büsse and Ware 2022). The extant species of *Epiophlebia* Tillyard 1917 were historically grouped with fossil taxa, forming the 'Anisozygoptera' (eg Nel 1993). The name reflects the conspicuous mixture of anisopteran and zygoptera

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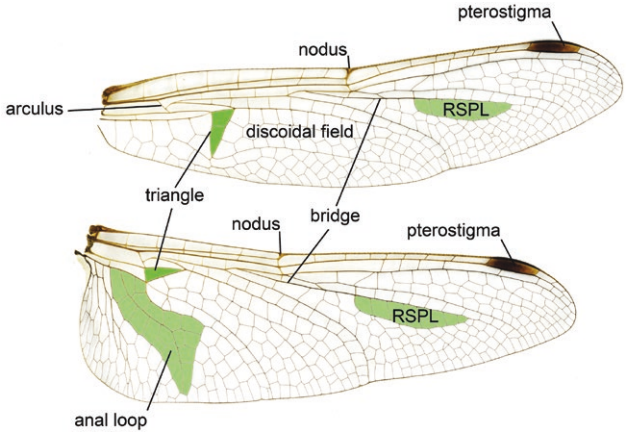


Fig. 7. Wing venation in Anisoptera; labeled wing of Sympetrum corruptum (Hagen 1861)

characters found in its extant species (Asahina 1954, Rüppell and Hilfert 1993, Büsse 2016). Previously, Nel (1993) showed that the term 'Anisozygoptera' represents a paraphyletic group of both fossils and extant species; however, for reasons of simplicity, the term 'Anisozygoptera' has continued to be used for extant species as suggested by Dijkstra and colleagues (2013) and in the World Odonata List (Paulson et al. 2024).

The 'Anisozygoptera' represents the sister group to the Anisoptera, together forming the group Epiprocta (Bechly 1996, Lohmann 1996); there are 3126 extant species in Epiprocta. This phylogenetic relationship between the extant group of *Epiophlebia* and the remaining Anisoptera is well-established and supported by numerous phylogenetic studies (Hovmöller et al. 2002, Bybee et al. 2008, 2021, Fleck et al. 2008a, b, Blanke et al. 2012, 2013, Misof et al. 2014, Letsch et al. 2016, Büsse et al. 2018, Kohli et al. 2021, Suvorov et al. 2021). The extant group of *Epiophlebia* is, due to its stenoecious lifestyle, restricted to areas of the Asian continent and shows a disjunct distribution restricting them to cold habitats, such as glacial refugia (eg Büsse et al. 2012 or, Goodman et al. 2024).

Synapomorphies for epiprocta

Body of extant adults robust with epiproct large in size for grasping females. In extant taxa, the frons is large (Rehn; 2003). Nymphs are robust, with internal anal gills present as rectal gills in extant taxa (but note that some extinct nymphs are Zygoptera-like in phenotype). Forewings and hindwings have a short petiole in extant taxa. The arculus is close to the first or second antenodal crossvein, and a fork in the RP is present at the midpoint of the nodus and arculus in Epiprocta, but convergent on some Zygoptera (Bechly 1996).

Anisoptera

There are 3123 species of Anisoptera (Paulson et al. 2024). Our recent work suggests that Aeshnidae + Austropetaliidae are sister to the remaining Anisoptera, with Petaluridae + Gomphidae sister to the Cavilabiata (ie, Cordulegastroidea + Libelulloidea); see Fig. 5 for a summary of past phylogenetic hypotheses.

Synapomorphies for anisoptera

Eyes large. Robust, large sizedthorax. Forewings and hindwings are different in size and shape. Nymphs of extant taxa are relatively stout compared to Zygoptera and with internal gills.

Aeshnidae

Aeshnidae Rambur 1842, is a family of medium- to large-sized dragonflies (ie, ~6–9 cm in length) that have a global distribution. They are distinct from other families of dragonflies for having large compound eyes that cover an extensive proportion of their head. There are 492 known species of Aeshnidae in 51 genera. In the past Aeshnidae have been placed together with Austropetaliidae and Neopetaliidae (Tillyard and Fraser 1940) as 'Aeshnoidea', or have been grouped together with Gomphidae and Petaluridae (eg Blanke et al. 2013). However, molecular studies in the last two decades have firmly placed Aeshnidae + Austropetaliidae as sister to the rest of the Anisopter a families. Few studies have explored the relationships within Aeshnidae except for the seminal work by Natalia Von Ellenrider (2002), which explores phylogenetic relationships within Aeshnidae using 58 adult and nymphal characters. Within Aeshnidae, the tribe Gomphaeschninae is considered a sister group of the remaining aeshnids (von Ellenrieder 2002). Other traditionally considered tribes in Aeshnidae are Brachytronini, Aeshnini, Anactini, Gynacanthagini, and Polycanthagini (eg Fraser 1936, Tillyard and Fraser 1940), which are not necessarily supported (von Ellenrieder 2002). There have also been several studies that have looked at relationships within specific genera in Aeshnidae. For example, *Boyeria* was evaluated (Kohli et al. 2014) and *Anax* (Clement and Saxton et al. 2022) using molecular datasets. Regionally, Mehmood et al. (2020) focused on Aeshnidae in a phylogenetic context from Pakistan. Shneider et al. (2023) published a phylogenetic hypothesis of the family using mitochondrial and nuclear evidence. They included representatives of 28 genera, mostly focusing on the Palearctic region; they suggest several changes finding some paraphyletic genera to be redefined (eg *Aeschnophlebia* Selys 1883, *Epiaeschna* Hagen in Selys 1883, *Nasiaeschna* Selys in Förster 1900, and *Brachytron* Evans 1845) and erecting a new genus *Isoaeschna* Schneider, Vierstraete, Kosterin, Ikemeyer, Hu, Snegovaya and Dumont 2023 to include the widespread European *Aeshna isoceles* (Müller 1767).

Synapomorphies for Aeshnidae

Large eyes touching along a majority of their length, forming an eye seam. Vertex with prominent tubercle between ocelli (Garrison et al. 2006). Hindwing and forewing triangles of similar shape. Triangles positioned equidistant from the arculus in the fore and hindwings. Abdominal tergae with carinae (Garrison et al. 2006). Male secondary genitalia with a deep median cleft in the anterior lamina (Garrison et al. 2006). Ovipositor in females is well developed. Nymph with flat prementum, elongated bodies, and widely spaced eyes.

Austropetaliidae

Austropetaliidae Carle and Louton (1994) is a species poor family composed of large to very large dragonflies (up to 12 cm in length) with an austral distribution in temperate forests of southeastern Australia and southern South America. There are 10 species of Austropetaliidae. The family is comprised of 4 genera; *Archipetalia* Tillyard 1917 which contains the sole species *A. auriculata* Tillyard 1917 distributed in Tasmania; *Austropetalia* Tillyard 1916, which is comprised by *A. annaliese* Theischinger 2013, *A. patricia* (Tillyard 1910) and *A. tonyana* Theischinger 1995, distributed in S.E. Australia; *Hypopetalia* McLachlan 1870 which contains the sole species *H. pestilens* McLachlan 1870 distributed in southern South America; and *Phyllopetalia* Selys 1858 that contains *P. altarensis* (Carle 1996, von Ellenrieder 2005) *P. apicalis* Selys 1858, *P. apollo* Selys 1878, *P. excrescens* (Carle 1996, von Ellenrieder 2005), *P. pudu* Dunkle 1985 and *P. stictica* Hagen in Selys 1858, distributed in southern South America. The monophyly of

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Austropetaliidae is proposed by Bechly (1996), following Carle and Louton (1994) and Carle (1995), and various analyses (eg Misof et al. 2001, Bybee et al. 2008, 2021, Carle et al. 2015) support the sister relationship of Austropetaliidae with Aeshnidae, together forming the superfamily Aeshnoidea. *Phyllopetalia*, the most diverse and probably the genus with the greatest taxonomic complexity and morphological variability was revised by von Ellenrieder (2005), who synonymized 4 genera, 4 species and one subspecies and presented diagnostic characters for genus and species.

