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Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeoLycopsid–arthropod associations and odonopteran oviposition on Triassic herbaceous *Isoetites*Philippe Moisan^{a,*}, Conrad C. Labandeira^{b,c}, Natalia A. Matushkina^d, Torsten Wappler^e, Sebastian Voigt^f, Hans Kerp^a^a Forschungsstelle für Paläobotanik am Institut für Geologie und Paläontologie, Westfälische Wilhelms-Universität Münster, Hindenburgplatz 57, 48143 Münster, Germany^b Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA^c Department of Entomology and BEES Program, University of Maryland, College Park, MD 20742, USA^d Department of Zoology, Biological Faculty, Kyiv National University, vul. Volodymyrs'ka 64, 01033 Kyiv, Ukraine^e Steinmann Institut für Geologie, Mineralogie, Paläontologie, Universität Bonn, Nussallee 8, 53115 Bonn, Germany^f Geologisches Institut, Technische Universität Bergakademie Freiberg, Bernhard-von-Cotta-Straße 2, 09599 Freiberg, Germany

ARTICLE INFO

Article history:

Received 8 February 2012

Received in revised form 8 May 2012

Accepted 20 May 2012

Available online 30 May 2012

Keywords:

Quillwort

Odonoptera

Archizyoptera

Oviposition

Madygen

Mesozoic

ABSTRACT

Associations between lycopsid and herbivorous arthropods are rare in the fossil record and equally sparse among the three surviving lineages of Lycopodiaceae, Selaginellaceae and Isoëtaceae. However, from the Middle–Upper Triassic Madygen Formation of southwestern Kyrgyzstan, we describe the first association between an isoetalean host, *Isoetites* (a quillwort), and a pattern of elliptical egg insertion scars that altered the host's live plant tissues. This ovipositional damage, in some cases deployed in a stereotypical zigzag pattern, was most likely caused by small damselfly-like insects from the extinct suborder Archizyoptera of the order Odonoptera (dragonflies). If this identification is correct, it indicates considerable behavioral stasis of dragonflies extending deep into the Mesozoic. Our detection of lycopsid ovipositional damage adds to the list of major plant hosts from the preangiospermous Mesozoic that were resources for host use by egg-laying dragonflies, particularly horsetails, ferns, and seed plants that included conifers, peltasperms, corystosperms, ginkgophytes, bennettitaleans and probably cycads.

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1. Introduction

Lycopsids are one of the oldest vascular plant lineages and were present among the earliest terrestrial ecosystems of the Early Devonian (Kenrick and Crane, 1997). Later in the Paleozoic, lycopsids became a significant and diverse component in a range of wetland environments (DiMichele and Phillips, 1985). Although their early presence is represented by several extinct basal clades, one early derivative group were the diverse Lepidodendrales, typically constructed as pole-like trees with limited woody tissues, whose uppermost reaches bore dichotomous branching limbs with scaly, needle-like leaves. The Lepidodendrales were especially prominent in equatorial environments, particularly swamps and marshes from the Middle Pennsylvanian of Euramerica to the Late Permian of Cathaysia (DiMichele and Phillips, 1985). By the end of the Permian, the Lepidodendrales were extinct, although another lineage, the Triassic Pleuromeiales attained similar arborescent growth forms as the earlier Lepidodendrales, but were more limited in stature and developed a new, cormose rooting structure (Retallack, 1975). Modern lycopsids had their origins during the

Paleozoic and early representatives coexisted with other typical wetland taxa from Pennsylvanian deposits (Taylor et al., 2009). Modern lycopsids are significantly scaled down compared to their Paleozoic forbearers, but are recognizable by their occurrence in humid environments or in arid environments with life-history traits to avoid desiccation. There are three principal lineages of modern lycopsids: the Lycopodiaceae (clubmosses, groundpines), the Isoëtaceae (quillworts), the subject of our discovery discussed below, and the Selaginellaceae (resurrection plants, spikemosses). All presently are herbaceous and commonly have prostrate growth forms (Pryer et al., 2004).

