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Original article

The natural history of oviposition on a ginkgophyte fruit from the Middle Jurassic of northeastern China

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Abstract

A distinctive pattern of oviposition lesions occurs on a ginkgoalean seed, *Yimaia capituliformis*, which likely was inflicted by a kalligrammatid lacewing with a long, sword-like, plant piercing ovipositor. This newly recorded oviposition type, DT272, occurs in the 165 million-year-old Jiulongshan Formation, of Middle Jurassic age, in Northeastern China. DT272 consists from three to seven, approximately equally spaced lesions with

surrounding callus tissue whose fabricator targeted fleshy outer and inner tissues of a ginkgophyte fruit. This distinctive damage also is known from the fleshy attachment pad surfaces of basal bennettitalean bracts. Examination of the life history of this probable ginkgoalean–kalligrammatid oviposition interaction indicates that the spacing of the eggs in substrate tissues disfavored inter-larval contact, but little can be said of defense and counterdefense strategies between the plant host and the newly hatched immatures.

Keywords: Daohugou, Inner Mongolia; Jiulongshan Formation; Kalligrammatidae, Ovule; *Yimaia*

Introduction

Oviposition, the process by which insects deposit or insert eggs in or on other organisms (Heming, 2003), is a ubiquitous feature of insect life history. An essential aspect of oviposition is the ability to access substrates for oviposition by a female insect that would promote the hatching, growth and survival to reproductive adulthood of her offspring, such that a succeeding generation is successfully produced (Denno & Dingle, 1981; but see Renwick, 1989). For those insects that oviposit into plant tissues, there are a variety of life-history strategies that are used, revealed by an extensive history of research (Zeh *et al*., 1989). These studies include the deposition of eggs either on or in plant tissues of closely related taxa (Müller & Rosenberger,

2006; Gültekin, 2007), the triggering of gall induction at oviposition sites (Formiga *et al.*, 2011), and the ovipositor probing of egg-insertion sites to assess plant-tissue suitability by agromyzid leaf miners (Sehgal, 1971; Winkler *et al.*, 2010). In addition, insect oviposition frequently activates counterdefenses by the host plant that include chemical defenses such as the generation of plant-host volatile chemicals as a response from oviposition lesions that attract egg parasitoids (Colazza *et al.*, 2004; Moraes *et al.*, 2008), and structural defenses such as egg-crushing wound response tissue from the plant hosts of certain leaf beetles (Desurmont *et al.*, 2012). The natural history of insect oviposition in plants has provided a major source of data and inferences as to how plants and insects interact on modern ecological and evolutionary time scales (Renwick, 1989; Childers, 1997). However, while the descriptive aspects of oviposition in the fossil record have been extensively explored (Vasilenko & Rasnitsyn, 2007; Popa & Zaharia, 2011; Gnaedinger *et al.*, 2014; Na *et al.*, 2014a), the natural history, including implications for behavioral evolution, of this archive of oviposition only recently has been studied to any significant degree (Hellmund and Hellmund, 1996a, 1996b; Sarzetti *et al.*, 2009; Winkler *et al.*, 2010; Ding *et al.*, 2014).

In addition to the vast spectrum of interactions that fossil plants have with feeding and ovipositing insects (Labandeira, 2006b, 2013), there also are related associations with mites, viruses, bacteria, fungi and nematodes (Labandeira & Prevec, 2014). These secondary infections

often alter the development and eventual appearance of the initial lesion, and can have a

significant effect on the fossil record of oviposition. For fossils, a formal classification of insect

feeding on plants was proposed by (Vialov, 1975), although he excluded oviposition as a related

category of "feeding" traces. Vasilenko (2005) suggested that oviposition should be added to the

taxa of fossil insect traces. By contrast, Zherikhin (2002), offered more complete descriptions of

ovipositional features and provided discussion of the morphological characteristics of their

producers, indicating that the preservation of fossil insect eggs in impression and compression

deposits provide a wealth of structural details that rarely are explored.

Patterns of fossil insect oviposition often show the vital link between plant and insect

relationships, insect reproductive biology that includes ovipositor structure, and the role of the

environment in modifying how, when and where oviposition occurs (Krassilov & Silantieva,

2007; Vasilenko & Rasnitsyn, 2007; Na *et al*., 2014a). Although insects lay eggs in plant tissues,

typically as a non-nutritive plant resource and principally for the shelter of eggs against predators

(Heming 2003; but see Moraes *et al*., 2008), the nature of the interaction has other effects, such

as production of callus and necrotic tissue that are associated with an informal type of

"herbivory". Oviposition and herbivory often are highly connected at the biochemical and

histological levels (Rodman, 1980), and there are instances of eggs negatively influencing

photosynthetic activity of the host plant in the immediate region of the lesion (Hilker & Meiners,

2011). Both the ovipositor- and mouthpart inflicted fossil record of damage provides a

significant archive in ferreting out the major patterns in host-plant use (Labandeira, 2006b).

