

# Insect egg sets on angiosperm leaves from the Lower Cretaceous of Negev, Israel

Valentin Krassilov<sup>a,b,\*</sup>, Natalia Silantieva<sup>a</sup>, Meinolf Hellmund<sup>c</sup>, Winfried Hellmund<sup>d</sup>

<sup>a</sup> Institute of Evolution, University of Haifa, Mount Carmel, Haifa 31905, Israel

<sup>b</sup> Paleontological Institute, 123 Profsoyusnaya, Moscow 117647, Russia

<sup>c</sup> Institute for Geological Sciences and Geisel Valley Museum, Martin-Luther-University Halle-Wittenberg, Domstr. 5, D-06108 Halle (Saale), Germany

<sup>d</sup> Von-Loe-Str. 31, D-53840 Troisdorf, Germany

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## Abstract

Egg set impressions on fossil leaves, a new field of palaeontological research, links insect palaeoecology with that of the host plant. Zygoteran egg sets from the Albian of Makhtesh Ramon, central Negev, Israel, were deposited on narrow leaves of an angiospermous *Acaciaephyllum*-like morphotype. Their pattern resembles the extant and Tertiary “Coenagrionid Type”, attesting to evolutionary conservatism of this oviposition mode since the time of early angiosperms. A comparison with the Palaeozoic–Jurassic proto-Odonata egg sets suggests a change in oviposition modes in several steps that can be related to the evolution of wetlands. The Albian remains are among the earliest of a modern aspect supposedly related to the advent of angiosperms. A wetland source community has been previously suggested for *Acaciaephyllum*-like leaves on taphonomic grounds, and the finding of damselfly egg sets provides additional evidence in favour of such a habitat, thus having a bearing on the palaeoecology of Early Cretaceous angiosperms.

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## 1. Introduction

Insect egg sets on fossil leaves is a recently emerging field of entomological, palaeoecological and evolutionary research. Fossil egg sets attributed to Odonata or proto-Odonata are known from the Late Palaeozoic onwards, with modern patterns emerging through the Cenozoic or, as the only Late Cretaceous record suggested, even earlier (Hellmund and Hellmund, 1991, 1996a, 2002b,c).

Here the first find of Early Cretaceous zygoteran egg sets is reported and their palaeoecological and evolutionary implications are discussed. This paper is part of a body of work on

habitation and feeding traces on Cretaceous plant remains as evidence of plant–arthropod interaction at the time of the advent, and expansion, of the flowering plants (Krassilov, 2007).

## 2. Stratigraphy and taphonomy of insect traces on plant remains from the Cretaceous of Negev

In Israel, non-marine and marginal marine Cretaceous deposits are widespread in the Negev Desert, cropping out on the western slope of the Arava Rift Valley south of the Dead Sea (Krassilov et al., 2005) and in the erosional windows (cirques, or makhteshim, in Hebrew) of central Negev (Fig. 1). The Gerofit and Qetura localities of Arava contain the most representative mid-Turonian angiosperm assemblage comprising 46 species (Krassilov et al., 2005) bearing abundant

\* Corresponding author. Institute of Evolution, University of Haifa, Mount Carmel, Haifa 31905, Israel.

E-mail address: [vkkrassilov@hotmail.com](mailto:vkkrassilov@hotmail.com) (V. Krassilov).