Synapomorphies for Austropetaliidae

Eyes meeting at a point in adults, rather than as a seam (eyes meeting in a seam in Aeshnidae). Vertex flat. Deep premental cleft in adults. Pterostigma with brace vein (shared with Aeschnidae), and costal margin with reddish brown spots. Triangles similar in fore and hindwings. Male posterior hamules with single tip, and anterior lamina with an elongated median cleft (Garrison et al. 2006). Nymph with wide labrum, projecting distally (Garrison et al. 2006). Lateral lobes on all 10 nymphal segments well developed (Carle 1996).

Gomphidae

The clubtails/club-tailed dragonflies (Gomphidae Rambur 1842) represent the second most species-rich group within the suborder Anisoptera and are notably diverse and widely distributed across all continents except Antarctica, encompassing approximately 90 genera and 1006 species the majority of which are restricted to running waters (Tillard 1917, Carle 1994, Corbet 1999). Gomphidae dragonflies have medium to large body size (~4–7 cm in length) and are often black with a distinctive yellow or sometimes green pattern. Compared to other families, such as Aeshnidae and Libellulidae, bright blue or red colors are rare They are distinguished within the Anisoptera suborder by their widely separated eyes (Farkas et al. 2012). While the monophyly of Gomphidae is well-supported, few genera within the family have been confirmed as monophyletic, and several groups remain unresolved (eg *Nihonogomphus* Oguma 1926 and *Onychogomphus* Selys 1854, species relationships within *Ophiogomphus* Selys 1854, and the subfamilies Octogomphinae, Hageniinae, Epigomphinae, and Gomphinae, as noted by Ware et al. 2017). To date, most phylogenetic analyses have included a few representative species from the Gomphidae family (eg Bybee et al. 2008, which included fossil and extant taxa in a morphological and molecular analysis; Carle et al. 2008, which focused taxon sampling on Coenagrionidae; Dumont et al. 2010, an ordinal phylogeny which used nuclear ribosomal genes; Ware et al. 2014, which focused taxon sampling on Petaluridae; Letsch et al. 2016, for which diversification rate analyses were done; and Carle et al. 2015, which included mitochondrial and nuclear data), but no comprehensive Gomphidae-focused, molecular-based phylogeny has been reconstructed. Crucially, the classification of the Gomphidae family varies depending on the dataset used for analysis. For example, studies using molecular data (eg Bybee et al. 2008, 2021, Carle et al. 2015, Kohli et al. 2021, Suvorov et al. 2021) place Gomphidae as a sister group to Petaluridae, while those using morphological data (eg Carle 1982a, Blanke et al. 2013) place it as a sister group to all other Anisoptera. A comprehensive study of more taxa and a robust molecular phylogeny is currently ongoing as part of the GEODE project; in an effort to hopefully resolve evolutionary relationships among the species within this family and revise the current taxonomy of the group.

Gomphidae species discovery is ongoing and while the potential for the discovery of new species in the Neotropical region is high (eg Datto-Liberato et al. 2022, Vilela et al. 2022), there is adequate knowledge for many genera, thanks to the extensive work of Belle (e.g. 1984; 1990, 1991, 1996), Garrison (1994a) and Needham et al. (2000) (eg *Aphylla* Selys 1854, *Erpetogomphus* Selys 1858, *Gomphus* Leach in Brewster 1815, *Phyllocycla* Calvert 1948, *Phyllogomphoides* Belle 1970, *Progomphus* Selys 1854). Several genera have been evaluated in a phylogenetic context, or revised in recent decades. For example, with molecular data, Kiyoshi and Sota (2006) used Sanger sequences to evaluate *Davidius*, and Park et al. (2022) sequenced a mitochondrial genome of *Asiagomphus coreanus* (Doi and Okumura 1937). Morphological revisionary works have been more common for Gomphidae genera than molecular studies; for example, Belle undertook a morphological revision of *Aphylla* (1992), Watson and O'Farrel (1985) assessed the intergeneric relationship of *Ictinogomphus* Cowley 1934, *Austrogomphus* Selys 1854 and other Australian Gomphidae and Garrison (1994) revised *Erpetogomphus*.

Synapomorphies for Gomphidae

Eyes separated equal to the amount of space between the lateral ocelli. Hindwing pterostigma are positioned distally in the wing, beginning at the latter third of the postnatal region (Garrison et al. 2006). Male auricles on segment 2 of the abdomen (as in other groups). Female ovipositor reduced or absent, bifid vulvar laminae present. Adult prementum not bifurcated. Nymphs with elongated or enlarged third antennal segment. Nymph with labial mask flat (see Fig. 6 for labeled prementeum image). Nymphal tibial spines are short and rounded.

Petaluridae

Petaluridae Tillyard 1917, is a family of medium to very large dragonflies (~7–12 cm) with a largely Pan-Pacific distribution. The family is typically regarded as sister to Gomphidae (Bybee et al. 2021, Kohli et al. 2021, Suvorov et al. 2021). The family is comprised of 5 genera and 11 species; *Tachopteryx* Uhler in Selys 1859 which contains only *T. thoreyi* is found in Eastern North America; *Tanypteryx* Kennedy 1917, which is comprised of *T. hageni* (Selys 1879) in Western North America and *T. pryeri* (Selys 1879) in Japan; *Phenes* Rambur 1842, containing *P. raptor Rambur 1842* from Patagonia (southern Argentina and Chile); *Uropetala* Selys 1858 comprised of *U. carovei* (White in Dieffenbach 1843) and *U. chiltoni* Tillyard 1921 from Aotearoa (New Zealand); and *Petalura* Leach 1815, containing *P. hesperia* Watson 1958 from western Australia, and *P. gigantea* Leach 1815, *P. litorea Theischinger 1999*, *P. ingentissima* Tillyard 1908 and *P. pulcherrima* Tillyard 1913 from Eastern Australia. We note that the status of *P. pulcherrima* remains debated in the literature (Mitchell et al. 2021, Tolman et al. 2024); no genomic resources exist for this putative species, and it is considered a species of concern by the Australian government (Pintor et al. 2019). *Petalura*, *Uropetala* and *Phenes* form a well-supported Gondwanan clade, while *Tanypteryx* and *Tachopteryx* form a well-supported Laurasian clade within the family (Tolman et al. 2024*)*. However, even with an AHE dataset, the relationships between the genera of the Gondwanan clade, and within *Petalura* receive low support (Tolman et al. 2024). Few generic studies have been undertaken using molecular data: Mitchell et al., (2020) focused on molecular phylogenetics of *Petalura*, and Tolman et al. (pers. comm) are working on a revision of *Uropetala* using genomics. With high-quality draft genome assemblies available for both *T. hageni* (Tolman et al. 2023b), and *U. carovei* (Tolman et al. 2023c) the Petaluridae are currently the most well-represented anisopteran family based on whole genome sequencing data. These genomes have been used to link gene family expansions to the

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semi-terrestriality of nymphs, and the long lifespan of these species (Tolman et al. 2023c).

Synapomorphies for Petaluridae

Eyes separated equal to the amount of space between the lateral ocelli. Occiput rounded (May et al. 2000). Hindwing pterostigma long and narrow, positioned in the middle of the postnatal region, apically to the tip of the wing. Triangles crossed, supertriangles free (Garrison et al. 2006). Female with distinct ovipositor. Sectors of arculus not fused at base. Adult prementum with a deep bifurcating cleft. Nymph with parallel wing pads, short antennae, and elongate bodies of relatively large size. Labial mask flat. Labial palps with spatulate end hooks (Carle 1995). Prominent tibial spurs present.

