

Fossil Ovipositions of Dragonflies: Review and Interpretation

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Abstract—The paper deals with the stratigraphic range and morphology of fossil formations on plants interpreted as insect ovipositions. Our analysis of the insect fossil record has shown that the endophytic ovipositions probably belong to the Kennedyina and Triadophlebiina (in the Paleozoic and Lower Mesozoic) and to the Calopterygina (in the Upper Mesozoic and Cenozoic).

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INTRODUCTION

Fossil ovipositions of insects on plant organs are among the rarest, but also the most revealing, traces of arthropod–plant interactions in the geological record. Compared to other, more frequent, traces, such as leaf feeding damage, galls, and mines, ovipositions can provide the most complete information about the biology and even morphological features of the insect that left them. Therefore, the study of fossil ovipositions on plants is extremely important both for the clarification of insect–plant coevolution and for the reconstruction of the reproductive biology of insects.

In this paper, we review the stratigraphic range and morphological and biological features of fossil ovipositions on plants and the interpretation of such ovipositions.

In the geological record, ovipositions on plants occur irregularly. We have found only one paper describing Upper Carboniferous ovipositions (Bethoux et al., 2004). Ovipositions on stem fragments of *Calamites* consist of considerably elongated eggs, arranged in parallel, at a short distance from each other, tending to form horizontal rows. From the Permian, only a single

find is known; a so far undescribed specimen from northern Russia (Upper Permian, Sukhona River). The shape and arrangement of the eggs, in an oviposition on a leaf of *Pursongia* (Pl. 15, fig. 1) differ slightly from Carboniferous examples. The most numerous pre-Cenozoic ovipositions are described from the Triassic; ovipositions on *Equisetites* from the Keuper of Germany and on leaves of *Taeniopteris* from the Ladinian of France (Grauvogel-Stamm and Kelber, 1996). The former ovipositions are the same elongate oval structure (occasionally, the eggs are in an indistinct zigzag arrangement), and the latter ovipositions include more rounded eggs arranged in closely packed rows, one after another. Several finds are known from Jurassic deposits (including the Jurassic/Cretaceous boundary): formations on leaves of the genera *Schmeissneria* and *Podozamites* from the Lower Jurassic of Germany (Konijnenburg-van Cittert and Schmeißner, 1999) and on leaves of *Ginkgoites*, *Desmiophyllum*, and *Pityophyllum* from three Transbaikalian localities of the Jurassic/Cretaceous boundary (Pl. 15, figs. 2, 3; Vasilenko, 2005) are similar to the Carboniferous, Permian, and Triassic ovipositions. Ovipositions with oval elongated

Explanation of Plate 15

Fig. 1. Fossil ovipositions on leaves of *Pursongia* sp., PIN, no. 3321/28, Vologda Region, Upper Permian, $\times 3.5$.

Fig. 2. Fossil ovipositions on leaves of *Ginkgoites*, PIN, no. 4626/483, Transbaikalia, Upper Jurassic–Lower Cretaceous, $\times 4$.

Fig. 3. Fossil ovipositions on leaves of *Pityophyllum* sp., PIN, no. 4626/481, Transbaikalia, Upper Jurassic–Lower Cretaceous, $\times 4$.

Figs. 4–6. Fossil ovipositions on leaves of *Querexia* sp., Amur Region, Upper Cretaceous: (4) PIN, no. 5140/10, $\times 5$; (5) PIN, no. 5140/2, $\times 4.5$; (6) PIN, no. 5140/1, $\times 10$.

Fig. 7. *Arctotypus sylvanensis*, fragment of a dragonfly of the suborder Meganeurina with a wide wing base, PIN, no. 1700/3245, Perm Region, Lower Permian, $\times 1.3$.

Fig. 8. *Paurophlebia lepida*, fragment of a dragonfly of the suborder Triadophlebiina with a stalked wing base, PIN, no. 2785/7, Kyrgyzstan, Triassic, $\times 3$.

