Reproduction Structures of Damselflies (Odonata, Zygoptera): are They Trace Fossils or not?

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Reproduction structures of damselflies (Odonata, Zygoptera): are they trace fossils or not?

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A b s t r a c t

Following a review of relevant mechanisms and structures, we propose to use binary nomenclature for characterizing and naming most fossil egg-sets, clutches and ovipositions of damselflies as trace fossils. We recommend to sharply distinguish between structures caused by insects and adjoining plant tissues. Only the former are trace fossils, the latter are not.

K e y w o r d s : Trace fossils, Odonata, oviposition, plant–insect interaction.

Dedicated to the late Dr. GÜNTER KRUMBIEGEL (1926–2014) in friendly commemoration

1. Introduction

The procedure of oviposition by extant damselflies results in a clearly arranged pattern within plant tissue, showing a special endophytic behaviour. Cavities are carved into plant tissue in a repeating series, creating a shelter for the eggs to develop into prolarvas. This plant-insect interaction has been preserved in a number of fossil plants (e.g., HELLMUND & HELLMUND 2013). Immediately after oviposition, the plant reacts to the damage caused by the damselfly with a noticeable swelling and/or 'staining effect', where the colour of the tissue around the wound is different. This reaction of the plant can even be observed in the fossil record.

The fossil record of damselflies (Odonata, Zygoptera), mainly from the Cenozoic, thus includes egg-sets, clutches and ovipositions (e.g., HELLMUND & HELLMUND 2013). These structures represent praeimaginal stages of hemimetabolic insect metamorphosis but have been treated as trace fossils by PENALVER & DELCLOS (2004), VASILENKO (2005, 2008) and KRASSILOV & RASNITSYN (2008). The latter authors (p. 69) accordingly proposed a new ichnotaxon, *Catenoveon undulatum* KRASSILOV et SILANTIEVA in KRASSILOV & RASNITSYN (2008). The question of whether or not fossil praeimaginal stages, egg-sets and egg clutches of zygopteran insects are trace fossils is difficult to answer. Here we discuss this issue using examples of fossil and recent biological material.

2. Definition of trace fossils

A trace fossil has been defined as follows: "… a morphologically <u>recurrent</u> structure resulting from the life activity of an individual organism (or homotypic organisms) modifying the substrate. […] The substrate may be rock, soft to firm sediment, dead organic matter (peat, wood, shell, bone), or (then) living organic tissue. […] Burrows and borings in plants (leaves, wood, etc.) undoubtedly are traces. There is a "grey zone" of dubious structures, however, that some workers include as trace fossils and others do not (BERTLING et al. 2006: 266)."

However, plant reaction tissues are "not traces", because they are the reaction from puncture by an insect during oviposition and are thereby excluded from the "grey zone" (BERTLING et al. 2006: 266–268 and table 1). Rather, they qualify as pathological evidence of a past injury.

3. Damselfly ovipositions today and in the fossil record

The fossilized praeimaginal stages of coenagrionid damselflies usually are arranged in "zig-zag band" or other discrete patterns. Four different modes of damselfly

oviposition have been recognized in the fossil record so far, showing clear evidence that this reproductive behaviour extends well back into Earth history (Fig. 1; e.g., Hellmund & Hellmund 2013). Studies of extant species reveal these patterns of oviposition to persist identically today (e.g., Hellmund 1991, 1992, 1994). Each egg is provided its own shelter as the female carves out a depression in the plant tissue using the ovipositor apparatus (Fig. 2). These egg-sets often exhibit preference for certain kinds of plants, e.g. in fossils of laurel leaves *Daphnogene* with praeimaginal stages of lestid zygopterans (Fig. 3).
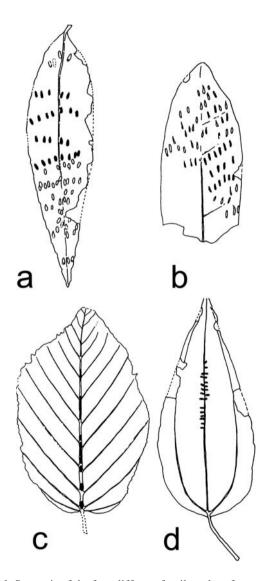

Fig. 2. Extant egg-set of the "Lestid-type" placed in the tissue of a plant stem, in a single discrete row. For one of these eggs, the covering plant tissue has been dissected while the other eggs shine through the covering tissue. Length of one egg ca. 1.40 mm, dissection and photograph: W. Hellmund.