Cordulegastridae and Chlorogomphidae

There are 52 species of Holarctic Cordulegastridae and 56 species of the tropical Asian family Chlorogomphidae (Paulson et al. 2024). Several studies have included members of Cordulegastridae or Chlorogomphidae in their analyses (eg Letsch 2007, Ware et al. 2007, Bybee et al. 2008, 2021, May et al. 2015, Kohli et al. 2021, Suvorov et al. 2021). Using molecular Sanger sequences Froufe et al. 2014 and Schneider (2021) solved many of the taxonomic issues in the largely western Palaearctic genus Cordulegaster. Schneider et al. (2024) published a ~280 specimen phylogeny of the family using Sanger sequences; their work provides support for 4 valid genera in the family, *Anotogaster* Selys 1854, *Cordulegaster* Leach in Brewster 1815, *Thecagaster* Selys 1854 and *Zoraena* Kirby 1890 while a fifth (*Neallogaster* Cowley 1934) was not sufficiently represented in the dataset to fully resolve its relation with *Anotogaster*. No phylogeny of Chlorogomphidae exists, but as for Cordulegastridae the family has been represented in other phylogenies that focused on the order or various families. Wilson (2021) assessed 2 species of *Chlorogomphus* Selys 1854 using morphology. Wang et al. (2023) published a complete mitochondrial genome for *Chlorogomphus shanicus* Wilson 2002.

Synapomorphies for Cordulegastridae

Eyes meeting only for a short length/point or narrowly separated. Prementum with cleft. Vertex forming tuberule between lateral ocelli. No brace vein on the pterostigma. Triangles in forewing and hindwing elongated longitudinally and similar in shape. Median space without crossveins. Male spines on the middle leg are quadrangular on the tibia (Garrison et al. 2006). Female with pronounced ovipositor, which exists as a long gonapophysis on segment 8 that is strongly sclerotized and extends past the tip of the abdomen. Nymph mouthparts with hooked teeth on the prementum, labial mask flat.

Synapomorphies for Chlorogomphidae

Eyes separated by a short distance. Auricles in males. Triangles similar in shape in forewing and hindwing. Median space with crossveins. Abdominal segments 3 and 4 constricted. Nymph elongate with broad labial mask; labial mask with deep crenulations (Orr 2003). Nymphs resemble those of Cordulegastridae but have more slender and shorter antennae.

Neopetaliidae

This family is represented by the sole species *Neopetalia punctata* (Hagen in Selys 1854), which is a medium sized dragonfly (~5–6 cm) endemic to the temperate forests of southern Argentina and Chile. The relationship of this family to other Anisoptera was addressed by Carle and Louton (1994), who based on nymphal characters (ie, the typical scoop-shaped labium of Libelluloidea) transferred Neopetaliidae Tillyard and Fraser 1940 to Libelluloidea and created Austropetalidae to include genera formerly included in Neopetaliidae (eg *Austropetalia*, *Phyllopetalia*, *Hypopetalia*). Subsequent phylogenetic analyses placed *Neopetalia* Cowley 1934 as sister to Cordulegastridae (eg Misof et al. 2001), and more recent classification schemes (Dijkstra et al. 2013) and phylogenetic analyses (Bybee et al. 2021) include Neopetaliidae within Cordulegastroidea, together with Cordulegastridae and Chlorogomphidae.

Synapomorphies for Neopetaliidae

Eyes meeting only at a point. Premental cleft present. Wings with elongated forewing triangle. Wings with reddish brown spots along the costa. Pterostigma with a prominent brace vein. Male middle legs with tibial spines that gradually taper (Garrison et al. 2006) and forelegs with tibial keels present. Male with bilobed posterior hamule tip and vertex with prominent tubercle (Garrison et al. 2006). Female with short vulvar lamina and 2 pairs of gonapophyses (Garrison et al. 2006); segment 10 of abdomen with sternum enlarged into a circular plate-like flap. Nymph with hook like teeth on the prementum and flat labial mask.

Macromiidae

Macromiidae Needham 1903, is a lineage of the superfamily Libelluloidea and a family of medium to large-bodied dragonflies (~6 cm to 8 cm in length). There are 125 species of Macromiidae. They have a Holarctic, Afrotropical, Oriental, and Australasian distribution. The highest diversity in this group is recorded in Southeast Asia and Sub-Saharan Africa. Macromiidae was formerly considered a subfamily of Corduliidae (Kirby 1890) until discovered to be monophyletic and upgraded to family level by more recent and robust studies in Odonata (Ware et al. 2007, Bybee et al. 2021). Historically, the family name 'Macromiidae' was proposed by Gloyd (1959) based on diagnoses from 3 genera, *Macromia* Rambur 1842, *Didymops* Rambur 1842, and *Epophthalmia* Burmeister 1839. She proposed the elevation of what was called the '*Macromia* group', to family status. Currently, this family consists of 4 genera—*Macromia*, which has been recovered as a sister genus to *Didymops*, and *Phyllomacromia* Selys 1878, which has been recovered as a sister genus to *Epophthalmia* (Bybee et al. 2021, Kohli et al. 2021, Ware et al. 2007, WOL). A genus-level study by May (1997) examining the status of *Phyllomacromia* and *Macromia* proposed the aforementioned intergeneric relationships. An earlier genus-level revision by Lieftinck (1932) confirmed the status of *Epophthalmia* as a genus within what was then called the sub-family Corduliinae. Additionally, a study by Williamson (1909) proposed the congeneric status of North American *Macromia* and *Epophthalmia* while confirming the generic status of *Didymops*. Djikstra (2005) revised the genus *Phyllomacromia* using morphological data. Overall, due to the paucity of species-level data, the relationships within and among these genera are yet to be parsed out and confirmed, respectively. With higher taxon sampling, current phylogenetic analyses are ongoing, confirming and redefining some of the taxonomic relationships within this group.

Synapomorphies for Macromiidae

Eyes meeting for a majority of their length. In most genera, eyes with evagination on the posterior margin. The distance between triangle and arculus is twice as long in the forewing than in the hindwing (May et al. 2000, Garrison et al. 2006). All adult members of this family share a unique sausage-like anal loop shape with a rounded

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heel located close to the base of the hind wing. As nymphs, they have a combination of wide, flattened bodies with long, spider-like legs (Tennessen 2019). Nymphs of most genera with nymphal horns. Nymphs with hand-like tibial spines. Nymphs with a spoon-like labial mask and deep, jagged teeth on the prementum.

Corduliidae

Corduliidae is a widespread, medium to large sized (3.5–7 cm in length) family of dragonflies commonly possessing metallic green bodies. Historically, Corduliidae consisted of 7 subfamilies (Fraser and Tillyard 1957, Bechly 1996), however, analyses by Ware et al. (2007) and Carle et al. (2015) revealed this classification to be polyphyletic, establishing a more restricted, but monophyletic Corduliidae consisting solely of members of the subfamily Corduliinae. Currently, Corduliidae consists of 22 genera and 167 species, however, half of these genera were added based exclusively on morphological traits (Bechly 1996, Fleck 2012). Current phylogenetic work (Goodman, pers. comm.) on Corduliidae does support its monophyly, with the inclusion of *Metaphya* Laidlaw 1912, an Australasian genus, which had never been sequenced before. However, the genera *Pentathemis* Karsch 1890, *Schizocordulia* Machado 2005, and *Aeschnosoma* form a monophyletic sister group to Libellulidae. The nymphs of *Pentathemis* and *Aeschnosoma* Selys 1870 are phenotypically similar due to the presence of lateral spines on the abdomen of the nymph that are elongate on the 9th segment; their distributions are disjunct as they exist in South America and Eastern Australia respectively (Fleck 2012, Fleck and Legrand 2013). The placement of *Aeschnosoma* + *Pentathemis* was unresolved in Bybee et al. (2021), as *Pentathemis* was recovered as sister to Libellulidae with low phylogenetic support. More taxon sampling is currently underway, which will recover these 3 taxa (as well as the malagasy genus Libellulosoma Martin 1906) within either family, or require the description of a new family. Several studies have focused on generic revisions, but a majority of genera have not been assessed with a phylogenetic treatment. Kormondy (1959), for example, presented a very thorough revision of *Epitheca* Charpentier 1840 (then considered *Tetragoneuria*). For the neotropical region, the genus *Navicordulia* Machado and Costa 1995 was revised by Fleck (2017) and Fleck and Juillerat (2019) providing taxonomic keys and updated distribution for all its species. *Neocordulia* Selys 1882 was recently revised by Ehlert et al. (in press), revising problematic mischaracterization of several species. Jödicke et al. (2004) assessed *Cordulia aenea amurensis* Selys 1887 and *C. shurtleffii* Scudder 1866 using morphological and Sanger genetic data. Several generic revisions are purported to be underway, and we look forward to a more accurate reflection of the phylogenetic history of these genera in future years.