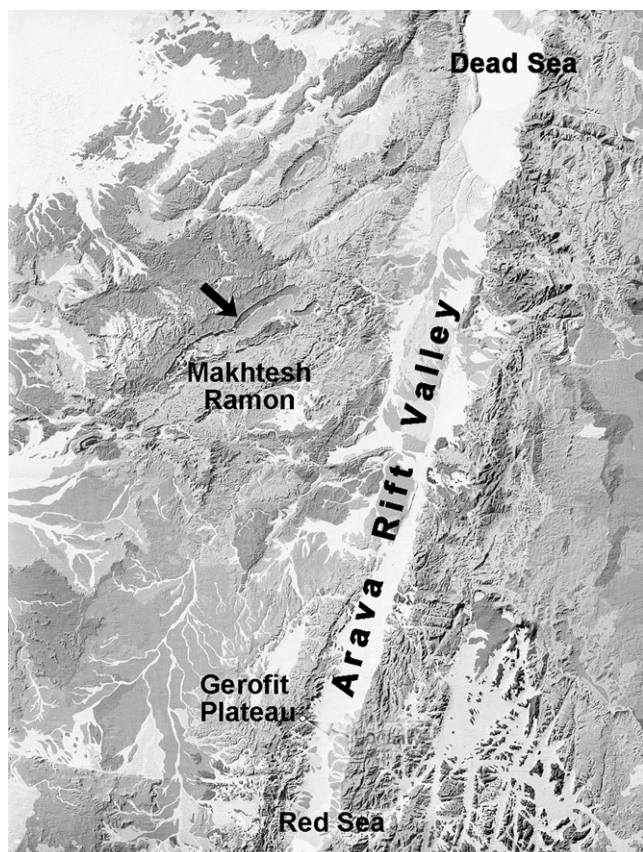


Fig. 1. Satellite photograph indicating the Albian plant locality with traces of zygoteran egg sets (arrow).

traces of exceptionally diverse phytophagous and phytocolous arthropods (Krassilov, 2007). Body fossils of Hemiptera, beetles, cockroaches, and a few other insects have been described from these localities (Dobruskina et al., 1997).

In the central Negev, the larger erosional cirque, Makhtesh Ramon, exposes a succession of Triassic–Early Cretaceous siliciclastic sediments overlain by Late Albian–Cenomanian platform carbonates. The angiosperm-like macrofossils (Krassilov et al., 2004) and angiospermous pollen grains (Schrank, 1992; Brenner, 1996) appear in the Lower Hatira Formation, which contains marine intercalations and is topped by the Ramon basalts and their covering of lateritic redbeds. On the evidence of invertebrate remains in the marine intercalations, as well as the palaeomagnetic and isotopic dating of the basalts, the Lower Hatira Formation has been dated as Barremian?–Early Aptian (Gvirtzman et al., 1996), and more recently as Aptian–Early Albian (Segev et al., 2005).

The conformable Upper Hatira Formation above consists of variegated cross-bedded sandstones with lenticular, finely laminated siltstones and marly clays (claystones) containing occasional marine fossils and locally abundant terrestrial plant debris. This paralic sequence is interpreted as mainly tidal flat sediments. It is bracketed between the Aptian–Early Albian Ramon basalts below and the Late Albian richly fossiliferous limestones above, which restricts its age to Early–Middle Albian. An Albian ammonite, *Knemiceras* Böhm, has been

reported from the middle part of the succession (Gvirtzman et al., 1996).

Early Cretaceous plant fossils, first reported by Lorch (in Nevo, 1968), have recently been collected by two of us (NS and VK) from several Upper Hatira localities on the northern slope of Makhtesh Ramon. The Albian plant assemblages consist of ferns, ginkgophytes, conifers and the earliest angiosperm macrofossils in the basin. They are much less diverse than the Turonian flora of Arava, and insect traces are relatively rare, reflecting an early stage of angiosperm–insect interaction.

Trunks, roots, fronds and particulate debris of *Weichselia* are numerically dominant in all of the Albian localities, indicating the close proximity of the source community of arboreal ferns to the tidal-flat depositional site (Silantieva and Krassilov, 2006). Next in abundance are narrow angiospermous leaves of several morphotypes, often forming mat-like bedding-plane accumulations that are constantly associated with *Weichselia*, supposedly representing a coastal wetland community within the *Weichselia* zone or adjacent to it. The other angiosperm morphotypes, such as peltate *Nelumbites* or subpeltate platanoid leaves, are relatively infrequent, poorly preserved and apparently allochthonous, suggesting an export of plant material from remote freshwater and dry-land sources. Together with occasional leaves and cone scales of araucariaceous conifers, the broadleaved angiosperms might reflect inland vegetation of a mixed mesic forest type (Silantieva and Krassilov, 2006).

Prominent in the narrow-leaved angiosperm assemblage are elongate, slightly inequilateral leaves with a strong midrib and long ascending, irregularly branched acrodromous laterals resembling *Acaciaephyllum* and *Rogersia* from the Albian flora of Maryland, eastern North America (Fontaine, 1889; Hickey and Doyle, 1977), but differing in the subparallel arrangement of the laterals. They probably represent a distinct morphotype, the taxonomy of which will be dealt with elsewhere. Systematic affinities of early angiosperms with such leaves are presently uncertain. On the basis of its venation pattern, *Acaciaephyllum* has been tentatively compared to monocotyledonous leaves (Doyle, 1978, 2001). The egg sets described in this paper cast some light if not on the taxonomic position, then on the habitats of angiosperms with *Acaciaephyllum*-like leaves.