Fig. 9. *Permepallage angustissima*, fragment of a dragonfly of the suborder Kennedyina with a stalked wing base, PIN, no. 66/117, Arkhangelsk Region, Upper Permian, $\times 1.3$.

Fig. 10. *Ditaxineurina* fam. gen. sp., fragment of the body of a dragonfly with a wide wing base, PIN, no. 1700/461, Perm Region, Lower Permian, $\times 1.5$.

Plate 15

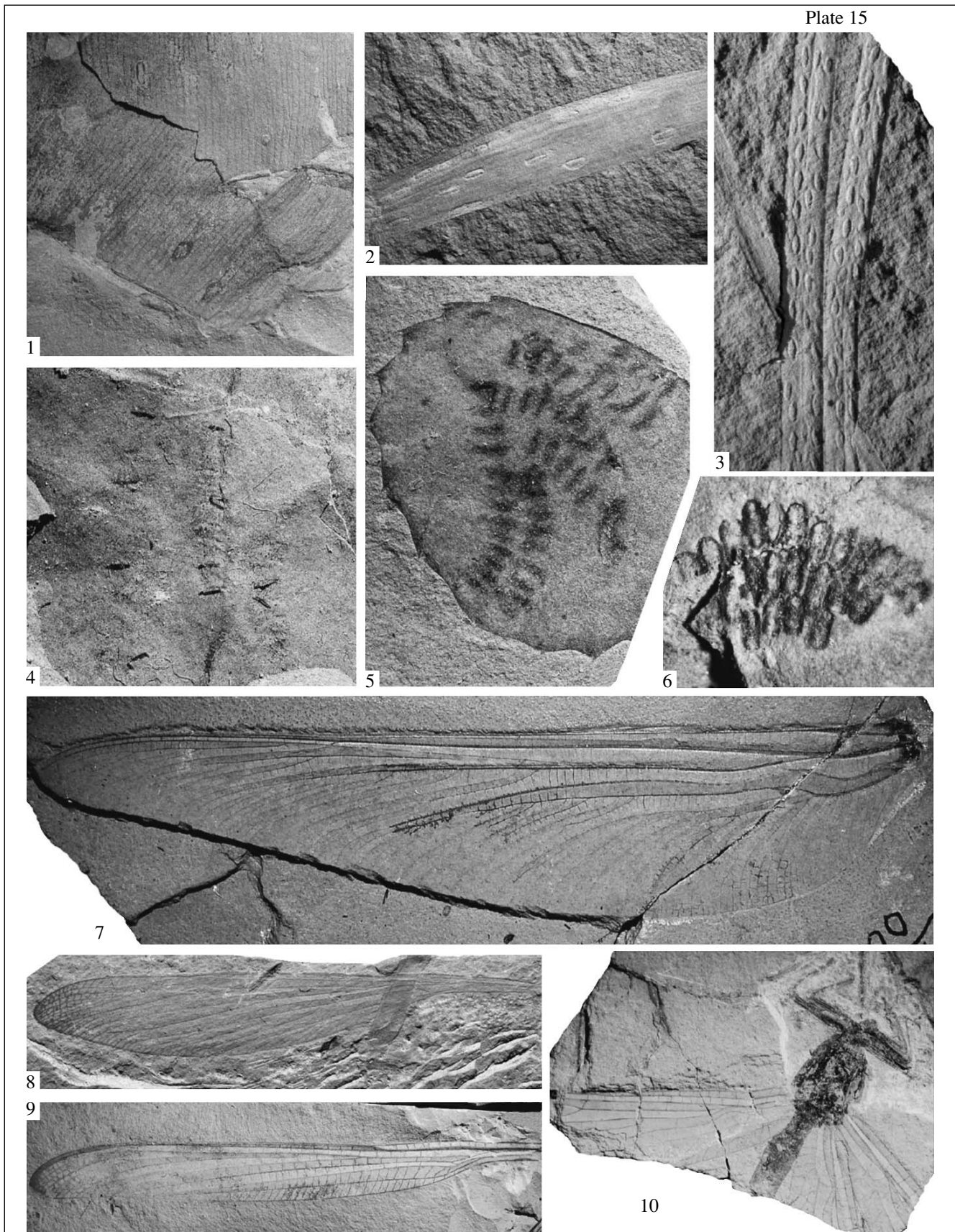
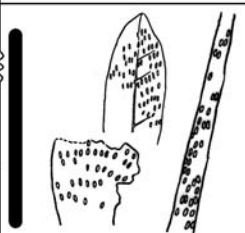
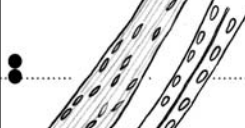
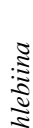
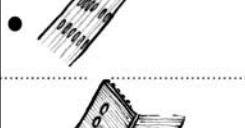
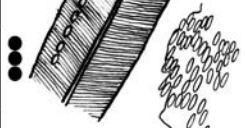
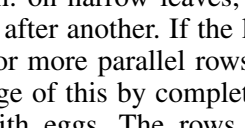
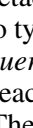
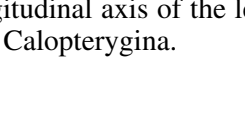