Perhaps no other interval of the deep past offers as much data for the historical development

of oviposition as does the Jurassic Period. Although there is evidence for Late Triassic

ovipositional on a variety of plant hosts (Labandeira, 2006a; Pott *et al*., 2008; Gnaedinger *et al*.,

2014; Wappler *et al*., 2015; Labandeira, *et al*., 2016), it was during the Jurassic that many

modern associations were launched largely on plant-host lineages that now are extinct. Much of

the evidence for Jurassic ovipositional damage on plants occurs especially in Eurasian deposits,

particularly Western Europe and China. Lower Jurassic ovipositional damage has been found in

Germany (Krausel, 1958; Weber, 1968; van Konijnenburg-van Cittert & Schmeißner, 1999), and

as clusters of egg scars on bennettitalean leaves in Romania (Popa & Zaharia, 2011). Plant

remains with damage caused by ovipositing insects were described from the Late Jurassic to

Early Cretaceous of Russia, such as lesions occurring on the a conifer leaf assigned to the

pinaceous host, *Pityophyllum* sp. (Vasilenko, 2005). Interactions involving a single oviposition

occurrence from the Middle Jurassic have been described in association with a ginkgoalean leaf

from Inner Mongolia of Northeastern China (Na *et al*., 2014a). Ding and colleagues (2015)

additionally reported several oviposition damage types from the same deposit.

Currently, examples of Jurassic oviposition from China have been described from the Jiulongshan Formation, at the two major Daohugou localities, of latest Middle Jurassic age, in Northeastern China. (Na *et al*., 2014b; Ding *et al*, 2015; Meng *et al*., unpublished data). In this contribution, we assess a new damage type (DT) occurrence, and provide a natural-historical account of its significance. The new ovipositional type is exceptional, as it represents a stereotyped behavior on an atypical plant organ, a ginkgoalean fruit. The specimen has been penetrated through the outer fleshy and inner hardened seed coats and has punctured into central megagametophytic nutritive tissue by several ovipositional lesions. Our description of this distinctive DT is the first description of this, new ovipositional mode from the fossil record.

Material and Methods

The locality

The specimen originates from a quarry adjacent the village of Daohugou, near Chifeng City, in Ningcheng County, Inner Mongolia Autonomous Region of China . The strata containing the specimen is assigned to the Callovian Stage of the late Middle Jurassic, and is part of the Jiulongshan Formation (synonym: Haifanggou formation) that has been radioisotopically age dated multiple times using the ^{40}Ar/^{39}Ar series dates at 165 million years (Chen *et al*., 2004; He *et al*., 2004), corresponding to the Callovian Stage (Cohen, 2013). We herein accept the

conclusion of (Chen *et al*., 2004), based on what is known of the established stratigraphy (Liu & Jin, 2002; Ren *et al*., 2002), whereby the Daohugou beds are underlain by volcanic rocks dated at 164–165 million years (Chen *et al*., 2004; He *et al*., 2004). Consequently, the Daohugou beds should be no younger than 164–165 million years in age. The Jiulongshan Formation has a lithology of grey, greenish and purplish tinged, fine-grained sandstones and volcanic tuffs that are intercalated with taupe colored conglomerates and brick-red mudstones. The formation ranges from 50 to 80 meters in thickness, of which the fossiliferous beds form a minor part. Geological studies emphasizing stratigraphic correlations from measured data strongly indicate that the Daohugou strata belong to the Jiulongshan Formation (Liu & Jin, 2002; Ren *et al*, 2002, 2010).

The stratigraphic data are consistent with other studies that indicate an assignment to the Jiulongshan Formation and an age date of latest Middle Jurassic. Comparative studies of a large number of fossil insects (Ren *et al*., 2002), conchostracans (Shen *et al*., 2003), bivalves (Jiang, 2006) and immature frogs (Yuan *et al*., 2004) are consistent with a latest Middle Jurassic age. Moreover, multiple age dates from isotope geochronologic analyses also support a latest Middle Jurassic age date. The floristics of plant fossils within the Jiulongshan Formation indicate an assignment either to the latter Middle Jurassic or earlier Late Jurassic, evidence for which includes ferns (*Coniopteris*), cycads (*Nilssonia*), ginkgophytes (*Baiera, Czekanowskia, Yimaia*),

bennettitaleans (*Anomozamites*, *Pterophyllum*, *Weltrichia*) and conifers (*Podozamites*, *Yanliaoa*) (Pan, 1977; Zhang, *et al*., 1987; Li *et al*., 2004; Na *et al*., 2014b). No angiosperms are known from the Jiulongshan Formation (Ren *et al*., 2009; Wang *et al*., 2010).