### 3. Material

The egg sets are preserved on two leaf fragments, one of which, representing the proximal part of an *Acaciaephyllum*-like leaf-blade, is 40 mm long (about one-third of the whole length), 15 mm broad, and gradually tapering to the base. The leaf blade is transversely folded and ruptured, except at the midrib, by micro-slumping of the clay matrix, the lower and upper parts of it being impressed at slightly different levels. It is preserved on a slab with several haphazardly arranged and overlapping fragments of conspecific leaves, which are easily distinguishable owing to their characteristic venation (Fig. 2).



Another leaf, overlapped by the larger fragment and strongly deformed, is infested with insect eggs of the same kind. The other plant remains on the slab are frond rachises, detached pinnules and sporangial clusters of *Weichselia*. After careful examination, a few poorly preserved egg holes were found on two more leaves of the same species.

The ferruginous leaf impressions show a thick midrib and slender laterals departing at an acute angle near the base and taking subparallel, slightly undulating courses towards the apex. Judging by the prominence of the veins, the distinctiveness of the sclerenchymous strands sheathing the midrib, and the locally discernible outlines of epidermal cells, the “impressions” are in fact the subcutaneous mineral replicas of the interior surface of the cuticle. This replication mode is described in Krassilov et al. (2005) and elsewhere, and is

particularly favourable for the preservation of endophytic egg sets.

The egg scars are better preserved in the lower part of the leaf; in the upper part, which is more weathered and intensely coloured, their contours are less distinct (Fig. 2A). On the second leaf, egg holes of the same kind are more widely spaced and appear somewhat stretched, conceivably by leaf growth after the eggs were deposited (Figs. 2B, 3D).

#### 4. Description of egg sets

The elliptical egg scars are strewn all over the leaf blade, avoiding the midrib and the stronger secondary veins, although they are occasionally placed quite near the latter (Fig. 3A, E). On the larger leaf fragment, the egg density is 18–20 per