Table 1. Stratigraphic ranges of various ovipositions on plants and main suborders of dragonflies

Era	Period	Epoch	Dominating type of endophytic ovipositions (schematized drawing)	Plant taxa with ovipositions (references)	Occurrence of main suborders of dragonflies
Cenozoic	Paleogene	Eocene		Various angiosperms (Helmund, Helmund, 1991, 1998, 2002)	 
		Paleocene			
Mesozoic	Cretaceous	Late		<i>Quereuxia</i> sp. (unpublished)	 
		Early		<i>Pityophyllum</i> sp. <i>Ginkgoites</i> sp.	
	Jurassic	Late		(Vasilenko, 2005)	 
		Middle		<i>Schmeisseria microsrachys</i> <i>Podozamites distans</i>	
		Early		(Konijnenburg van Citter, Schtißner, 1999)	
	Triassic	Late		<i>Taeniopteris angustifolia</i> <i>Equisetites arenaceus</i> <i>Equisetites foveolatus</i> <i>Equisetites platyodon</i>	
		Middle		(Graufogel-Stamm, Kelber, 1996)	
		Early			
Paleozoic	Permian	Late		<i>Pursongia</i> sp. (unpublished)	
		Middle			
		Early			
	Carboniferous	Late		<i>Calamites cistii</i> (Bethoux, Galtier, Nel, 2004)	

eggs depend on the leaf width: on narrow leaves, the eggs are situated in rows, one after another. If the leaf is wide enough to place two or more parallel rows of eggs, the insect takes advantage of this by completely filling the available space with eggs. The rows are always situated along the longitudinal axis of the leaf, like to ovipositions of modern Calopterygina.

In the Upper Cretaceous of the Amur River region (Maastrichtian), two types of ovipositions are found on floating leaves of *Quereuxia*, fundamentally differing in arrangement from each other and older ovipositions (Pl. 15, figs. 4–6). The first type includes elongate and widely spaced eggs arranged in weakly arching rows (Pl. 15, figs. 4, 5); and the second type includes more

rounded and densely packed eggs in short arching rows (Pl. 15, fig. 6). Unlike all the above-mentioned examples, the latter oviposition bears traces of a protective cover and was definitely situated on the leaf surface (exophytic oviposition).

It should be pointed out that, like other evidence of interactions between arthropods and plants (galls, mines, and feeding damage), the number of ovipositions on plants sharply increased in the Late Cretaceous, and certain changes in their morphological and biological characteristics occurred. In the Cenozoic, ovipositions on plants are even more numerous, occurring on various plants, predominantly angiosperms. Table 1 shows the stratigraphic range of finds, type of oviposition, plant taxon, references, and the stratigraphic range of main suborders of dragonflies.

