## 3.9 The relevance of palaeontological data for understanding the age and origin of extant odonates

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**Paleontological evidence** provides direct or indirect minimum ages for the existence of recent lineages and the concerning phylogenetic splitting events, and thus also is of crucial importance as independent evidence for calibrating molecular clock data. Furthermore, fossils provide independent tests for theoretically reconstructed evolutionary scenarios of character transformation and reconstructed ancestral ground plans.

The earliest stem group representatives of odonates belong to the protodonate grade (Erasipteridae and Namurotypidae) and have been found in the lowermost Upper Carboniferous (Namurian B, 319 mya) of Hagen-Vorhalle in Germany. The morphologically more primitive Eugeropteridae from the Upper Carboniferous of Argentina are not reliably dated and probably somewhat younger. Even protodonate larvae are known from the Upper Carboniferous Mazon Creek locality in U.S.A. and already were aquatic with prehensile mask. Adult protodonates did not possess a male secondary genital apparatus and thus could not mate in wheel position, but probably transferred external spermatophores like apterygote insects. The oldest fossil record of odonates with secondary male genitalia is provided by the protozygopteran *Engellestes* from the latest Early Permian of Tshekarda (ca. 278 mya). Typical structures of modern odonate wing venation, like nodus, discoidal cell, and pterostigma, are already known from a few protozygopteran damselflies (*e.g. Bechlya* and *Luiseia*) of the Upper Carboniferous of New Mexico (299 mya) and England (307 mya).

The first fossil record of crown group representatives of Odonata is represented by isophlebioid damsel-dragonflies from the Upper Triassic (Carnian, ca. 232 mya) Schilfsandstein of Bavaria and the Australian Ipswich coal mines (*e.g.*, Mesophlebia), which belong to the stem group of Epiprocta and still had larvae with three caudal gill lamellae like Zygoptera. The earliest true Zygoptera is a still undescribed Hemiphlebiidae from the Upper Jurassic (Tithonian) limestones of Painten (150 mya) and Solnhofen (148 mya) in Bavaria. The oldest known relative of extant Epiophlebiidae is the recently described, small damsel-dragonfly Burmaphlebia from the Lower Cretaceous amber of Myanmar (99 mya). The earliest stem group Anisoptera is an undescribed Liassophlebiidae from the Lower Jurassic (Liassic alpha) of Bavaria (200 mya) and many more are known from the Liassic Posidonia shale (180 mya) of Middle Europe, but the first crown group representatives of Anisoptera (Cymatophlebia) appear in the Upper Jurassic Malm beta (154 mya) of the Swabian Alb. Of many modern families, the oldest representatives (stem group or crown group) can be found in the Lower Cretaceous (*e.g.*, Crato Formation). Fossil damselflies and dragonflies from the Paleogene (*e.g.*, Baltic amber, Middle Eocene, 44 mya) and especially the Neogene often can already be attributed to modern genera, but only Quartenary fossils from the Pleistocene are conspecific with modern species.