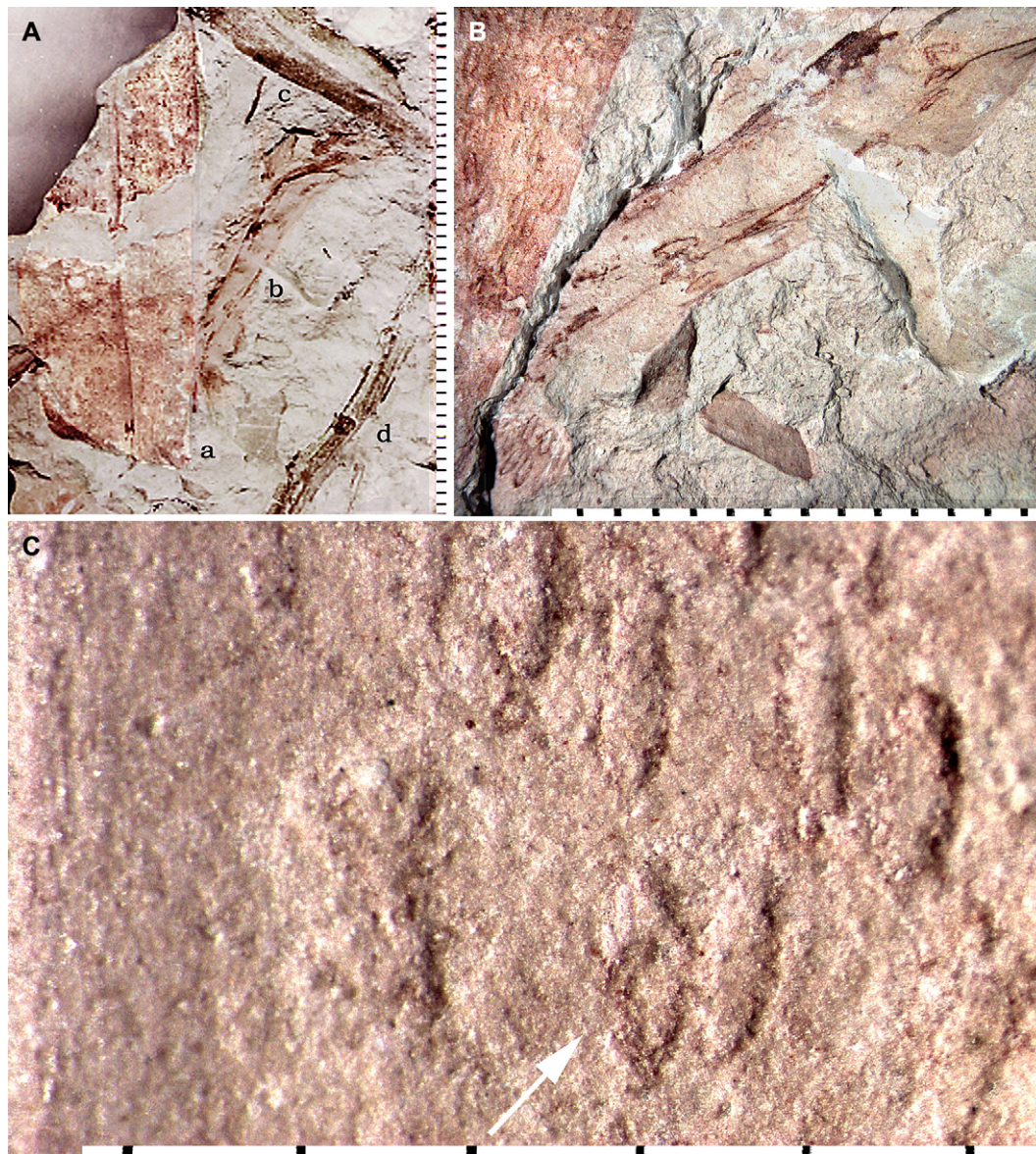


Fig. 2. Zygopteran egg sets on angiosperm leaves from the Lower Cretaceous of Negev. A, IMR-A2-303, clay slab with two infested leaf impressions (a, b), uninfested leaf fragment of the same species (c), and a frond rachis of *Weichselia* (d). B, IMR-A2-303b, leaf fragment with egg holes. C, IMR-A2-303a, egg holes, arrow points to impression of a dark inner body. Scale bars in mm.





Fig. 3. Zygopteran egg sets on angiosperm leaves from the lower Cretaceous of Negev. A, IMR-A2-303a, lower part of infested leaf showing density of egg scars. B, IMR-A2-303a, egg scars with short mucronate ends. C, IMR-A2-303a, plicate contour of egg hole. D, IMR-A2-303b, egg scars stretched by elongation of the leaf blade; one on the left side deformed. E, IMR-A2-303a, showing egg set orientation with respect to the midrib and secondary veins. Scale bars in mm.

5 mm<sup>2</sup> of leaf surface and the total number of eggs per leaf fragment (40 × 15 mm, about one-fifth of the whole leaf) is about 250. Occasional punctures between the egg scars probably mark failed egg-laying attempts.

At the first glance, the egg scar pattern may look chaotic, but on closer inspection certain patterns emerge, in particular in the basal part of the leaf where the scars are arranged in concentric arches with up to ten scars on both sides of the midrib. The arches follow the ascending lateral veins for some distance, but then converge upon the midrib. The egg files wobble

across the path. They are mostly well-spaced, but are occasionally close to each other. The distances between consecutive scars of a file are variable within the range of 0.1–0.5 mm. Zigzag arrangements are discernible at several points along the arches (arrows in Fig. 4). Occasional scars are paired (Fig. 3c).

In the upper part of the leaf fragment, the pattern of egg scars is less distinct. The scars are orientated nearly parallel or oblique to the veins at various angles, usually increasing towards the leaf margins. Some are in line with each other,



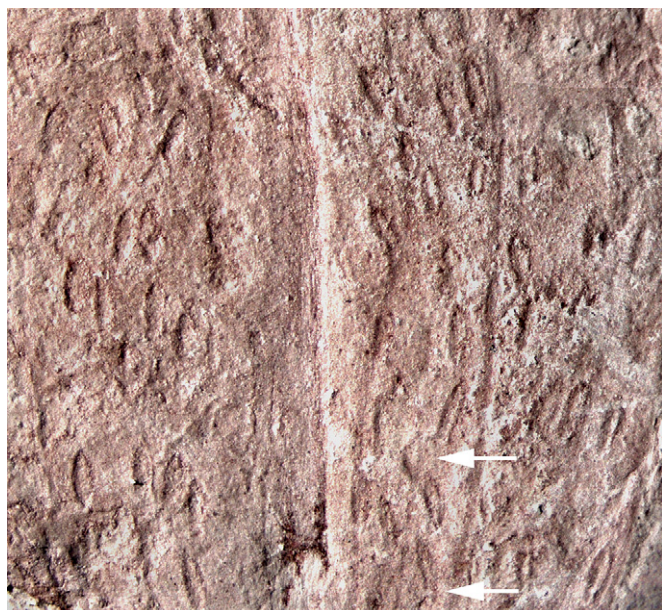


Fig. 4. Zygopteran egg sets on angiosperm leaves from the lower Cretaceous of Negev, IMR-A2-303a; concentric pattern of egg scars arranged in wobbling arcuate files on both sides of the midrib; arrows pointing to zigzag scars.

forming short arches or S-figures of irregular zigzag arrangement. A coulisse-like arrangement of adjacent scars is quite common. Close to the leaf margin, the egg scars are spread out in a fan-like manner, which might have resulted from the interference of two sets of concentric arches.