Synapomorphies for Corduliidae

Eyes meeting for a considerable distance (greater than the length of the occipital triangle in the crepuscular genus Neurocordulia Selys 1871). Male with auricles (absent in Hemicordulia Selys 1870). Triangles in fore and hindwings are dissimilar. Distance between the triangle and the arculus is more than twice as long in the forewing than in the hindwing. Second crossvein between RP1,2 and IRP2 not oblique. Nymph with a spoon-like labial mask. Nymph with prementum possessing only very shallow crenulations.

Synthemistidae

Synthemistidae Tillyard 1911 (Tigertails) is the most species poor libelluloid family and is sister to the remaining Libelluloidea (Davis et al. 2011) (28 genera, 149 species), whose members are predominantly stream-dwelling Australasian endemics (Theischinger and Hawking 2006), and with the exception of the largely European *Oxygastra* Selys 1870, all members of this family are either found in the tropics or in the temperate parts of the Southern Hemisphere. Species richness of genera within Synthemistidae varies considerably, with 25% being monotypic, while the most speciose genus *Idionyx* Hagen 1867 contains 29 species. Such variability likely reflects the taxonomic inclinations of those who have worked on this group (eg lumper versus splitter philosophies), but it might also suggest high degrees of endemism, ecological specialization, and/or variable rates of extinction. This will be assessed through phylogenetic works currently underway for this group assessing topologies and branch lengths (Goodman, pers. comm). The earliest classifications of Synthemistidae consisted only of the Australian genera: *Synthemis* Selys 1870, *Eusynthemis* Förster 1903, *Choristhemis* Tillyard 1910, and *Synthemiopsis* (Tillyard 1917). Phylogenetic studies by Ware et al. 2007 revealed a monophyletic group ('GSI' clade), sister to Synthemistidae (*sensu* Tillyard 1917), consisting of several now defunct families hypothesized by Bechly 1996: (Gomphomacromiidae, Austrocorduliidae, Oxygastridae, Idionychidae, and Cordulephyidae). Letsch 2007 recovered Idomacromiidae (Bechly 1996) within the 'GSI' clade (sensu Ware et al. 2007), which was unsampled in Ware et al. 2007. Finally, Carle et al. (2015) expanded the family Synthemistidae to include all 'GSI' clade taxa. Analyses utilizing Anchored Hybrid Enrichment (AHE) and transcriptomes recover the monophyly of Synthemistidae (Bybee et al. 2021, Kohli et al. 2021), however only 12 taxa were used, a majority of which were *Synthemis* and *Eusynthemis*. Currently, families hypothesized by Bechly 1996 are being evaluated (Goodman, pers. comm.), and Goodman's work supports the monophyly of the Australian Synthemistidae as described by Tillyard (1917). Ware and Samways (2009) evaluated the relict Cape-genus *Syncordulia* Selys 1882, estimating its origination at 60 mya. Pinto evaluated *Lauromacromia* Geijskes 1970 using phylogenetic analyses, revising the genus and proposing new species.

Synapomorphies for Synthemistidae

Eyes meeting for a considerable distance (greater than the maximum width of the occipital triangle), and absence of lateral abdominal carinae (except for *Apocordulia* Watson 1980 in both traits). Auricles are present, with Australian Synthemistidae (including Pseudocordulia and Austrocordulia), South American Gomphomacromia and Lauromacromia, and *Idionyx* possessing spines. Nymph wing pads are divergent in Australian Synthemistidae and Idionyx, lateral spines on abdominal segments of nymphs varies (absent in Australian Synthemistidae, present on multiple segments in *Austrocordulia, Austrophya, Hesperocordulia, Cordulephya* and *Lauromacromia*). Nymph possess spoon-like labial masks as in Corduliidae, however the teeth of the labial palpus varies greatly in length, regularity, and width; the most striking example is in the Australian taxa *Cordulephya* Selys 1870, possessing exceptionally prominent, irregular teeth (Fig. 6). Wing venation varies as well within Synthemistidae. The anal loop can range from compact (Australian Synthemistidae and *Macromidia* Rambur 1842), elongate with a zigzag midrib (*Gomphomacromia* Brauer 1864, *Micromidia, Austrophya* Tillyard 1909, *Lathrocordulia* Tillyard 1911, *Austrocordulia* Tillyard 1909, *Syncordulia, Apocordulia*), or elongate but no inflated tip (*Idionyx, Neocordulia, Oxygastra, Idomacromia* Karsch 1896), however no taxa possess inflated tips (boot-shaped pattern) at the posterior end of the anal-loop as observed in Libellulidae and Corduliidae. The triangle of *Cordulephya* Selys 1870 and *Neophya* Selys 1881 are quadrangular.

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Libellulidae

There are 1038 species of Libellulidae. In Ware et al., (2007), Pilgrim and von Dohlen (2007), Carle et al., (2015), Bybee et al., (2021) and Kohli et al., (2021), nearly all the libellulid subfamilies defined by Fraser (1957), Davies and Tobin (1985), and Steinmann (1997) failed to receive support as monophyletic; one notable exception is the Libellulinae which is consistently recovered across studies. In Libellulinae, various members of the subfamily have been sequenced: *Agrionoptera* Brauer 1864, *Orthetrum* Newman 1833 and *Ladona* Needham,1897 (AHE data, Bybee et al. 2021), *Misagria* Kirby 1889, *Hadrothemis* Karsch 1891, *Neodythemis* Karsch 1889, *Agrionoptera* Brauer 1864, *Orthemis* Hagen 1861, *Ladona, Plathemis* Hagen 1861, *Libellula, Lyriothemis* Brauer 1868 and *Orthetrum* Neumann 1833 (Sanger data, Ware et al. 2007), *Agrionoptera, Cratilla* Kirby 1900, *Libellula, Orthetrum, Orchithemis* Brauer 1878, and *Lyriothemis* (Transcriptome data, Kohli et al. 2021). In each case, the subfamily is strongly supported with measures of phylogenetic support.