Botanical context

The examined specimen that exhibits oviposition scars was collected from latest Middle Jurassic Daohugou beds, detailed above. The specimen is a seed, a mature fertilized ovule, from the pedunculated ginkgoalean ovulate organ (fruit) of *Yimaia capituliformis* Zhou, Zheng & Zhang, 2007, each of which subtends a cluster of four to eight ovules or seeds. *Yimaia capituliformis* reproductive organs are affiliated with five-lobed *Ginkgoites huttonii* leaves, a form genus consisting, at least in the Jiulongshan biota, of a morphological series ranging from morphs with wider and shorter lobes to those with narrower and longer lobes (Zhou *et al*., 2007). Both petiolate *Ginkgoites huttonii* foliage, and pedunculate *Y. capituliformis* organs and pollen organs are attached to *Ginkgoitocladus* short shoots that are borne by typical, undiagnosable, mid-Mesozoic ginkgoalean woody branches. The oviposited specimen was found as a detached element from a *Y. capituliformis* cluster; all morphological features of this specimen indicates that it is from *Y. capituliformis*. Dispersed ovules or seeds of *Y. capituliformis*, typical of the oviposited specimen, are assigned to the form genus *Allicospermum* (Zhou, 2009). Pollen organs affiliated with *Y. capituliformis* apparently are unnamed but the pollen is referred to

Ginkgocycadophytus and resembles closely that of modern *Ginkgo biloba* (Zhou, 2009). The whole-plant taxon to which the oviposited seed or ovule belongs consists of *Ginkgoites huttonii* leaves, *Yimaia capituliformis* ovulate organs and unnamed pollen organs with *Ginkgocycadophytus* pollen attached to *Ginkgoitocladus* short shoots borne on typical ginkgoalean branches (Zhou, 2009). *Yimaia capituliformis* is an Eurasian taxon that ranges from the Early Jurassic to Middle Jurassic and perhaps early Late Jurassic that was described initially from Europe (Braun, 1843; Schenk, 1867; Black, 1929; Harris & Millington, 1974; Kirchner, 1992) but subsequently has been found in Northeastern China (Zhou *et al*., 2007; Zhou, 2009; Wang *et al*., 2012).

The oviposited specimen of *Y. capituliformis* is housed at the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Science at Capital Normal University in Beijing, China (CNUB; Dong Ren, curator). The basic damage-type terminology and classification system used for this specimen follows the system outlined in Version 3 of the *Guide to Insect (and Other) Damage Types on Compressed Plant Fossils* (Labandeira *et al.*, 2007). The description of plant anatomical features follows the terminology of Gifford and Foster (1989).

Methods

The oviposited specimen was examined using a Nikon SMZ18 stereomicroscope. Microphotographic images of oviposition damage were taken on a Nikon SMZ18 dissecting microscope, connected to a Leica DFC500 camera with a Nikon DS-Ri-2 digital camera system. The resulting images were photomerged by Adobe Photoshop version CS5 to produce the images in Figure 1. Morphological features such as egg size, egg shape, and if possible chorion sculpture, were noted, as were biological features that included egg arrangement and the average interval between adjacent egg insertion scars. These features are the basis of modern insect oviposition classification (Bogdanov-Kat'kov, 1947). The length of each egg scar was measured along the midline from the anterior to the apex and the width was measured across the broadest part of the egg. Our approach follows explicit criteria in which each oviposition type should be classified based on their formal characters (Sarzetti *et al*., 2009; Gnaedinger *et al*., 2014).

Description and Natural History of the Specimen

Provided below is the formal description, biological context and related remarks of new DT272, a novel ovipositional type not previously mentioned from the fossil record. These new data will be added to the next version of the *Guide to Insect (and Other) Damage Types on Compressed Plant Fossils* (Labandeira *et al*., 2007).

Holomorphotype of DT272.

CNU-PLA-NN2011-663P/C, part and counterpart (Fig. 1A–E).