The egg-scar shapes are elongate to fusiform, 1.0–1.1 mm long, symmetrically pointed at both ends or with one end bluntly and the other acutely pointed, occasionally with a minute mucro (stitch mark) preserved (Fig. 3B). The mucronate ends point towards the leaf apex, betraying the direction of oviposition.

Some egg holes are deeper and more strongly marked than the others; these perhaps belong to non-simultaneous sets. At high magnifications under a stereomicroscope, the contours of egg scars are slightly undulating and transversely plicate, as if they have shrunk (Fig. 3C). A few egg impressions show a slender, twisted, dark body inside (Fig. 2C), probably representing a dried yolk or embryonic larva (cf. the organically preserved larval remains figured in Hellmund and Hellmund, 1996a, figs. 6, 13).

## 5. Discussion

Fossil egg sets are evidence of insect reproductive behaviour that, in the case of egg deposition on plants, is pertinent to the evolution of plant-insect interactions through time. Insect habitation, feeding and reproductive traces on fossil plants are often left by species that are not represented as body fossils, therefore revealing a hidden part of biological diversity. Even in cases when finds of body fossils coincide with traces left by the same group of insects, the latter provide indispensable information on behavioural traits that might

have evolved at rates different from those of morphological traits.

In particular, the record of egg sets on the leaves of early angiosperms are evidence of insects exploiting a new and rapidly expanding group of plants, exerting an impact on their ecology and evolution. Such records, therefore, link insect ecology with that of their plant hosts, at the same time shedding light on the habitats of early angiosperms. These aspects of endophytic egg sets from the Albian of Negev are discussed further below.

### 5.1. Summary of previous records

Endophytic oviposition is known to have occurred since the Late Palaeozoic (Labandeira, 2002a; Rasnitsyn and Quicke, 2002; Béthoux et al., 2004). Although remains of endophytic egg sets are conventionally attributed to Odonata, it should be noted that at least superficially similar egg patterns may belong to aquatic Coleoptera and Hemiptera. In Dytiscidae, the water beetles, eggs are more often glued to the substrate, but endophytic oviposition occurs in several genera (reviewed in Hinton, 1981), among which *Agabus*, for instance, produces long, bead-like strings of closely set eggs (Wesenberg-Lund, 1943; Hinton, 1981). The eggs are rounded or bluntly pointed and the strings are straighter than the oviposition habits of modern Odonata would ever produce (see below).

Extant Hemiptera, like Odonata, infest stems, leaves, petioles and other floral organs of aquatic and waterside plants (Jordan, 1952). Water bugs exploit not only fresh water but also marine habitats, on account of which their traces can be expected in paralic settings, such as in Palaeozoic coal basins. The eggs are different from those of Odonata in their sophisticated aeration system, but the scar shapes can be similar. Endophytic oviposition occurs in at least 12 families of Hemiptera (Hinton, 1981), but, unlike Odonata, the eggs are commonly inserted in natural crevices, slits or stomatal chambers (Wesenberg-Lund, 1943). When deposited in pits made by the ovipositor, the eggs are often laid in groups of three to many. The linearly arranged eggs are upright or continuously connected end to end, or even overlap. Their anterior ends are only rarely flush with the leaf surface.

The fusiform scars on *Calamites* trunks described by Béthoux et al. (2004) are irregular, up to 38.5 mm long, and each contains more than one egg. Their attribution to Odonata is, therefore, improbable, although the possibility of an unknown group of proto-Odonata comprising very large insects (like those described by Brauckmann and Zessin, 1989) with peculiar oviposition habits cannot be excluded.

Early Mesozoic oviposition scars vaguely comparable to those of Odonata are found on stems (leaf sheaths) of large equisetaleans (Heer, 1877; Roselt, 1954; Geinitz, 1855; Kräusel, 1958; Weber, 1968; Grauvogel-Stamm and Kelber, 1996, and work cited therein). Detailed descriptions are available for those on *Equisetites arenaceus* from the Lower Keuper of Frankonia (Grauvogel-Stamm and Kelber, 1996). The scars are fairly dense, of variable size, up to  $3 \times 9.5$  mm, which is more than four times larger than the upper size limit of eggs in modern

Odonata. An irregular zigzag pattern is reconstructed for them, but not quite convincingly, because the scars seem to have been partly obliterated on the stem impression. Moreover, an unusual feature seen on fig. 14 in [Grauvogel-Stamm and Kelber \(1996\)](#) is a contiguous disposition of scars along the parallel files. The authors seem to be justified in assigning these scars to proto-Odonata rather than Odonata.