Some taxonomic groupings that have been recovered are marked departures from previous morphology-based conclusions. *Pantala* Hagen 1861 and *Trithemis* Brauer 1868, for example, are recovered as sister groups by Ware et al., (2007), Pilgrim and von Dohlen (2008). Further, Bybee et al., (2021) and Ware et al., (2007) recovered *Pantala* in a larger clade that included *Zygonyx* Selys in Hagen 1867 and *Nannophlebia* Selys 1878; the migratory, flier *Pantala* is markedly different in appearance and behavior than any of the 3 other taxa recovered in this globally distributed larger clade. The recovery of *Diastatops* Rambur 1842 + *Perithemis* Hagen 1861 and *Zenithoptera* Selys 1869 in clades separate from *Palpopleura* Rambur 1842 was similarly surprising, since these taxa have been commonly placed in the subfamily Palpopleurinae based on their wing coloration and the presence, in some taxa, of a concave costal vein. Although revisions are needed in the most species-rich genera of the Neotropics, some genera as such as *Erythemis* Hagen 1861, *Nephepeltia* Kirby 1889 and *Orthemis* have been revised and have taxonomic keys (von Ellenrieder 2012, 2014, Palacino-Rodriguez et al. 2015), as well as the *connata* group of *Erythrodiplax* Brauer 1868 (del Palacio 2021), the most diverse genus of the Americas. Country level revisions are also available in some genera, such as *Oligoclada* Karsch 1890 or *Perithemis* in Argentina (von Ellenrieder and Muzón 1999, von Ellenrieder and Garrison 2008and).

Synapomorphies for Libellulidae

Eyes meeting for considerable distance. Distance between arculus and triangle is longer than twice as long in the forewing compared to the hindwing. Triangles in the forewing and hindwing differ in shape. The second crossvein between RP1, 2 and IRP2 is oblique in shape (Bechly 2006, Garrison et al. 2006). The shape of the anal loop in the hind wing resembles a boot or a shoe and possesses a well developed mid-rib (Fraser 1957; however, several taxa have a greatly reduced anal loop). Males lack tibial keels on prothoracic leg and lack auricles on segment 2 of the abdomen.

A note about nymphs

Taxonomic progress on the nymphs (larvae, naiads) of Odonata has lagged profoundly behind that of adults, which is understandable yet lamentable because of the potential for phylogenetic information. Of the world's 6420 currently recognized species (Paulson et al. 2024), the nymphs of fewer than 3200 have been discovered and documented (either described in detail or partly characterized or diagnosed). Interest in discovering and characterizing nymphs did not begin in earnest until a century after Linnaeus published his system of binomial nomenclature. Beginning in the mid 1800s, Hermann Hagen in Germany became interested in nymphs, describing 2 European species, and later his student, Louis Cabot, published a three-part treatise (1972, 1981, 1989) describing and illustrating about 20 species (some definitely determined, others by supposition). Shortly afterward, James G. Needham began his odonatological studies, embarking on a long career of rearing and describing nymphs from around the world. Soon a wave of studies on North American nymphs began to appear, with contributions from C. Francis Byers, Philip P. Calvert, Philip Garman, Clarence Hamilton Kennedy and Edmund M. Walker. In other parts of the world, C. DeGeer, L. Dufour, W. J. Lucas, R. J. Tillyard, R. Ris, M. A. Lieftinck and Paul Andre Robert published descriptions of nymphs from Europe, Asia, Africa and Australia.

The majority of the species still unknown in the nymph stage occur in the more diverse tropical regions of the world, where new species are being discovered at a fairly steady rate per decade (Fig. 2). The rate that nymphs are being associated with these new species is much slower, and it will take many more decades to describe them and accumulate corroborating phylogenetic data. The state of affairs is different in the temperate regions, as a vast majority of the species have been quite thoroughly treated. However, characters that might provide phylogenetic information have yet to be tested on a wide scale. Examples of nymph morphology being used to contribute to phylogeny include Blanke et al., (2013), Carle et al., (2015), Kohli et al., (2014), Letsch et al., (2016). The value of nymph characters in helping resolve generic boundaries has been amply demonstrated, for example, by Westfall (1988), Ramirez and Novelo-Gutiérrez (1999) and Fleck et al., (2008a,b).

Most Anisoptera genera are now known in the nymph stage. We estimate that at least 80% of the 368 genera have been discovered and associated. However, many genera are known based on only one or a few species, and more time is needed to analyze generic nymph characters to test whether they corroborate phylogenetic data based on adults. Another setback is that many genera have been diagnosed based on very few species, and we have yet to see if those diagnoses will hold up when more species are discovered.

The period of time between publication of a new species and description of the nymph varies depending on the taxon at hand. In comparing temperate and tropical genera, it appears there is greater lag time for tropical genera by a factor of 1.2–1.7. For example, in the family Aeshnidae, the average length of time between adult and nymph descriptions for *Aeshna* (all species are known) was 79 years compared to 100 years for the few *Gynacantha* that are known (it is possible that less than 20% are known). Comparatively, the proportional lag time for gomphids was more, 27 years for *Ophiogomphus* (a north temperate genus) and 43 years for *Progomphus* (predominantly Neotropical), even though the interval was surprisingly less than for aeshnids; it is not clear why the proportional lag time is more for some genera than others. In the Libellulidae, we compared *Leucorrhinia* Brittinger 1850 (a north temperate genus, with all species known in the nymph stage) having a lag time of about 60 years with *Erythrodiplax* (a western hemisphere, predominantly tropical/subtropical genus in which less than half are known as nymphs) in which the lag time was much longer, over 100 years.

Because species systematics are almost exclusively based on adult morphological characters (some species have been discovered by molecular studies; eg Damm et al. 2010), researchers have had to rear nymphs to adult stage in order to associate and identify them with certainty. However, many of the unknown nymphs belong to rare or hard to find species, some of which live in habitats that are difficult to access; others are lotic species which can be more difficult

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to rear than most lentic species. With DNA sequencing as a tool, it is now possible to associate un-reared, field-collected nymphs with adults of their species (eg Ruiter et al. 2013), bypassing the often tedious task of rearing. This approach should be pursued to advance our knowledge of the nymphs as it most certainly will pay huge dividends for phylogenetic understanding.

Nymph descriptions and identification guides are based almost entirely on the last instar. Earlier instars of very few species have been examined and diagnosed. For those species in which early instars have been studied, it is clear that the characters that differentiate species in the last instar usually have not yet appeared in earlier instars, although generic determinations can often be made. Collecting eggs from gravid females and rearing the hatchlings to final instar is a time-consuming task, and nymphs or exuviae of each instar must be preserved for morphological examination. Specific rearing conditions and feeding live prey of the appropriate size present challenges. These challenges evidently have been deterrents to rearing more species. Our lack of knowledge is further hampered by the fact that many past nymph descriptions are brief and not well-illustrated, revealing a need for reexamination; it is likely that some older descriptions are based on misidentifications, especially those based on supposition. More research on museum collections is needed.

One more promising field of study involving nymphs that is receiving attention is that of environmental DNA (eDNA), which is extracted from the water in which the nymphs live (Schmidt et al. 2021). This technique, still in its infancy, could allow people conducting field surveys to detect the presence of species without the laborious task of dip-netting for them, an effort which can fail to obtain specimens, leading to 'false negatives' in diversity surveys. Detection of nymph presence using eDNA will provide crucial data for addressing habitat/conservation concerns.

Dragonfly morphology studies

A brief history of convergent morphology used in systematics

It is common for molecular and morphological evolution to occur at different rates (Patterson et al. 1993), and interpretation of morphological characters, especially, is complicated by functionally driven convergent evolution. Dragonfly wing venation features, for example, may be highly correlated (eg Carle 1982b, Pilgrim and von Dohlen 2008), and flight behavior may influence vein density, the shape and size of the wing, and the venation pattern. As discussed in Pilgrim and von Dohlen (2008), for example, Trameinae (*sensu* Fraser 1957, Davies and Tobin 1984; not supported as monophyletic by molecular data) have similarly shaped wings, with broad bases and expanded anal regions. This area of the wing has been thought to be correlated with flight behavior (eg Bechly 1996, Pilgrim and von Dohlen 2008). Several of the venation patterns commonly used in dragonfly morphological matrices (such as the number of cells in the RSPL (Fig. 7), the presence of undulation in the R_{4+5}, and the angle of the anal loop midrib) may affect chordwise flexibility, spanwise stiffness and wing twisting or camber (eg Fraser et al. 1957).

