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History of dragonfly flight

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From their earliest appearance in the fossil record, dragonflies have clearly taken a different approach to flight than other insect groups. Even the superficially similar Neuroptera do not fly like dragonflies. Flight specialisation has enabled dragonflies to occupy a range of niches, as specialised predators of flying insects, for around 300 My.

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The Pterygote insect lineage may have first appeared in the fossil record some 400 million years ago (Mya) – recorded as a single mandible in the Rhynie chert beds (Grimaldi & Engel, 2005; Tillyard, 1928) – but the assignment of this specimen is presently thought to be problematical (Haug & Haug, 2017). There then follows a long break with no suitable terrestrial fossil deposits known. Around 320 Mya insects appear in Earliest Upper Carboniferous deposits (Grimaldi & Engel, 2005). At this point the group are already both diverse and fully flighted, with numerous lineages.

Within Insecta the Odonata belong to the division Palaeoptera, so named by Martynov (1924) in the belief that the palaeopterous condition, where wings cannot be twisted to lie over the abdomen, represented a "primitive" condition preceding the evolution of the neopterous condition. There remains debate on the evolution of the insect wing base with arguments over the status of a neopteran ancestor or of a diaphanopteroid palaeopteran structure (Ninomiya & Yoshizawa, 2009). However, the dragonfly wing base is clearly a derived condition, arrived at by a process of reduction through fusion of wing base sclerites.

The earliest dragonfly fossils come from the later Namurian, about 320 to 313 Mya, and are among the earliest insects. There are a series of closely dated discoveries that in evolutionary terms are essentially simultaneous. The specific-to-Odonata secondary copulatory apparatus did not occur in the Hagen-Vorhalle lagerstätte material, however it had clearly evolved by the Late Permian in the Protozygoptera (Zessin, 2008).

A difficulty in understanding arises because a large number of forms (and hence names) were recovered within a notional age period of perhaps 20 My, and tree-building heuristics always build trees – hence over-interpretation is an ever-present danger. By the time they appear in the fossil record the dragonfly grouping was already diverse and had clearly radiated significantly.

At first record these animals had in the wingbase the peculiar-to-dragonflies triple vein structure (RP + M + CuA of Trueman & Rowe, 2019), high aspect ratio wings, and long narrow

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abdomens, indicating they were already committed to an ecological niche close to that occupied today.

Whilst the triple vein was present, few other of the characteristic structures of dragonfly wings were present in these earliest forms; most obviously both nodus and pterostigma were absent. The diverse wings of early odonatoid groups (Protodonata, Meganisoptera) are figured in Carpenter (1992) and Nel et al. (2009), among others. In ecology these early dragonflies might have resembled present-day Ascalaphidae (Neuroptera), which, while lacking the highly specialised wing structures and flight mechanisms of crown Odonata, still operate as aerial predators.

Within 15 My of the oldest dragonfly fossils, by *c*.305 Mya, the Protozygoptera lineage had appeared in the record (Jarzembowski & Nel 2002). As at the end-Permian great extinction only some lineages from within the Protozygoptera made it through we can gloss over the other "experiments", even though some forms were successful for tens of millions of years. Features of the surviving Protozygoptera lineages included both a form of "nodus" and a pterostigma. For purely mechanical reasons protozygopteran wing function must therefore have closely approximated that in living Odonata.

We have no idea why some Protozygoptera survived the end-Permian event. It might have been something to do with their biology: size, habitat, larval biology; but it may have been just luck. Most Protozygoptera species probably went extinct together with all the other odonatan lineages.

Protozygotera had a stemmed wingbase, so this is the plesiomorphic state, and retained by the Zygoptera.

In the earliest Triassic, starting about 250 Mya, there was a very rapid radiation of dragonfly types. The lineages of Zygoptera and Anisoptera (including the "Anisozygoptera") separated at this time (Thomas, Trueman, Rambaut, & Welch, 2013). Whereas Zygoptera retained the general petiolate wing shape of the ancestral Protozygoptera, the anisopteran line has variously evolved a secondarily broadened wingbase including, in the hind wing, a neoanal field. Within both lineages there is variation in the detailed form and the functioning of the wings. The diversity of extant dragonfly wings is indicated in Wootton (this volume, Figure 1 p. 34). The functioning of the various wing forms, and their evolution in response to selection pressures are reviewed in Wootton & Newman (2008).

Dragonfly flight is inherently unstable about all three axes: pitch, roll, and yaw. Flight control is maintained dynamically, using sensory input and neural processing to balance the outputs of each of the four wings. Dragonflies "fly by wire". Dragonflies can loop, roll, slip sideways under any flight conditions, hover with body horizontal, fly backwards, accelerate to over $10\,\mathrm{m\,s^{-1}}$, or stop, in a few wing strokes, spin about an axis in two wing strokes, and even fly upside down while grappling with a rival. Clearly wing forms capable of such flight have been around for over 250 My (the separation of Zygoptera and Anisoptera) and perhaps 300 My (the early records of Protozygoptera).

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