Gradual decrease in egg size in the proto-Odonata occurs through the Jurassic. Whereas Early Jurassic forms scarcely differ from those of the Triassic in plant host preference and size ranges, being only slightly smaller than the latter ([Kräusel, 1958](#); [Van Konijnenburg-van Cittert and Schmeibner, 1999](#)), those of the Late Jurassic fall within the size range of modern Odonata and are found on gymnospermous leaves ([Vasilenko, 2005b](#)). Among them, the scattered elongate scars reportedly found on *Ginkgo* leaves from Tchernovskiy Kopi, Transbaikalia ([Vasilenko, 2005b](#), pl. 5, fig. 2) are orientated irrespective of the vein pattern (digitate in *Ginkgo*), which does not comply with the advanced oviposition types in which the male–female tandem uses the vein pattern for orientation ([Wesenberg-Lund, 1943](#)), but occurs in a less advanced unattended oviposition on fern leaves ([Kumar and Prasad, 1977](#)).

The Cenozoic records of odonate egg sets are rather numerous and of modern aspect (examples in [Hellmund, 1988](#); [Hellmund and Hellmund, 1991](#); [Schaarschmidt, 1992](#); [Johnston, 1993](#); [Labandeira, 2002b](#)). [Hellmund and Hellmund \(1991, 1996b, 2002a\)](#) described two scar patterns: “Coenagrionid Type”, for which the arcuate and zigzag arrangements are the modal configurations (the “Bogenmodus” and “Zickzackmodus”), and the “Lestid Type”, in which the files of paired egg scars follow the stronger veins.

One can assume that modernization of oviposition habits mainly took place during the Cretaceous, but Cretaceous egg records are currently scarce. While Jurassic and pre-Jurassic records of Zygoptera have mostly been invalidated ([Rasnitsyn and Quicke, 2002](#)), recognizable representatives of modern families appeared during the latest Jurassic and Early Cretaceous ([Jarzembowski et al., 1998](#); [Vasilenko, 2005a](#)). Our findings indicate that the coenagrionid egg set configuration might have appeared at about the same time or somewhat later, remaining essentially unchanged for at least 100 million years.

## 5.2. Oviposition palaeoecology of Albian Zygoptera

In present-day Odonata, oviposition habits are quite diverse. Eggs are attached in dense masses to, or inserted in, a variety of emerging, submerged or terrestrial waterside substrates. Endophytic oviposition is considered to be relatively specialized, and the eggs implanted in plant tissues differ from those externally deposited in their elongate form and thin transparent shell. The techniques of endophytic oviposition also vary from indiscriminate to highly specialized in relation to the host plants.

Examples of the latter are vividly described in [Wesenberg-Lund \(1943\)](#). The insects work in pairs, the egg-laying female being guided by her male partner over a rotating or wobbling

track producing the concentric or zigzag egg-set patterns respectively. The concentric lines of equidistant eggs laid by *Agriion* on the lower surface of nymphaeacean leaves are described as “die niedrigste Nadelarbeit die man sich denken kann” ([Wesenberg-Lund, 1943](#), p. 70), whereas on the long peduncles of these plants, up to six pairs of *Erythromma* work simultaneously “als wiegende blaue Guirlanden”, the hind part of their bodies moving incessantly, as a result of which “die ersten Eier werden dicht unter der Blüte in Zickzacklinien eingebort” ([Wesenberg-Lund, 1943](#), p. 76).

Such oviposition techniques imply a changing orientation, either rotation or wobbling, of the female’s body, resulting in the arcuate or zigzag patterns of their egg scars that are disposed at regular intervals. Perhaps a less advanced oviposition technique is described by [Kumar and Prasad \(1977\)](#) in the tropical zygopterid Calopterigidae, in which a submerged female, unattended by her partner, keeps changing her position while moving against the current. The resulting egg sets are irregular on leaves but more or less parallel to the fibrous ridges on stems, as in the Palaeozoic egg sets (see above).