Description. Linear series of lenticular to elongate-ovoidal lesions, exhibiting thick, confluent reaction rims that occur on fleshy tissues of reproductive organs. Each egg insertion scar occurs from the same direction and forms one in a series of several egg lesions that are evenly arranged in a single, linear row with approximately the same inter-egg distances. The linear series of insertion scars is directed perpendicular to the long-axis of the lesions. The central part of each insertion lesion is preserved as a convex bulge (epirelief in the part) or concave depression (hyporelief in the counterpart). Scars range from three to seven in number (also based on additional bennettitalean material not described here). Lengths of individual scars generally range from 1.0 to 1.8 mm, and the widths from 0.4 to 0.6 mm. The distance between adjacent scars is approximately 1.0 mm.

Measurements. The entire oviposition trace covered a length 8.57 mm across the outer seed-coat surface. From left to right, the size of each egg (length × width, in mm) are: 1.13×0.44, 1.18×0.48, 1.02×0.59, 1.22×0.64, 1.23×0.56 and 1.82×0.49. The seventh scar along the seed margin was not measured due to possible taphonomic distortion. The exact distances between adjacent scars ranged from 0.90 to 1.29 mm.

Occurrence. Jiulongshan Formation, of Middle Jurassic age, assigned to a $^{40}Ar/^{39}Ar$

radioisotopic date of 165 Ma, equivalent to the Callovian Stage. Daohugou locality, Inner

Mongolia Autonomous Region, Northeastern China.

Functional feeding group. Oviposition. We note that oviposition has been treated as a

functional feeding group in the fossil plant–insect associational literature (e.g., Labandeira *et*

al., 2007, 2016a), a practice that is attributable to the feeding-like damage that it causes and a

persistent fossil record analogous to other functional feeding groups (Ding *et al*., 2015).

Specialization level. 3.

Host plant. *Yimaia capituliformis,* Zhou, Zheng, Zhang, 2007. (Ginkgoales: Yimaiaceae).

Inferred culprit. The most likely maker of DT272 damage was an early, Callovian-age

species of the subfamily Oregrammatinae (Neuroptera: Kalligrammatidae), based on the

ovipositor structure of *Oregramma illecebrosa* from the younger Yixian Formation of

Northeastern China (Labandeira *et al*., 2016b; Meng *et al*., unpublished data).

Figured material. Figure 1. A–E, Specimen of *Yimaia capituliformis*, illustrating

oviposition DT272; A, Entire image of host-plant ovule or seed; specimen

CNU–PLA–NN–2011663P*;* B–D, Enlarged figures of various oviposition lesions; E,

Oviposition lesions on counterpart of specimen (CNU–PLA–NN2011–663C). Scale bars: A–C, E, represent 1mm; D represents 0.5mm.

Other material. DT272 has not been found on other specimens of *Yimaia capituliformis*, but it does occurs on several of the basal attachment pads of *Cycadolepis* bracts on a specimen of *Williamsonia* sp. (CNU-PLA-NN-2013-225). This latter occurrence will be described in related, future publication (Meng *et al*., unpublished data).

Repository. Paleontological Collections, College of Life Sciences, Capital Normal University, Beijing, China.

Remarks. DT272 is very distinctive, robust oviposition mark characterized by a thickened, encompassing reaction scar. The occurrence of DT272 on *Yimaia capituliformis*, a ginkgophyte seed or ovule, is the first recognition of this DT in the fossil record. This seed or ovule consisted of an outer, thick and fleshy outer seed coat and a more hardened, thin inner seed coat, which in turn, surrounded innermost megagametophytic nutritive tissue that is the histological equivalent of angiosperm endosperm. Undoubtedly the target of the eggs was the megagametophytic tissue that would have provided accessible and abundant nutriment for hatching eggs and emerging nymphs or larvae. The outer, fleshy substrate of the outer seed coat may have provided a series of visual or chemical cues for attracting an ovipositing insect. This type of oviposition also is found on the fleshy pads revealing the attachment-scar surfaces of *Cycadolepis* bracts at the base

of the bennettitalean *Williamsonia*, from the same formation as the DT272-bearing *Yimaia*

specimen (Meng *et al*., unpublished data). Based on these occurrences and knowledge of the

ovipositor structure of the younger kalligrammatid lacewing *Oregramma illecebrosa* of the

Yixian Formation that probably was associated with bennettitalean pollinators (Yang *et al*.,

2014a, 2014b; Labandeira *et al*., 2016b), we infer that this type ovipositor structure originated

for slashing deep into fleshy tissues. Such an ovipositional habit may have been tracking a

particular, fleshy tissue type throughout the Jiulongshan flora among unrelated plant hosts.