1.1. The fossil and modern record of lycopsid–arthropod associations

Of the major land-plant groups, lycopsids arguably provide the least evidence for arthropod detritivory, especially when they were prominent during the late Paleozoic (Labandeira et al., 1997). In addition, fossil (and modern) lycopsids are one of the least herbivorized of land-plant groups when examined for the diversity and intensity of associations with arthropods (Gerson, 1979; Labandeira, 2002a). The earliest evidence in the fossil record for consumption of lycopsids comes from the Early Devonian Rhynie Chert of Scotland, in which primitive lycopsid spores occur in the coprolites of early microarthropods (Kevan et al., 1975; Habgood et al., 2004), with ingestion

* Corresponding author.

E-mail address: f_mois01@uni-muenster.de (P. Moisan).

probably favoring detritivory over herbivory (Labandeira, 2007). From the younger Calcareous Sandstone Series, also from Scotland but of Early Mississippian age, Scott (1977) illustrated from a small coprolite a spore type very reminiscent of a lycopsid. However, it was from younger, Early Pennsylvanian sediments of the Yorkshire Coal Measures that Scott (1977) reported the lycopsid spores *Lycospora*, *Densosporites*, cf. *Crassispora*, and ?*Cristatisporites* in numerous, small arthropodan coprolites that could be attributable to detritivory or herbivory. During the Middle Pennsylvanian in Euramerican wetland habitats there is evidence that the large, ground-dwelling myriapod, *Arthropleura*, consumed plant litter, including xylary tracheids identified as lycopsid in origin (Rolfe and Ingham, 1967), probably representing a detritivorous diet in habitats laden with fallen bark, tree stumps and other plant litter (Rolfe, 1985). By contrast, an arboreal herbivorous association is represented by a diaphanopterodean nymph, probably a species of *Prochoroptera*, with unaltered, entire, lycopsid spores as gut contents (Kukalová-Peck, 1987), possibly representing a major dietary mode for some palaeodictyopteroid taxa. The most pervasive Paleozoic lycopsid–arthropod association, however, is the detritivory represented in the stems and leaf cushions (*Lepidophloios*, *Diaphorodendron*) and cones (*Lepidocarpon*) of several dominant lycopsid taxa from coal-ball bearing basins occurring in wetland environments throughout the Pennsylvanian of eastern North America (Labandeira et al., 1997). In all of these reports, there are no records of distinctive, frequently robust lycopsid cuticles (Hübers et al., 2011) in arthropod guts or as coprolitic contents. Additionally, there are no published lycopod–arthropod associational records after the Paleozoic, a consequence largely attributable to demise of plant communities that harbored large amounts of lycopsid biomass, and their replacement during the Triassic by more diminutive, less abundant, and especially better defended taxa that have persisted to the Holocene (Berenbaum and Siegler, 1991; Popper and Fry, 2004; Markham et al., 2006; Holtum et al., 2007; Setyawan, 2011).