The Albian egg sets from Makhtesh Ramon resemble those of extant damselflies (Zygoptera, Odonata), in particular the “Coenagrionid Type” described by [Hellmund and Hellmund \(1991, 1996b, 2002a\)](#), for which the arcuate and zigzag arrangements are the modal configurations. In our material, the egg sets cover the entire width of a leaf fragment measuring  $40 \times 15$  mm, in which 250 egg scars were counted. For comparison, a similarly arranged egg set covering the entire leaf-blade in a Late Oligocene *Apocynophyllum*-like leaf fragment measuring  $60 \times 15$  mm contains 111 egg scars ([Hellmund and Hellmund, 1991](#), fig. 3), and the greatest number counted so far is 416 on an undetermined angiosperm leaf, about  $135 \times 25$  mm in size, from the lower Middle Eocene of Messel. It was suggested in such cases that several females (or mating tandems, as is commonly the case in extant damselflies) were simultaneously at work.

As was pointed out in the description, over the distal, perhaps better exposed, part of the leaf, the scars are less distinct and their pattern is less regular than down to the base. The irregularities might have been caused by an overlap of simultaneously or, in the case of well-marked scars overlapping faint scars, of consecutively deposited egg sets, as well as by interruptions inflicted by such external influences as a high number of damselflies competing for room on the leaf, by a cloudy sky or rain drops or, in unattended females, by the repeated approaches of a male. Such interruptions have been observed in the course of studies of modern behaviour ([Kumar and Prasad, 1977](#); [Hellmund and Hellmund, 1998](#)).

However, even the more regular arrangement over the proximal portion of the leaf blade betrays a somewhat inconsistent combination of arcuate and zigzag patterns. Also, whereas in extant damselflies egg-spacing is fairly constant, controlled by the arch of the abdomen ([Wesenberg-Lund, 1913, 1943](#)), in our material the distances between adjacent egg scars are highly variable, suggesting a less advanced mechanism of egg deposition in the Early Cretaceous form.

### 5.3. Early angiosperm palaeoecology

Leaves of early angiosperms are classified as morphotaxa of problematic affinities to natural taxa. The choice of extant ecological equivalents is, in most cases, arbitrary and unreliable. The peltate long-petiolate *Nelumbites* morphotype is commonly recognized as representing floating leaves of aquatic forms (the comparable leaves of *Nelumbo* and *Nymphaea* are often infested with zygopteran eggs, but we found no egg holes on Albian leaves of this sort), whereas the narrow-leaved entire-margined morphotypes might come from a range of wetland and dry habitats. Various ideas on their ecological confinements are affected by controversial views of upland vs. lowland settings of angiosperm origins.

In the case of early angiosperms, lithofacies and the taphonomy of leaf remains can be more instructive than morphology or taxonomic assignments. Even before the egg sets were found, a supratidal marsh-like habitat had been suggested for the narrow-leaved angiosperms on taphonomic evidence (Silantjeva and Krassilov, 2006). In the Albian localities of Makhtesh Ramon, such leaves are found in tidal-flat deposits, often amassed on the bedding planes and associated with *Weichselia*, a fern genus dominating the coastal habitats of the Mediterranean realm and elsewhere. Any independent evidence, even if oblique, is beneficial in such cases.

Because zygopteran larvae must hatch in water or fall into water immediately after hatching (otherwise they perish), the eggs are laid on aquatic or waterside substrates. Thus, such egg remains are strong evidence of aquatic or semi-aquatic, at least periodically submerged, habitats. For present-day damselflies, angiosperms provide the most frequently used substrate for endophytic oviposition, perhaps for the simple reason that the most abundant and widespread aquatic/wetland plants are angiospermous, but fern leaves can also be infested (examples in Kumar and Prasad, 1977).

Cenozoic damselflies sometimes show a marked preference for a particular type of angiosperm leaf, e.g., for the leathery *Cinnamomum*-type leaves in the case of a lestid species recovered from the Upper Oligocene of Rott, Germany. Proximity of the source plants to water bodies is suggested on taphonomic grounds (Hellmund and Hellmund, 1991). However, coenagrionid species from the same locality seem to have been less selective, depositing their eggs not only in angiosperm leaves but also occasionally in the floating leaves of aquatic ferns (Hellmund and Hellmund, 1991, fig. 5).

For Albian damselflies, there were ample opportunities to use ferns as a substrate for their eggs, since fern wetlands were the most widespread plant community and some aquatic ferns with floating leaves were also present. Yet only one of several narrow-leaved angiosperm leaf species is infested, which suggests a fairly narrow range of host choice. In addition, on the leaf with less dense egg scars, the latter appear to have been stretched by subsequent growth of the leaf blade, which implies oviposition on the living plant rather than on debris. On the second leaf, the egg pattern is more regular near the base, conceivably because this part of the leaf blade was submerged or better sheltered from external disturbances.

