Jessica L. Ware, American Museum of Natural History, NY, NY, 10024
jware@amnh.org

Quick guide
Odonata

What are dragonflies and damselflies?
Dragonflies and damselflies, which make up the order Odonata (6300 species), have terrestrial adults and nymphs that inhabit freshwater. Dragonflies comprise ~3100 species in the suborder Anisoptera. Although dragonflies vary in colour, shape and size, they have a general "gestalt". Dragonflies tend to have thick abdomens, and a majority extend their wings laterally at rest. There are 10 recognized dragonfly families. Some families have their eyes spaced apart ("clubtails", aka Gomphidae), and others have eyes which seem fused together, forming a central seam ("darners" aka Aeshnidae). Dragonfly nymphs respire using internal gills located in their rectum. Damselflies comprise ~3200 species in the suborder Zygoptera. Damselflies have slender abdomens, and a tendency to hold their often petiolate wings over their back when at rest (or slightly apart as in "Spreadwings", Lestidae). There is debate about the number of valid damselfly families, which may be >35. Damselflies have eyes that are spaced apart. Damselfly nymphs respire using external gills (caudal lamellae). A third taxon, suborder Anisozygoptera, consists of 3 Asian species. Anisozygopterans have thick bodies and petiolate wings. All odonates are voracious predators. Nymphs will eat both invertebrates (such as juvenile flies) and vertebrates (such as small fish). Adult odonates consume insects, even cannibalistically. Dragonfly and damselfly families differ in habitat preferences, preferring lentic (e.g. lakes and ponds) or lotic (flowing water like that found in rivers or streams) habitats .

How do they reproduce?
Dragonflies and damselflies reproduce in freshwater, where females lay eggs (oviposit) either in plant material or on the surface of the water. Females are capable of storing sperm in internal sperm storage organs called the bursa copulatrix and spermatheca. Males have two sets of genitalia, with sperm produced in the testes at the tip of the abdomen and then transferred to the vescia spermalis (secondary genitalia) at the base of the abdomen. When reproductive behaviour begins, males solicit mating by clasping females behind the head using appendages on the 10th abdominal segment. Depending on the species, females may have small pits on the thorax dorsum in which the male appendages fit as a species specific lock-and-key, but lock-and-key structures are more common in damselflies. If a female is receptive to mating, she will bend her abdomen to bring her vulvar lamina to meet the male's secondary genitalia; mating pairs thus form what is called the "copulatory wheel". Sperm transfer takes place after a period of sperm displacement, wherein the male uses his secondary genitals to either pack deeply in or scrape out any previous male's sperm from the female sperm storage organs. Females lay their eggs either with an egg laying apparatus called an ovipositor (all damselflies, some dragonflies), which they use to place eggs in plant material, or they lay their eggs without such a structure by tapping their abdomen on the water's surface to disperse their eggs (some dragonflies).

How do they fly?
Dragonflies and damselflies are known to be highly visual predators who hunt on the wing. They possess two sets of densely veined, corrugated wings, which move synchronously to produce lift. Odonates are capable of highly acrobatic flight, with some families capable of very short turning radii; this maneuverability facilitates escape from common predators such as frogs, fish and birds. Such maneuvers also aid in mating displays, as intrasexual selection has selected for acrobatic competitive territorial mating “dances” in males looking to mate with females aggregating at freshwater. Dragonflies are known to be particularly fast fliers, and most larger dragonflies capable of velocities of 10 m/s.

How old are odonates?
Odonata are among the earliest diverging groups of flying insects, and are considered an ancient insect group. The fossil record of odonates is extensive, both in compression and amber fossils. The oldest crown odonate fossils are thought to be ~Triassic to Jurassic in origin, and recent molecular transcriptomic work suggests that odonate suborders diverged from each other in the Permian period.

What have we learned from molecular work?
Most early classification in this group was based on wing venation characters, which have shown to be unreliable for some levels of classification given that they are often correlated with flight behaviour. Molecular systematics has allowed the reclassification of intrafamilial relationships (invalidating most subfamilies in speciose groups such as the skimmers, Libellulidae), and largely resolved the backbone of the Anisoptera tree of life. Zygoptera interfamilial relationships remain chaotic, despite years of study.

Where can dragonflies and damselflies be found?
Dragonflies and damselflies are globally distributed. They have been found on every continent but for Antarctica, from the arctic to the southernmost regions of the southern Hemisphere. There is a rich diversity of odonates around the equator, with high species biodiversity in the tropics. Sadly, many regions of the world are considered data deficient with respect to dragonfly and damselfly conservation status.