Fig. 1. Synopsis of the four different fossil modes of zygopteran egg-sets (known so far), placed within fossil angiosperm leaves of Cenozoic localities. **a**, **b:** Coenagrionid-type: zig-zag mode (a) and curved mode (b). **c, d:** Lestid-type: single-row mode (c), double-row mode (d). Sketches are not to scale. Images adapted from Hellmund & Hellmund (2002b).

Coenagrionid damselflies, however, do not seem to prefer a certain plant type in the fossil record (e.g., Hellmund & Hellmund 1991, 1996).

After insertion, hemi metabolic metamorphosis of the damselfly prolarva begins. It is accompanied by an instantaneous reaction of the plant. In extant examples, the tissue swells and often has a reddish flare of natural stain (anthocyanes) surrounding each egg (Fig. 5; Hellmund & Hellmund 1991). This plant–insect interaction was found remarkably preserved at the Late Oligocene Rott Fossillagerstätte, Siebengebirge, Germany (Hellmund & Hellmund 1991, 1996). There, a laurel leaf of *Daphnogene* had up to 15 eggs inserted, each with a notably elevated margin, indicating plant-insect interaction (Figs. 3–4). Other fossil angiosperm leaves from Rott preserve damselfly egg-sets as well, but lack evidence of plant reaction. In these cases, the damselflies may instead have been laying their egg-sets on dead leaves, or the leaves were embedded soon after oviposition. A single angiosperm fossil leaf specimen from Rott has dark remains preserved (1.2–1.5 mm in length) that are recognizable within some of the egg cavities, even suggesting fossilized egg material remains within the leaf tissue (Hellmund & Hellmund 2013). Hellmund (1997) summarized further reports of zygopteran-plant interactions from slightly older (middle Oligocene) locations in Saxony, Germany.

A much older fossil example of elevated margins around eggs is reported by Pott et al. (2008) in which they describe a leaf of *Nilssoniopteris angustior* (Stur ex Krasser, 1909) comb. nov. from the Late Triassic of Austria. However, they were not sure whether these were caused by a damselfly or a beetle.
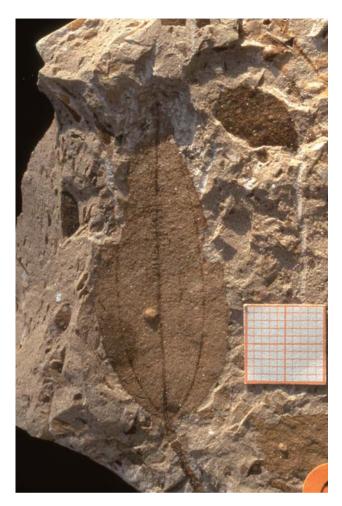
Fig. 3. Fossil egg-sets laid within an angiosperm leaf (*Daphnogene*), placed in a partial double row (overview), from the Late Oligocene Rott Fossillagerstätte, near Bonn (Germany). Length of one egg ca. 1.20 mm – ca. 1.40 mm; taken from HELLMUND & HELLMUND (2013).

Fig. 4. Enlarged detail of Fig. 3, showing the dark swollen margins of the plant tissue surrounding each egg. Length of one egg = 1.20 mm – 1.40 mm (from HELLMUND & HELLMUND 2013).

4. Taxonomic treatment of damselfly ovipositions

Fossil egg-sets of damselflies were reported as far back as 1846 (GOEPPERT 1846), although they were not identified as such. GOEPPERT (1846, pl. 14, fig. 1) misinterpreted these remains preserved on fossil angiosperm leaves as belonging to epiphytic fungi, *Hysterium opegraphoides* (GOEPP.) HEER and *Hysterites opegraphoides* GOEPP. despite their distinct orderly arrangement (Fig. 6). Epiphytic fungi typically settle on a substrate, covering it in an irregular fashion without any distinct pattern. For further details, see BENEDIX et al. (1974: 324), HELLMUND & HELLMUND (2002a), HELLMUND & HELLMUND (2013: 36) and Fig. 7.