Modern examples of herbivory may provide a sense of the types of lycopsid–arthropod associations that were present during the Mesozoic and Cenozoic. Many of these associations (Gerson, 1979; Mound et al., 1994) probably evolved from arthropods whose immediate ancestral hosts were angiosperms, but subsequently and recently colonized lycopsids. Of the three principal lineages of extant Lycopsida, overwhelmingly the most extensively herbivorized is the Selaginellaceae, probably a consequence of their greater ecological and biogeographical breadth and several-fold greater species diversity than either the Lycopodiaceae or Isoëtaceae. For the Selaginellaceae, represented only by *Selaginella*, there are several rare records of external foliage feeding caused by lepidopteran larvae, including the Panamanian *Euptychia westwoodi* and Costa Rican *E. jesia* and *E. mollis*, nymphalid butterflies (Singer et al., 1971; DeVries, 1987); Philippine *Ragadia luzonia* and *Acrophtalmia artemis*, also nymphalid butterflies (Fukuda, 1983); and the larvae of a Bornean species of *Callopietria*, an obligately fern-feeding noctuid moth (Holloway, 1989). *Selaginella* also is externally consumed by adult *Haaniella echinata*, a walking stick (Phasmatodea: Phasmatidae) (Blüthgen et al., 2006); larvae and adults of the scorpionfly *Boreus reductus* (Mecoptera: Boreidae) (Penny, 1977); and the small wasp *Encarsia sueloderi* (Hymenoptera: Aphelinidae), a parasitoid of the similarly *Selaginella*-feeding, piercing-and-sucking whitefly *Aleurotulus pteridophytae* (Hemiptera: Aleyrodidae) (Mound et al., 1994) perhaps a case of a herbivore parasitoid later colonizing the plant host of its former larval host. Other piercing-and-sucking insects occurring on *Selaginella* are the scale insect *Phenacoccus solani* (Hemiptera: Pseudococcidae) (McKenzie, 1967); and the thrips, *Echinothrips selaginellae* (Thysanoptera: Thripidae) (Mound et al., 1994). Last, there are two unidentified gallers that occur on *Selaginella*, a gall midge from Indonesia (Diptera: Cecidomyiidae) (Strasburger, 1873; Docters van Leeuwen, 1938); and a gall wasp from India (Hymenoptera: Cynipidae) (Bera et al., 1994; De and Bera, 1995). Barton (2005) provides a global listing of arthropod herbivores on *Selaginella*.

The Lycopodiaceae and Isoëtaceae are more rarely attacked by insects. For the Lycopodiaceae, *Lycopodium* is attacked in Hawai'i by the pith-boring larvae of *Scoparia lycopodiae*, a member of the lepidopteran Pyralidae (pyralid moths) (Swezey, 1910); and *Huperzia* is consumed in Japan by the leaf-mining larvae of *Temnosira czurhini*, a member of the dipteran Pallopteridae (flutter-wing flies) (Kato, 2002). The Isoëtaceae occur in wet environments, and their spores may be dispersed by annelids (Duthie, 1929) and insects. The minimal-ist leaf tissues of *Isoëtes* are consumed by generalist external herbivores such as the limnephilid *Limnephilus* of the Trichoptera (Cronin et al., 1998). And lastly, Lieftinck (1949) reported exuviae of the coenagrionid dragonfly *Ischnura isoetes*, attached to *Isoëtes* near the water's surface in peat-bog swamps of north-central Indonesian New Guinea.

1.2. A brief fossil history of oviposition (Table 1)

The earliest record of ovipositional damage on fossil plants is from the Late Pennsylvanian sphenopsid *Calamites cistii* (Béthoux et al., 2004). During the Pennsylvanian and Permian, and until the expansion of sphenopsids during the early Mesozoic, conifer stems and especially seed-fern foliage were the preferred plant substrates for the Odonatoptera, Palaeodictyopteroidea, Orthoptera, and perhaps basal holometabolous clades with prominent, external ovipositors such as the aptly named sawflies of the Hymenoptera (Labandeira, 2006a; Vasilenko and Rasnitsyn, 2007). These mostly Paleozoic clades bore laterally compressed ovipositors, often ridged and with marginal serrations, that were modified for slicing into plant tissues in laying eggs (Sharov, 1968; Carpenter, 1971; Kukalová-Peck, 1972; Naito and Huang, 1988; Labandeira, 2006a; Prevec et al., 2009). Throughout the Triassic and Jurassic, a variety of pteridophytes and seed plants of aquatic and wetland habitats were used as substrates principally by the Odonatoptera, as the Palaeodictyopteroidea and other Paleozoic ovipositing clades became extinct around the Permian–Triassic boundary. The major ovipositional plant substrates during the earlier Mesozoic were sphenopsids (Roselt, 1954; Kräusel, 1958; Weber, 1968; Geyer and Kelber, 1987; Kelber, 1988; Labandeira, 2006a), probable cycads (Kelber, 1988; Grauvogel-Stamm and Kelber, 1996), voltzialean conifers (Labandeira, 2006a; Gnaedinger et al., 2007), probable pinaceous conifers (Vasilenko, 2005), peltasperms (Vasilenko, 2011), corystosperms (Labandeira, 2008, personal observation), ginkgophytes (van Konijnenburg-van Cittert and Schmeißner, 1999; Vasilenko, 2005), and bennettitaleans (Pott et al., 2008). From the Early Cretaceous until the Miocene almost all plant hosts with ovipositional damage were angiosperms (Table 1), although numerous nonangiospermous substrates are used for oviposition today such as conifers (Codella and Raffa, 2002) and cycads (Donaldson, 2008).