What don’t we yet know about odonates?
Despite their ubiquity around lakes, gardens, and even cities, very little is known about odonate population sizes, or individual travel distance (daily and lifetime). Although we know females store sperm, we don’t yet know how sperm is chosen during egg fertilization. Although some behaviours have been well studied many species lack basic life history information. For many taxa, adult and larval forms have not been associated, or larvae are undescribed. Information on ancestral biogeographical patterns is lacking for most taxa, and we have rudimentary understanding of the climate change impact on odonates.

What does the future hold for odonate research?
With the advent of computerized tomography (CT), internal morphology descriptions for both nymphs and adults is possible. Genome sequencing allows study of dragonfly colour vision, and

transcriptomes have inferred robust phylogenies. Artificial intelligence has extracted dragonfly wing features, and working groups have been formed to study odonate global abundance. The future of odonate research is rooted firmly in a collaborative community that seeks to cooperatively train others in these novel techniques, in hopes of using Odonata as model organisms for evolutionary and ecological study.

Where can I find out more?

Bried, Jason Leslie Ries, Brenda Smith, Michael Patten, John Abbott, Joan Ball-Damerow, Robert Cannings, Adolfo Cordero-Rivera, Alex Córdoba-Aguilar, Paulo De Marco, Jr, Klaas-Douwe Dijkstra, Aleš Dolný, Roy van Grunsven, David Halstead, Filip Harabiš, Christopher Hassall, Martin Jeanmougin, Colin Jones, Leandro Juen, Vincent Kalkman, Gabriella Kietzka, Celeste Searles Mazzacano, Albert Orr, Mary Ann Perron, Maya Rocha-Ortega, Göran Sahlén, Michael Samways, Adam Siepielski, John Simaika, Frank Suhling, Les Underhill, Erin White. (2020). Towards Global Volunteer Monitoring of Odonate Abundance, *BioScience*, biaa092.

Büsse, S., Hörnschemeyer, T., & Gorb, S. N. (2017). The head morphology of Pyrrhosoma nymphula larvae (Odonata: Zygoptera) focusing on functional aspects of the mouthparts. *Frontiers in Zoology*, 14(1): 1-13.

Corbet, P. S. (1999). Dragonflies: behaviour and ecology of Odonata. Harley books.

Kohli, Manpreet, Harald Letsch, Carola Greve, Olivier Béthoux, Isabelle Deregnaucourt, Shanlin Liu, Xin Zhou, Alexander Donath, Christoph Mayer, Lars Podsiadlowski, Ryuichiro Machida, Oliver Niehuis, Jes Rust, Torsten Wappler, Xin Yu, Bernhard Misof, Jessica Ware (2020). How old are dragonflies and damselflies? Odonata (Insecta) transcriptomics resolve familial relationships. *bioRxiv*.

Nakahara, M., & Tsubaki, Y. (2007). Function of multiple sperm-storage organs in female damselflies (Ischnura senegalensis): Difference in amount of ejaculate stored, sperm loss, and priority in fertilization. *Journal of Insect Physiology*, 53(10): 1046-1054.

Ruppell, G. (1989). Kinematic analysis of symmetrical flight manoeuvres of Odonata. *Journal of Experimental Biology,* 144: 13-42

Suvorov, Anton, Nicholas O. Jensen, Camilla R. Sharkey, M. Stanley Fujimoto, Paul Bodily, Haley M. Cahill Wightman, T. Heath Ogden, Mark J. Clement, and Seth M. Bybee. (2017). Opsins have evolved under the permanent heterozygote model: insights from phylotranscriptomics of Odonata. *Molecular Ecology,* 26 (5): 1306-1322.

Waage, J. K. (1986). Evidence for widespread sperm displacement ability among Zygoptera (Odonata) and the means for predicting its presence. *Biological Journal of the Linnean Society*, 28(3): 285-300.

Figure 1 :

Images of dragonflies and damselflies: (a) *Neopetalia* nymph (photo credit: Jessica Ware), (b) Flame tailed pondhawk (photo credit: Greg Lasley), (c) American rubyspots in copulatory wheel (photo credit: Greg Lasley), (d) Swamp darner (photo credit: Greg Lasley), (e) Blue fronted dancer (photo credit: Greg Lasley)