PENALVER & DELCLOS (2004) described fossil egg-sets from the Miocene of Spain as "ichnofossils", stating that they were "ovipositions, mines and chew marks". VASILENKO (2005, 2008) introduced a "formal classification" for odonatan egg-sets. The author describes these as "oval or lentiform structures (eggs) with regular distribution over substrate" and that they represent "plant damages" as well. The word "over" is incorrect here, and must be replaced by "within", because egg-sets and clutches have been deposited actively within plant tissue. KRASSILOV & RASNITSYN (2008) proposed "binary nomination" for "arthropod eggs and oviposition scars". Interestingly, these authors practiced two methods for characterizing arthropod eggs and oviposition scars, following both the descriptive characterization introduced by HELLMUND & HELLMUND (1991) and parallel the use of binary nomenclature.

Fig. 5. Extant endophytic "Coenagrionid-type" egg-sets (clutches), zig-zag mode, on a leaf of the water lily *Nymphaea*. Swollen margins around each egg are visible, as well as red stain concentrations (anthocyanin) caused by the plant–insect interaction. Length of one egg ca. 1.20 mm, photograph: W. HELLMUND.

Fig. 6. Fossil angiosperm leaves from the middle Miocene of Salzhausen (Hesse, Germany) preserved within organic substratum, figured as a lithograph in GOEPPERT (1846). The specimen in the centre displays fossil egg-sets of damselflies. GOEPPERT (1846) described and identified them erroneously as epiphytic fungi. The total length of the leaf with egg-sets (centre) is about 8 cm, photograph taken from the lithograph by W. HELLMUND.

5. Conclusions

Fossils of damselfly reproduction comprise three different types of structures: a) depressions carved into host plants by the insect, b) relics of praeimaginal stages contained in hollows within plant matter, and c) wound tissue produced by the plant around the lesion. From the viewpoint of taxonomy, these structures must not be treated together, because they are not produced simultaneously but subsequently. We discuss and attribute them in chronological appearance in the following paragraphs.

At first, the mother insect actively modifies a plant substrate when carving out a depression. It thus clearly creates a trace fossil according to the definition of BERTLING et al. (2006, p. 266). In creating these pits, the damselfly follows a specific recurrent behaviour of moving sideward, back and forward, thus creating a special pattern of
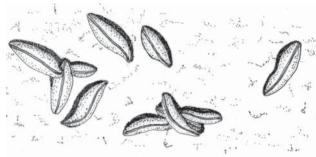

Fig. 7. Sketch of extant epiphytic fungi of *Farlowiella carmichaeliana* (BERK.) SACC. Length of each fungus is ca. 3 mm. Note the irregular pattern on the plant tissue, clearly differing in size and morphology from zygopteran egg-sets. The fruiting bodies of the fungi display a more or less sunken slit. Sketch by W. HELLMUND, modified from BENEDIX et al. (1974).

distances and angles between individual depressions (e.g., HELLMUND & HELLMUND 1996, Fig. 21). This behaviour thus is quasi-simultaneous with carving depressions, as it follows the underlying plan. Strictly speaking, two types of behaviour may become preserved here: the body movement of the insect over the leaf surface and the scraping of pits. Accordingly, these two types of behaviour might receive two names, but only the pit is a trace fossil – the substrate is not manipulated or modified during the movement of the imago yet. This movement may become obvious, however, by the pattern in which the oviposition occurs. It may be disputed whether the resulting fossils are compound trace fossils (see PICKERILL & NARBONNE 1995), but they at least have an important ichnologic constituent. Following the example of *Hillichnus* (BROMLEY et al. 2003) and according to BERTLING et al. (2006), the

pits and their arrangement should be united under one ichnotaxon. This approach has been applied by PENALVER & DELCLOS (2004), VASILENKO (2005, 2008) and KRASSILOV & RASNITSYN (2008).

In a second step, an egg is deposited. If organic matter of it or a larva is preserved inside the hollows, it qualifies for a body fossil, even though not identifiable at any subfamily level. Alternatively, it may be identified parataxonomically as an ootaxon (e.g., HIRSCH 1994; MIKHAILOV et al. 1996), if sufficient morphological and/or structural details are visible.

Finally, "plant reaction tissues are not traces" (BERTLING et al. 2006), as neither are embedment structures. The form and extent of the wound rim around the original depression must not be an ichnotaxobase for damselfly ovipositions therefore. A similar situation prevails in the ichnotaxonomy of drill holes *Oichnus* as clarified by WISSHAK et al. (2015).

We suggest to make use of the approach of KRASSILOV & RASNITSYN (2008) based on the behavioural groupings introduced by HELLMUND & HELLMUND (1991; Fig. 1), which has since been adopted by several authors.

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