Evolutionary changes in the ovipositor shape of sawflies revealed by early fossils

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Considering taxonomic diversity, extant Xyelidae represent a very small subset of the past diversity of the family. Its earliest representatives are the Triassic sub-families Archexyelinae and Madygelinae. New, well-preserved Madygellinae specimens found from the Upper Triassic Ominé locality (Momonoki Formation, Mine Group; Carnian; Japan). The six specimens can be assigned to four new species, belonging to three genera, one being new. Two of the specimens expose body parts and wings. It is the first discovery of such well-preserved remains for this sub-family, providing important information for updating the systematics of Madygellinae, especially regarding ovipositor morphology. This organ plays an important role in Hymenoptera ecology, as herbivorous sawflies use it to lay eggs into plant tissues. To appreciate in more details the evolution of this ecologically important organ, we considered ovipositor shape in both fossil and extant Xyelidae. All known Triassic representatives display high aspect ratio types, namely ‘needle- (long and narrow)’ or ‘dagger-like (long and wide)’ ovipositors, while extant forms display both extremes of the range of ovipositor types, namely the high aspect ratio ‘dagger-like’ and ‘needle-like’ types (in Xyelinae) and the low aspect ratio ‘short and wide’ type (in Macroxyelinae only). The fossil record of Middle Jurassic to Lower Cretaceous sawflies shows the highest diversity of ovipositor types for the family, with the high aspect ratio ones present in Xyelinae, Daohugoinae and Macroxyelinae (‘dagger-like’ and, in Xyelinae only, ‘needle-like’ ones); and the ‘short and wide’ type in Macroxyelinae. Afterwards, the range of ovipositor types slightly declined but, more importantly, concentrated on the two, very distinct types known nowadays. Also, specialisation in ovipositor type diversity seemingly occurred during the Jurassic-Cretaceous transition for the Xyelinae, while Macroxyelinae displayed a peak of diversity during the Lower Cretaceous. In other words, decline in disparity was probably not contemporaneous in Xyelinae and Macroxyelinae. As for the latter sub-family, the appearance of the ‘short and wide’ ovipositor indicates a transition from deep to subsurface insertion of the egg and, by implication, a departure from the endophytic development, within a male conifer cone (still preserved in extant *Xyela* species), in favor of the external dwelling on leaves of pre-angiosperm plants (with further transformation into the feeding on leaves of elms and hickories by larvae of the extant *Macroxyela* and *Megaxyela*, respectively). It can then be assumed that ovipositor shape transition was accompanied with a larval diet change in Macroxyelinae (in contrast to at least some Xyelinae).