Of interest is the fact that very similar endophytic ovipositions of separate elongate eggs, more or less regularly situated on leaves (occasionally in zigzag rows) are known since the Carboniferous. They differ from each other mostly in size, which varies in a relatively wide range (attaining a maximum in the Paleozoic). The biggest eggs in ovipositions of the most stable type (with elongate oval eggs) are observed in the Carboniferous and Triassic: up to 18.0 and 9.5 mm long, respectively. In the Permian, Jurassic, Cretaceous, and Cenozoic, the length of eggs does not exceed 2 mm and is generally from 1.0–1.2 mm. The sizes of eggs within one oviposition also vary: the maximal range again is observed in the Carboniferous.

Such eggs deposited on plants of different systematic groups never provoke the plants to form galls or identifiable overgrowth of tissues. Ovipositions made by modern dragonflies also never lead to such reactions, in contrast to those made by some other insects, such as dipterans and hymenopterans. So far known fossil ovipositions were probably not restricted to particular plant taxa, in most cases insects simply oviposited on any suitable plants.

Modern ovipositions are traditionally characterized by two pools of characters: morphological (shape, size, and surface structure of the egg) and biological (relative position of eggs to each other and to the substrate, protecting covers, and the type of the substrate on/in which eggs were deposited) (Bogdanov-Kat'kov, 1947). Almost all these features are observable in fossils as well.

INTERPRETATION

Most authors believe that the Upper Mesozoic and Cenozoic endophytic ovipositions consisting of elongate eggs were left by damselflies (suborder Calopterygina). This supposition is substantiated by the similarity of morphological and biological features of eggs and ovipositions. Damselflies are among few insect taxa of a high rank the members of which nowadays deposit elongate oval or flattened elongate eggs in the tissues of living or dead plants. The main modes of ovi-

position of modern damselflies and the general appearance of their oviposition on plants are shown in Fig. 1.

Only Late Cretaceous and Cenozoic eggs can be relatively reliably assigned to particular insects. Indeed, elongate and oval eggs most probably belong to the Calopterygina, the morphology and biology of which are adapted for such activity.

Thus, the interpretation of geologically young ovipositions represents no major problems, and we will focus on the older ovipositions, which are more or less uniform and are known since the Carboniferous.

Several points should be taken into account for the identification of the group of insects that oviposited in plant tissues from the Paleozoic to the Jurassic and, probably, earliest Cretaceous. First of all, the similarity between ovipositions suggests that they were probably made by one particular group of organisms. Further still, these organisms were able to oviposit into cuts in plant tissues; therefore, our search is limited to insects with a cutting ovipositor. These are dragonflies, palaeodictyopteroids (Dictyoneuridea), diverse members of the Cimiciformes, including several Paleozoic orders (Caloneurida, Blattinopseida, and Hypoperlida) and surviving Hemiptera, some holometabolous insects (extinct miomopterans or Palaeomanteida and extant hymenopterans), and orthopterans (Rasnitsyn and Quicke, 2002).

The majority of the above-listed orders have a limited stratigraphic range and are unknown either in the Carboniferous (often also in the Permian) or in the Mesozoic. The exclusion of these orders leaves only dragonflies, orthopterans, and miomopterans. However, the latter group did not survive to the Late Jurassic, and, above all, these insects were small to medium sized, and could not have deposited eggs of 10, or more so 18 mm. Orthopterans are slightly more plausible candidates. However, oviposition in living plant tissues is secondary in this group and represents a later (Late Mesozoic or Cenozoic) acquisition.

This leaves only dragonflies. The lifetime of their ancient order Meganeurida corresponds well with the ovipositions under discussion: Middle Carboniferous–Lower Cretaceous. The dynamics of change in body sizes are also appropriate: their body sizes were very large during the Paleozoic and became much smaller by the Cretaceous (the system developed by Pritykina (1989) for higher taxa of dragonflies is used here as it is more appropriate for our purposes). In addition, the Meganeurida, unlike other dragonflies, were most probably not aquatic insects (Rasnitsyn and Quicke, 2002), which is also in agreement with our data about ovipositions.