Wing venation is often cited as a character-set prone to convergence (eg Carle 1982b, Bechly 1996), but morphological characters unrelated to venation could also be highly homoplasious. Nymphal morphology, for example, may also be homoplasious. Nymph morphology may be linked to nymph habitat and behavior, such as water current speed, burrowing behavior, nymphal position in the stream (since terrestrial, bank dwellers, rock clingers and nymphs dwelling among plants in the middle of the stream may have different adaptations) and the presence of predators or competitors. Dorsal spines on the nymphal abdomen, for example, have been shown to differ in *Leucorrhinia* with fish predator presence (Mikolajewski and Johansson 2004, Hovmoller and Johansson 2004). Still other studies have suggested that spines may help stabilize the nymph during recoil from labial protraction (Nestler 1980) or when crawling through vegetation (Aguiar 1989). Other characters, such as the prothoracic epaulets, have been suggested to protect eyes during burrowing in mayflies (Edmunds and Traver 1959).

Male dragonflies use their secondary genitalia to remove sperm from competing males, and this behavior may have led to highly variable, often extremely elaborate vesica spermalis (penile) structures, the homologies of which are sometimes difficult to assess for the purposes of morphological analyses (eg Miller 1991). Miller (1991) extensively investigated the highly varied vesica spermalis structures within Libellulidae. Using the classification scheme from Davies and Tobin (1985), Miller was unable to reconcile the often complex vesica spermalis structures with libellulid taxonomy. A comparison of Miller's data to current phylogenetic hypotheses suggests no obvious phylogenetic patterns in the arrangement and length of these structures. Several vesica spermalis characters have been found to vary greatly between species within a single genus.

A morphological renaissance

The first milestone in dragonfly morphology was the book 'The Biology of Dragonflies' by R. J. Tillyard in 1917. More than 100 years and hundreds of published articles on odonates morphology later, new methods allow for detailed insights into dragonflies; opening the venue for dragonflies as models for functional morphology, biomechanics and biomimetics (eg Büsse 2023). As for insects in general, high-resolution microcomputed tomography (μCT) was the 'renaissance of morphology', as Friedrich and Beutel called it in 2008, also for odonates (eg Rajabi et al. 2017, Chitsaz et al. 2020). Researchers started to address their research questions using μCT as an efficient and non-destructive technique to allow for higher throughput (eg to histology) and a better spatial (3D) understanding of the studied anatomy. Nowadays, studies on integrative taxonomy and comparative morphology, but especially, functional morphology and biomechanics benefit from the 3D-anatomical understanding μCT allows for. Furthermore, these 3D-likenesses can be used, for example, in numerical approaches like finite element modeling (FEM) or musco-skeletal modeling and 3D-manufacturing like fused deposition modeling (3D-printing).

In combination with other methods, such as confocal laser scanning microscopy (CLSM), mechanical testing (like nanoindentation and atomic force microscopy (AFM)) or high-speed videography, studying odonates fosters our understanding of sophisticated processes and allows for biomimetic applications, using, for example, dragonfly wings (eg Khaheshi et al. 2021a, 2021b, 2021c), the flight of dragonflies (cf. the 'BionicOpter' from FESTO, Germany) or the predatory strike of dragonfly nymphs (Büsse et al. 2021).

Morphological studies on dragonflies are pushing the boundaries from the use of traditional protocols to the applications of biophotonic, material sciences, chemistry and engineering protocols that can be employed to reveal accurate phylogenetic relationships among and within the odonates (Watson et al. 2010, Nguyen, et al. 2014, Mainwaring et al. 2016, Zhou et al. 2024). For instance, in Ghana, the morphological adaptations of odonates across environmental gradients are being assessed (https://odonataingha.myportfolio.com/home). In this research, variations in wings' ultra- and nano- structures, cuticular hydrocarbon profile, hydrophobicity,

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antimicrobial and transmission properties of odonates that have enhanced wing durability in varying environmental stressors are being captured using Scanning–Electron Microscopy (SEM), optical profilometer, goniometer, UV-VIS-NIR spectroscopy, Raman microscopy, and AFMs. It is expected that these protocols will reveal apomorphic character(s) within different odonate taxa to provide better resolution of unresolved clades.

Behavioral and ecological studies

Odonates, as one of the basal clades of Class Insecta, are useful for comparative studies of behavior and ecology in Insecta. For example, they are generally believed to have integumental structures with limited capability to withstand extreme environmental stressors. This assumption is primarily due to their relatively thin exoskeleton compared to other insect groups. However, preliminary research using simulations has indicated the possibility of chemical and structural adaptations that might reinforce these integumental structures, providing some degree of resistance to environmental challenges (Nguyen, et al. 2014, Hoffman et al. 2018, Córdoba-Aguilar 2023). Understanding these adaptations is essential, as they could play a significant role in how odonates respond to ongoing and future environmental changes, including climate change.

Despite these presumed structural limitations, dragonflies are known for their outstanding thermoregulation abilities through a combination of physiological control of hemolymph circulation and behavioral strategies (May 1976, Guillermo-Ferreira and Gorb 2021). Recent thermophysiological studies on tropical mountain dragonflies have shown their thermal tolerances are broader compared to damselflies, which may help them adapt to complex and rapid climatic changes (Bota-Sierra et al. 2022). These findings suggest that dragonflies could serve as valuable bioindicators for understanding the ecological impacts of climate change on aquatic ecosystems (Sigutová et al. 2023).

Ecological studies of Odonata have highlighted several key patterns in distribution, behavior, and how this can also help elucidate evolutionary history. For instance, research has shown that odonate species composition and abundance can vary significantly across different habitats, such as forested streams, open ponds, and urban environments (Monteiro et al. 2014, Miguel et al. 2017). These variations are often linked to specific habitat characteristics, such as water quality, vegetation structure, and availability of prey. In Amazonian streams, for example, studies have found that dragonfly communities are strongly influenced by both local abiotic factors (eg water temperature, pH) and regional factors (eg forest cover), demonstrating the complexity of ecological interactions in tropical freshwater systems (Brasil et al. 2018, Oliveira-Junior and Juen 2019).

Moreover, ecological research has revealed behavioral adaptations that odonates employ to survive and thrive in diverse environments. For instance, many dragonflies exhibit basking behaviors to regulate body temperature, while others adjust their flight activity to avoid the hottest parts of the day. In urban areas, some species have adapted to artificial water bodies, demonstrating flexibility in habitat use and behavioral plasticity. Recent studies show that in cities, certain species are hunting more efficiently, possibly due to higher prey concentration or the absence of natural predators (Suárez-Tovar et al. 2024). However, this occurs alongside a loss of behavioral diversity, which could negatively impact the resilience of assemblage (Resende et al. 2021). Furthermore, the way species interact with environmental changes is influenced by phylogeny, highlighting the complexity of these ecological responses in a rapidly changing world (Bastos et al. 2021).

Another important area of study is the variation in color patterns, body structures, and thermal tolerances among different taxonomic groups. Comparative studies on color distributions and patterns, vision, and the structural durability of body parts have suggested that these traits could have evolved as responses to specific environmental pressures, such as predation, mating, and thermoregulation. For instance, some species, such as *Aeshna cyanea* (Müller 1764), *Austroaeschna multipunctata* (Martin 1901), and *Diplacodes bipunctata* (Brauer 1865), have evolved traits including self-cleaning, low adhesion, superhydrophobicity (anti-wetting), antibacterial activity and biocompatibility (Sun and Bhushan 2012, Mainwaring et al. 2016, Zhou et al. 2024). These adaptations are thought to provide advantages in terms of water repellency, minimizing microbial load, and reducing drag during flight. Additionally, UV protection through wax coverage has been reported (Guillermo-Ferreira et al. 2015), which may help mitigate the damaging effects of solar radiation, especially in high-altitude or high-latitude environments. The evolutionary history of these traits remains an active area of research. It is essential to generate information on how many taxa possess these different abilities, their evolutionary purposes, and how these traits have varied over time. This knowledge is particularly critical in a world undergoing rapid climate change.