The relative scarcity of egg-bearing specimens in the large accumulation of *Acaciaephyllum*-like leaves collected from the tidal-flat deposits may suggest that the infested leaves were transported from a more distant supratidal wetland beyond the influence of tidal waters. Remarkably, the ratio of the egg-bearing to unaffected leaves is approximately the same as in the Oligocene occurrences (Hellmund and Hellmund, 1991).

### 5.4. Possible co-evolution of Odonata and plant communities

Although the fossil record is still too sparse to reveal the evolution of oviposition habits in Odonata with respect to vegetational changes, certain preliminary considerations can be ventured. The Palaeozoic representatives were large insects that required massive plant parts of considerable surface area for oviposition. They laid their large eggs exclusively or preferentially in the cortex of *Calamites*, a dominant articulate wetland form of the time. During the Permian–Triassic transition, the *Calamites* (*Paracalamites*) wetlands were replaced by the *Equisetites*-*Neocalamites* wetlands of thick-stemmed horsetails, which, although different taxonomically, seem to have been quite similar to their Palaeozoic predecessors in their growth forms and habitats; hence, there were no essential changes in oviposition habits of insects that infested their stems.

The insects might have changed their preferential habitats with the decline of articulate wetlands since the mid-Jurassic and through the Cretaceous. Both *Neocalamites* and large horsetails disappeared in the Late Jurassic, being replaced by slender horsetails with stem diameters of less than 2 cm. Their parasitic insects might have first responded by diminution of their body size and eggs. They also added leaves to their oviposition substrates, which signalled a major change in the wetland life forms.

Through the Mesozoic, wetland biomass was relocated from stems to leaves: the microphyllous wetland dominants, lycopsids and articulates, were gradually replaced or overwhelmed by macrophyllous plants, which preconditioned a switch from stems to leaves as a preferential oviposition substrate. A habit of ovipositing in fern leaves that appears less advanced in the present-day Odonata might have been inherited from the Jurassic, a period of extensive fern wetlands. The latest Jurassic egg sets were found on *Ginkgo*, not a wetland plant, which suggests indiscriminate oviposition into floating leaf debris.

Horsetail swamps survive to this day and are still used as reproductive sites, if only in a minor way, by dragonflies and damselflies. Far more common hosts for their eggs are aquatic and semi-aquatic angiosperms, although indiscriminate use of floating plant debris is also common. It does not seem too much to assume that the appearance of aquatic and waterside angiosperms opened new venues for odonate adaptation, in which parsimonious egg deposition has fallen under the influence of such features as venation pattern and anisotropy of cuticle, epidermis, and mesophyll. The advanced



types of oviposition patterns found in present-day coenagrionids and lestids might have developed with the advent of angiosperms in response to the complexity of their growth patterns and several-order venation. Our data suggest that both midribs and the long ascending secondary veins were used for orientation and that the essential features of coenagrionid oviposition pattern had already been developed by the end of the Early Cretaceous.

## 6. Conclusions

Zygopteran egg sets from the Albian of Makhtesh Ramon, central Negev, Israel, are endophytically deposited into narrow lanceolate angiosperm leaves of an *Acaciaephyllum*-like morphotype, for which a supratidal wetland habitat has been postulated on taphonomic evidence (Silantiev and Krassilov, 2006). Since in the Odonata, only aquatic or waterside substrates are used for oviposition, the egg scars provide additional evidence for wetland habits in the early angiosperms.

The egg set can be assigned to the “Coenagrionid Type” (Hellmund and Hellmund, 1991), attesting to great antiquity and evolutionary conservatism of the pattern. The features of arcuate and zigzag modes, distinct in Tertiary and extant forms, are, however, mixed in the Albian form, and the egg-spacing is less constant, suggesting a somewhat less advanced oviposition technique.

The available fossil data suggest a stepwise change of oviposition habits from the Palaeozoic proto-Odonata to the modern Odonata with respect to the gradational replacements of the dominant wetland types during Mesozoic times. The major evolutionary events seem to have been related to a decline in thick-stemmed articulates and their substitution by slender horsetails and macrophyllous forms in the mid-Jurassic, and then to the spread of wetland angiosperms in the Cretaceous. Modern-type Odonata and basal angiosperms apparently belonged to a new-type of wetland ecosystems that originated in the Early Cretaceous.

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