The ovipositions were most probably terrestrial, since no oviposition is known on aquatic plants in the time interval under consideration. As for the Paleozoic, no aquatic immatures of insects were found (Carboniferous), or no such aquatic immatures are known from

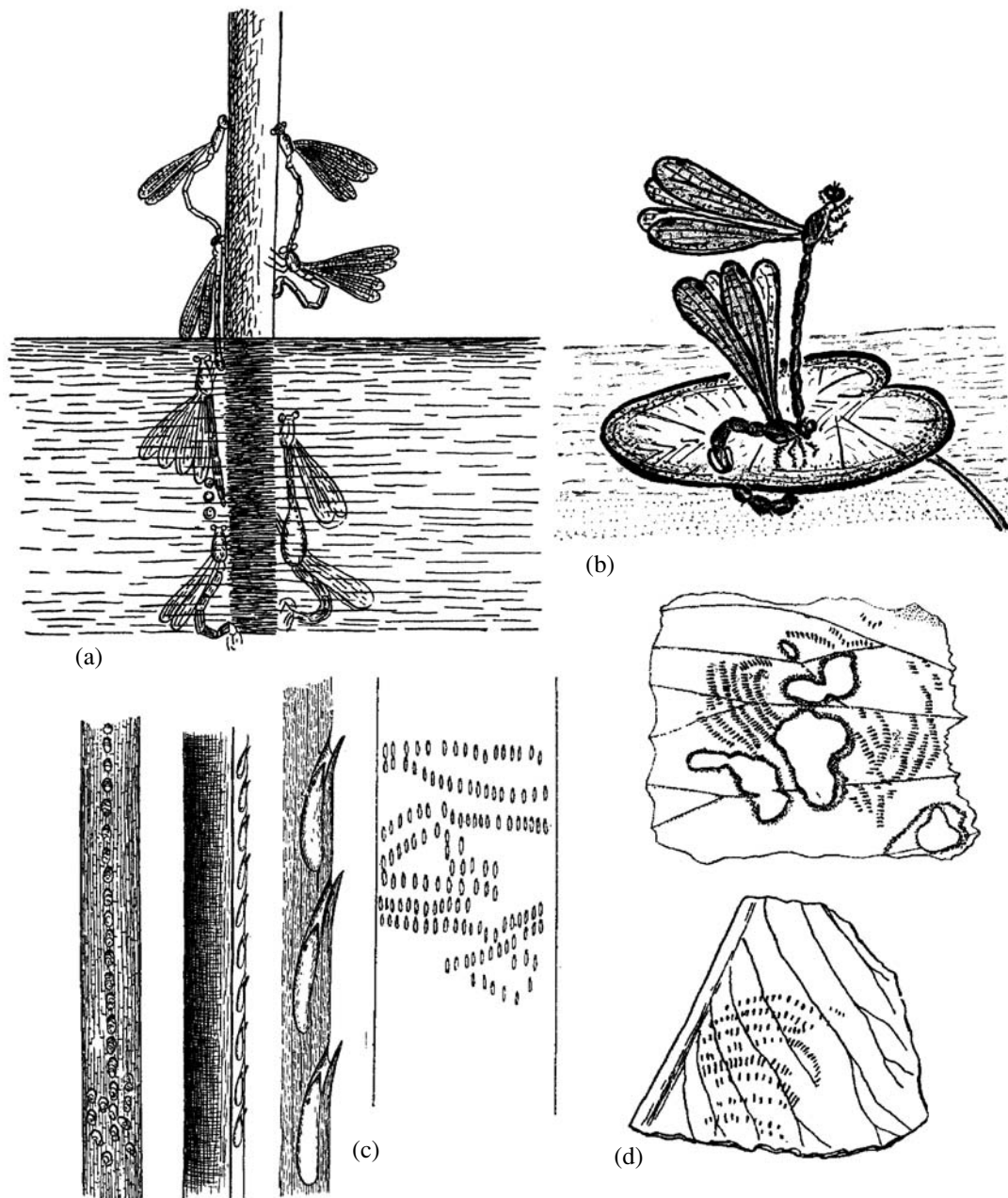


Fig. 1. Main types of ovipositions of dragonflies of the suborder Calopterygina: (a) egg deposition of modern dragonflies *Erythemis najas* on plant stems; (b) egg deposition of modern dragonflies *Coenagrion pulchellum* on floating leaves of plants; (c) general view of an oviposition on stems or elongate leaves; (d) general view of an oviposition on wide leaves (after Popova, 1953).

groups in which the female imago had a cutting ovipositor (Permian).