In addition to morphological and physiological traits, recent studies have also investigated the ecological and evolutionary dynamics of odonate life history strategies, such as migration, reproduction, and predation. For example, migratory species like *Anax junius* (Drury 1773) and *Pantala flavescens* (Fabricius 1798) display remarkable navigation abilities over long distances, which may be influenced by environmental cues such as wind patterns and geomagnetic fields (eg Ware et al. 2022). These behaviors are critical for understanding odonates' dispersal and colonization dynamics, especially in fragmented landscapes and under shifting climate regimes.

Despite the growing body of knowledge, there remains a need for comprehensive empirical research that compares these various traits across taxonomic groups and under different environmental conditions. Understanding how these traits interact and vary over time and space will provide a more holistic view of odonates ecology and evolution, potentially aiding conservation efforts. The integration of molecular tools, such as DNA barcoding and genomic studies, alongside ecological and physiological data, will be essential for advancing our understanding of odonate adaptations and their potential for persistence in an era of rapid environmental change. Presently, odonate genomics is not yet being used to uncover the basis of these traits due to limited taxon sampling; with increased taxon and population level sampling the genetic basis of key traits driving Anisoptera evolution can be better understood.

Biogeographical studies on dragonflies

With their impressive age (~325 million years), broad distribution, and habitat specificity, dragonflies hold great potential as study organisms in understanding the changing face of our globe (Beatty et al. 2022, Sánchez-Herrera and Ware 2012, Sánchez-Herrera et al. 2020). Studies have demonstrated how the movement of the continents, the rise and fall of mountain ranges, shifting sea levels, and the advance and retreat of glaciers have been reflected in the current distribution of odonate species, and how their diversity has been shaped by these ancient geographic and climatic events (Low et al. 2017, Pinkert et al. 2018, Goodman et al. 2024, Tolman et al. 2024). At the regional and local levels, assessment of odonate species assemblages across land use types and landscape types along climatic gradients may help assess species shifts (Hickling et al. 2005, Hassall

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2015, Simaika and Samways 2015, Brasil et al. 2018, Alves-Martins et al. 2019, Deacon et al. 2020, Cerini et al. 2021). Some odonates thrive in human-altered landscapes (Suárez-Tovar et al. 2022, Abbott et al. 2022) while others do not; studies of these species at multiple scales can reflect how human activities affect odonates and the aquatic habitats they rely on (Dingemanse and Kalkman 2008, Verheyen et al. 2019, Smith et al. 2023). Further, the dispersal patterns among taxa are highly variable with many largely sedentary species but also many species capable of readily colonizing new habitats as evidenced by the many species expanding their range due to climate change. In some species long range migration is part of the life history, the best examples of which are *Pantala flavescens* in which there is a annual migration spanning 2 or more generations between Africa and Asia (Hobson et al. 2012) and *Anax junius* in which the spring generation migrates northwards to the north of the US and Canada with their offspring migrating back to the south in autumn (May and Matthews 2008). Another incredible example is *Hemianax epphippiger* Burmeister 1839 (which is also recognized as *Anax ephippiger* (Bermiester) in the World Odonata List), which colonized the Caribbeans from Africa in the past 2 decades (Hedlund et al. 2020). All these species provide the opportunity to explore the mechanisms and systems allowing such relatively small-bodied animals to perform these energy-demanding tasks (Smallshire and Swash 2020, Hedlund, et al. 2021).

Genetics and genomics studies

As genomic resources continue to become more accessible and affordable, including the use of long-read and transcriptome sequencing techniques, the taxonomy and systematics of dragonflies will advance significantly (Wellenreuther et al. 2022, Bybee et al. 2024, Fuller and Wellenreuther 2024). Indeed, studies of the relatively few genomes (ie, ~10 high quality genomes from damselflies and dragonflies) that are currently available have already shed light on the evolution of Odonata, revealing that the autosomes remain remarkably conserved across more than 250 million years of evolutionary history (Tolman et al. 2023a). The continued integration of genomic data with traditional taxonomic methods will significantly enhance the accuracy of species identification, helping to resolve long-standing taxonomic ambiguities. Beyond clarifying these uncertainties, genomic advances will also play a crucial role in assessing a species' evolutionary potential. For example, by measuring genomic vulnerability (ie, an estimation of the amount that allele frequencies would need to change in order to keep pace with environmental change), researchers can improve predictive models to forecast how species will respond to changing climate and environmental conditions across their distribution areas (Newton et al. 2023, Tolman et al. 2023d).

Dragonflies also offer unique opportunities to explore the fluidity of species boundaries and the complexities of hybridization and subsequent genomic introgression (Suvorov et al. 2021). Research on odonates has already shown that species distinctions in some genera, such as *Macromia*, are not as rigid as previously thought, with considerable genetic mixing occurring across populations of *M. illinoiensis* Walsh 1862 and *M. illinoiensis georgina* (Selys 1878) (Ware, pers. comm) for example; hybridization is likely not uncommon in parts of the ranges of several Anisoptera and species level assessments are needed for many taxa. Future research should prioritize understanding these dynamics to refine species identification and improve taxonomic frameworks.

We must pay close attention to the taxonomic foundation of our knowledge. While genomic data is rapidly accumulating in public databases like the National Center for Biotechnology Information (NCBI), there remains a significant imbalance between model and non-model species. Future efforts should thus prioritize gathering sufficient resources to cover a diverse range of species, across various geographical scales and over time, employing different methodological approaches. Expanding research beyond the well-studied species in the northern hemisphere to include a more diverse array of dragonfly species worldwide will be essential (egWellenreuther et al. 2022). Such efforts will facilitate comparative analyses that uncover general patterns and processes in speciation and diversification.

One promising outcome of modern genomic methods is the study of functional genomics, through which we can understand the genetic diversity of species and how that diversity relates to morphological, physiological, and behavioral attributes of species. As we expand our knowledge through genome assembly and population genomics research, our ability to investigate gene function will greatly increase, allowing for a more fundamental understanding of adaptive evolution in dragonflies. This future research not only has implications for our understanding of dragonflies, but through comparative methods, we can better understand evolutionary function and processes in other insect orders.

Regional and global study of dragonflies

As for other charismatic groups of organisms, there is a broad group of amateur naturalists, community scientists and academics working together at regional and global scales to promote the study of Odonata. Globally, there are 2 organizations, the World Dragonfly Association, and the Societas Internationalis Odonatologica that promote the study and conservation of Odonata, publishing the *International Journal of Odonatology* and *Odonatologica* respectively. In the Western Hemisphere, there are the Dragonfly Society of the Americas and the Sociedad de Odonatología Latinoamericana, as well as provincial and country-wide efforts. In the Eastern Hemisphere, there is the European Congress of Odonatology, as well as country wide efforts across Europe, Asia, Oceania and Africa (eg the Indonesian Dragonfly Society, Die Gesellschaft deutschsprachiger Odonatologen). Here we provide 2 case studies of work being done in Latin America and West Africa.