Kalligrammatid lacewings also were long–proboscid pollinators that likely pollinated

gymnosperms such as *Williamsonia* that provided rewards of pollination drops and pollen

(Labandeira *et al*., 2016b). Additional understanding of the relationships between the fleshy

tissues of ginkgoalean and bennettitalean plants, kalligrammatid ovipositors, and the pollination

biology between kalligrammatids and bennettitaleans and possibly ginkgoalean hosts await

additional plant–insect studies of the Jiulongshan biota.

Discussion

The relationships between plants and insects are an important feature that provides much of the

ecological functioning in terrestrial ecosystems (Denno & Dingle, 1981). Insects use plants both

as a food resource and as shelter. Like gallers, leaf miners and seed predators, ovipositing insects

prefer laying eggs on or in the most appropriate plant hosts to access nutrients for their progenies

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(Resetarits, 1996; Lundgren *et al*., 2008). For such endophytic insects, the choice of an appropriate oviposition site is one in which hatching success, larval performance, recruitment and parental fitness is greater than plant-host selection against egg size, egg number and the confounding properties of substrate texture, hairiness or presence of chemical substances (Severson *et al*., 1988, 1991; Dwumfour, 1992; Resetarits, 1996), The simultaneous provision by the plant host of cover to allow protection from predators, parasitoids and pathogens must be assured (Forget *et al*., 2004). In particular, oviposition simultaneously incurs benefits and costs for the host plant and the intruding insect. Costs for the host plant include injury resulting in decreased photosynthetic capacity and the production of complex volatile biomolecules to signal the availability of a resource to potential enemies of the oviposited insect (Dwumfour, 1992; Childers, 1997; Moraes *et al*., 2008). Costs to the oviposited insect include compressive callus tissue that can destroy the oviposited inhabitant, especially at the egg stage, but also the production of various chemical and structural counterdefenses to those imposed by the plant host (Müller & Rosenberger, 2006; Formiga *et al*., 2011; Hilker & Meiners, 2011). And of course, the ultimate cost is successful predation of the oviposited insect by a predator or more frequently a parasitoid wasp or fly.

Direct evidence for the variety of these defensive, counterdefensive and counter-counterdefensive phenomena are difficult to establish. This difficulty is attributable to

the virtual absence of documentation, such fine-grained ecological patterns in the deep

paleobiological history of associations between vascular plants and their insect interactors

(Labandeira, 2002). On rare occasions, unhatched oviposited eggs visibly occur in lesions in the

fossil record, such as a half-emerged, intact egg from a *Glossopteris* host (Labandeira &

Currano, 2013). Nevertheless, the ovipositional relationship mentioned in this report is supported

by data. A female insect, most likely a kalligrammatid lacewing based on a lanciform ovipositor

structure (Labandeira *et al*., 2016b; Meng *et al*., unpublished data), inserted her ovipositor in a

behaviorally stereotyped fashion into a *Yimaia capituliformis* fruit, producing lesions that match

the relevant ovipositor size and shape. The ovipositor punctured the fleshy outer seed coat and

penetrated the hardened inner seed coat to reach the softer, nutritive, megagametophytic tissues

of the central ginkgoalean fruit. The same pattern was repeated on the surfaces of fleshy bract

attachment pads at the base of *Williamsonia* fructifications (Meng *et al*., unpublished data). This

highly stereotyped oviposition DT indicates a life history involving the targeting of fleshy plant

tissue by the same or closely related group of kalligrammatid lacewings, and endophytic,

immature phases of the insect that avoided interactions such as cannibalism, inferred from the

inter-lesion spacing of the egg insertion sites. It remains unknown whether the cascade of

defenses and counter defenses from chemical and physical sources were present to ward off

insect predator and pathogen attack and attract parasitoid consumers to the oviposited immatures.

Disclosure

The authors declare that there are no financial competing interests (political, personal, religious,

ideological, academic, intellectual, commercial, or any other), nor are there other competing

interests in the production of this manuscript.

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Figure Captions

Fig. 1. New damage type DT272. A–E, A *Yimaia capituliformis* ovule or seed with seven

oviposition lesions of DT272 arrayed in a single file. **A**, Entire seed with the fleshy outer seed

coat compressed as a black carbonized zone along the margin. The light brown color surrounded

by the black carbonized zone is the exposed outer surface of the inner seed coat. The micropyle

is at the top and the attachment area is at the bottom. This specimen is the part

(CNU-PLA-NN-2011663P). **B–D**, Enlargements of oviposition lesions occurring on the part. **E**,

Enlargement of oviposition in the counterpart (CNU–PLA–NN–2011663C). Note dark hued

reaction rims surrounding each oviposition lesion.