An additional piece of evidence in support of dragonflies being the producers of the ovipositions under discussion, is the close resemblance (although not identity) of the ovipositions to those of modern Calopterygina.

Archaic dragonflies of the order Meganeurida are the only group with a cutting ovipositor that remained more or less ecologically stable from the Carboniferous to the Mesozoic. Meganeurina were insects of varying

size (wingspan 90–630 mm) with broad stratigraphic and geographic ranges. In the Late Carboniferous–Early Permian, they reached their peak, and were widespread. By the end of the Permian, their diversity declined, and only the single family Triadotypidae survived into the Triassic. In the Late Carboniferous, the suborder Ditaxineurina (=Protanisoptera + Permianisoptera) appeared in the paleontological record. These dragonflies of moderate size (wingspan 50–130 mm) became common in the Permian. Some members of the subor-

der appeared as early as the Late Carboniferous, but all of them disappeared by the end of the Permian and did not cross the Permian/Triassic boundary. In the Late Carboniferous, members of the suborder Kennedyina (Propozygoptera + Archizygoptera) appeared, which are ancient analogues of the present day damselflies (Calopterygina). The Kennedyina reached its peak in the second half of the Permian; however, as early as the Early Permian members of the Kennedyina were already much more numerous than members of the Meganeurida with a wide wing base (Meganeurina and Ditaxineurina). Dragonflies of this suborder were small and moderate in size (wingspan 25–190 mm) and had strongly petiolate wings, resembling the Calopterygina. Among the Meganeurida, the Kennedyina were the last to disappear (in the Early Cretaceous). In the Triassic, one more suborder (Triadophlebiina) appeared among the Meganeurida; however, it did not survive into the Jurassic. Ecologically, they were close to the Kennedyina, but slightly larger in size.

In the Triassic, members of the modern order Libellulida appeared; particularly, the suborder Heterophlebiina (=Anisozygoptera), which existed until the end of the Early Cretaceous. Lower Jurassic deposits are marked by the appearance of one more suborder, the extant Libellulina. Individual specimens of members of archaic modern families of the suborder Calopterygina have been recorded from the Upper Jurassic–Lower Cretaceous.

The petiolate wing is believed to be adapted to rather slow, but highly maneuverable flight, which is particularly characteristic of inhabitants tangled vegetation (e.g., Calopterygina, Tipuloidea, and Bittacidae). The same is probably true for ancient dragonflies of the suborders Kennedyina and Triadophlebiina, which had petiolate wings. Those extant Odonata with petiolate wings, the damselflies (Calopterygina), oviposit in plant tissues, and the same strategy is conceivable for the Kennedyina and Triadophlebiina. Taking into consideration the stratigraphic distribution of endophytic ovipositions, i.e., their relative scarcity in the Carboniferous and Permian, increase in the Triassic, relative decline in the Jurassic, apparent absence in the Lower Cretaceous, and their increase in number (almost to the modern level) in the Upper Cretaceous and Cenozoic (see above for more detail), a conclusion can be drawn about the relation between endophytic ovipositions and the Kennedyina in the Carboniferous, Permian, and Jurassic and the Kennedyina and Triadophlebiina in the Triassic. Plate 15 shows Permian and Triassic dragonfly

fossils with different types of wing base: wide (Pl. 15, figs. 7, 10) and petiolate (Pl. 15, figs. 8, 9).

Therefore, there are no obvious contradictions in correlation between Paleozoic and Mesozoic (up to the Upper Cretaceous, when the Calopterygina spread) endophytic ovipositions and meganeurids with petiolate wing, i.e., the Kennedyina, and, possibly, Triadophlebiina. In the Carboniferous–Jurassic time interval, the size of both meganeurids and the ovipositions under discussion unidirectionally and steadily diminished.

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