Odonata efforts in Latin America

Progress in the knowledge of the regional dragonfly diversity has increased in recent decades (Muzon et al. 2017). The establishment of the Sociedad de Odonatología Latinoamericana (SOL) has played a crucial role in advancing this knowledge. One of SOL´s first projects was the assessment of all the species in the region for the IUCN Red List, where 1104 species were evaluated. Among these, 296 were classified as data deficient due to their rarity and the lack of information necessary to estimate their extinction risk, underscoring the substantial research effort still required in the region. The results of this assessment have become a significant base for research and conservation in the region (the tropical Andes assessment report was published in 2016 (Bota-Sierra et al. 2016), and the remaining assessments can be found at the IUCN portal). Several Latin American countries have a vibrant research network, with native researchers investigating a number of different topics with odonates; Argentina, Brazil, and Colombia are the most active at the time (eg Alves-Guillermo-Ferreira et al. 2014, Oliveira-Junior et al. 2015, Brasil et al. 2019, Martins et al. 2019, Lozano et al. 2020, Ferreira et al. 2023, Bota-Sierra et al. 2024). Countries like Belize, Costa Rica, Ecuador, French Guiana, and Panama are well sampled by visiting researchers, mainly from North America and Europe (Mauffray and Tennessen 2019, Paulson and Haber 2021, Rochas et al. 2022). Peru and

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Venezuela are megadiverse countries which were intensely explored in the past (eg De Marmels 1988, Hoffmann 2008, Vivas-Santeliz and De Marmels 2017), but current research in these countries has slowed in pace for various reasons. In Peru, new studies have begun to be published (Medina-Espinosa et al. 2024), and a new generation of researchers is being trained. Some countries such as Bolivia, El Salvador, Nicaragua, Chile or Paraguay, remain underexplored and are awaiting for native students to unveil their odonata richness.

SOL has been instrumental in fostering greater integration among regional researchers, promoting collaborations, joint research projects, and networked publications. This collaborative approach is exemplified in recent research efforts, such as the study by Alves-Martins et al., (2024), which emphasizes the importance of regional collaborations to address conservation challenges and advance scientific understanding of the Neotropical odonate fauna. Such initiatives highlight the potential for continued growth in odonatological research through regional and international partnerships.

Odonata efforts in West Africa

Elliot Pinhey, a taxonomist from the Netherlands who was active 1950–1981 described 47 species of African taxa; a majority of these were from East Africa however he published on several species from West Africa in his 1962 paper on tropical Odonata of Africa (Pinhey 1962). The knowledge of Odonata fauna in West Africa in particular is relatively limited compared to other regions of the world, and studies of Odonata taxonomy are mainly based on morphology. Biodiversity studies comprise some of the earliest and most important baseline data that advanced the knowledge of Odonata in Nigeria (eg Gambles 1971, 1980). Records of odonate specimens by the great curator, Mr. Oboite, at the Museums of Natural History of University of Ibadan date back to 1951 while those from Ahmadu Bello University Zaria, by J C Deeming, M. J Parr and R. M Gambles date back to 1957. Presently, efforts to establish a strong West African Odonata collection that would support further research on the entire fauna are ongoing.

Over the years, West African researchers and their colleagues have surveyed several geographical regions. Of the West Africa countries, Nigeria has had perhaps the most extensive recent research on odonates (Adu and Ogbogu 2011, Adu et al. 2014, 2015, 2016, 2022a,b, Kemabonta et al. 2016, 2018, 2019a, b, 2020a, b, Zakka et al. 2017, Ekpah et al. 2020a,b, 2021, Adu. 2022, De Vries et al. 2024) but current efforts in Ghana (https://www.nsf.gov/awardsearch/showAward?AWD_ID=2246257) will likely lead to published biodiversity assessments in the near future. The establishment of a Citizen Science platform for nature enthusiasts and a network of local and international experts focused on Odonata in 2020 has greatly increased the community of odonate workers in the region; this forum of dedicated Odonatologists and nature lovers facilitates the exchange of information, ideas, and mentorship support and has led to the digitization of nearly 7,000 individual specimens in databases such as GBIF. Work is ongoing in West Africa on developing biomonitoring and bioindicator tools, while also evaluating ecology, taxonomy, and conservation of dragonflies using morphology and molecular datasets, including environmental DNA (Uche Dike, pers. comm.).

Global collaboration

Research on Anisoptera has been collaborative, but much more needs to be done to promote global participation and capacity building. Although past research often depended heavily on morphological characters for taxonomic identification that were prone to convergence, there is a morphological renaissance underway with new techniques allowing for functional morphology studies and understanding of internal anatomy. Ongoing collaboration among researchers in the global research community has also facilitated the sub-genomic, genomic and Sanger sequencing of many species, with GEODE aiming to sequence a majority of species in the Odonata. Making sure that everyone in the global odonate community has access to modern morphological tools as well as molecular and bioinformatic tools and skills should be at the forefront of our community efforts. Overall, there is a pressing need for continuous training and education of local odonatologists involved in taxonomy, systematics, ecology, behavior, population genetics and genomics, and odonatology needs to work to ensure equitable distribution of resources, access to specimens, and skill set building.

Human cultural research is important for conservation

Dragonflies have been documented in cultures and communities around the world (Lucas 2002, Mitchell and Lasswell 2005), and different regions have numerous common names for dragonflies. Within the United States they are known as devil's darning needles, snake doctors, mosquito hawks, Tanilai, Shumakolowa and Pinao (Lucas 2002, Mitchell and Lasswell 2005). In Brazil, they are Aguadera, Cavalo da Judea, Jacina, Lavadeira, Pito de demo. In Russia they are called Strecosa, Kiil, and Enegarak. On different islands in Polynesia we see many names with a common pattern: Kisikisisi-wai, Bukaroo, Caicai-Wai, and Tivai vai. Usually these names indicate the group at large but some are descriptive of the color and size; in Japan Kino-Tombo is translated to yellow-dragonfly or Aka-Tombo red dragonfly. In some cases, common names reflect the behavior or life history of dragonflies. One common name in Brazil is 'lava-bunda', which roughly translates to English as 'tail-washer' or 'butt-washer', probably based on the observation of females ovipositing into water by dipping the tip of their abdomen (Aguilera and Silva 2021). Some rare common names identify particular species: Kapokapowai in Māori makes reference to the petaltail species in genus *Uropetala* Selys 1858. Dragonflies have often been used to tell stories in different cultures, like the devil's darning needle that would sew a children's eyes or mouth shut if they misbehaved. They have also been used to predict which fish you will catch or how much rain will fall as well as water quality.

While we have information on numerous groups we still lack information in many countries regarding folklore and indigenous knowledge. Why are naming and stories about species important to different cultures around the world? Dragonflies are becoming an important source of ecotourism in many regions (Lemelin 2009, Ngiam et al. 2017). Publication of field guides and digital tools focused on general audiences, including scientific and common names, is crucial to attract more people to the dragonfly world (eg Dunkle 2000, Bota-Sierra et al. 2019). All of these names communicate various ideas and thoughts that could be further explored. What use do these common names have in science communication and conservation? Common names in different cultures communicate perspectives that could be explored. How do these stories make you feel or respond to dragonflies? Do they help you connect to the group and motivate you to conserve the habitat and species? A common phrase is *you need to know what species there are in order to conserve them*. What is the best way to communicate about these species to the public so we can conserve them? What motivates people to want to donate money, vote or create habitat for them to thrive? How can scientists, local leaders, community members, science communicators, and government officials work together to ask and answer questions that benefit both dragonflies and the communities they live in? Some work has been done in science communication to strategically communicate and work with communities where these

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species live but so much work needs to be done (Nisbet and Scheufele 2009, Nisbet and Markowitz 2016, National Academy of Science, Engineering and Medicine 2017, Besley et al. 2016, Garlick and Fallon 2023andand). As we work to answer these questions, there needs to be communication and collaboration between taxonomists, systematists, ecologists, conservation biologists, local leaders, community members, government officials, social scientists practiced in ethnography, and science communicators to truly leverage dragonflies in this broader effort.

Our conclusion about the future of Anisoptera systematics

As reviewed here, the field of Anisoptera systematics is incredibly active. New revisionary work continues to build on historical definitions, and the amount of morphological, genetic and genomic data available for many families is steadily increasing. The dragonfly research community is working hard to be cohesive and equitable, and the future of this discipline is as global as the animals we study.

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