Our extensive review of the literature reveals no evidence of oviposition on fossil lycopsids. Moreover, there are no fossil records for any type of herbivory on lycopsids; the only evidence of arthropod damage to lycopsids corresponds to mite detritivory from Pennsylvanian age coal-swamp forests (Labandeira et al., 1997). In this paper we report the first case of oviposition on lycopsids. Ovipositional scars of endophytically inserted eggs were found on the leaf surfaces of the herbaceous lycopsids *Isoetes madygensis* and *I. sextelliae* from the Middle–Late Triassic Madygen Formation of Kyrgyzstan. Based on comparisons of ovipositional scar features of fossil and recent dragonflies, it is likely that the eggs were laid by a member of the Archizyoptera, an extinct suborder of dragonflies (order Odonatoptera) that included major Paleozoic taxa (Nel et al., 2012). This interpretation is supported by the occurrence of several fossil forms of the Odonatoptera–Archizyoptera (Table 2) in the Madygen fossil biota. This unique discovery represents new information for understanding the plant–insect associational complexity of this exceptional Triassic ecosystem, recognized as one of the most spectacular Mesozoic Lagerstätten worldwide. This ecosystem may eventually represent the greatest abundance and diversity of animal and plant taxa and their associations for any

Table 1

A compilation of evidence for oviposition in the fossil record.

Host plants	Locality/occurrence	Age	References
Angiosperm leaves	Ribesalbes, Castellón, Spain	Early Miocene	Peñalver and Delclòs (2004)
Angiosperm leaves	Randecker Maar/Grube Messel, Germany	Early Miocene/Middle Miocene	Hellmund and Hellmund (1996a,b)
Angiosperm leaves	Randecker Maar/Berzdorf/Bad Salzhausen, Germany	Early Miocene/Middle Miocene	Hellmund and Hellmund (2002c)
Angiosperm leaves	Voselberg, Bad Salzhausen, Germany	Middle Miocene	Goepfert (1841); Hellmund and Hellmund (2002a)
<i>Cedrela</i> (angiosperm)	Palo Pintado and San José formations, Argentina	Middle and Upper Miocene	Horn et al. (2011)
Angiosperm leaves	Hammerunterwiesenthal, Germany	Early Oligocene	Hellmund and Hellmund (1998)
Angiosperm leaf	Seifhennersdorf, Germany	Middle Oligocene	Hellmund and Hellmund (1996b)
Angiosperm leaves	Rott, Siebengebirge, Germany	Late Oligocene	Hellmund and Hellmund (1991, 1993)
Angiosperm leaves	Rott, Siebengebirge, Germany	Late Oligocene	Wappler (2010); Petrulevičius et al. (2011)
Angiosperm leaf	Sourdough, Wyoming, USA	Early Eocene	Wilf (2008)
Angiosperm leaves	Laguna del Hunco/Río Pichileufú, Argentina	Early Eocene/Middle Eocene	Sarzetti et al. (2009)
Angiosperm leaf	Grube Messel, Germany	Middle Eocene	Schaarschmidt (1988)
<i>Alnus</i>	Republic, Washington, USA	Middle Eocene	Lewis and Carroll (1991); Lewis (1992)
Angiosperm leaf	Benton County, Mississippi, USA	Middle Eocene	Johnston (1993)
Angiosperm leaves and <i>Ginkgo</i>	MacAbee, British Columbia, Canada	Middle Eocene	Labandeira (2002b)
Angiosperm leaf	Mücheln (Geiseltal), Germany	Middle Eocene	Hellmund and Hellmund (2002b)
Angiosperm leaves	Bohemia, Czech Republic	Late Cretaceous	Hellmund and Hellmund (1996a)
<i>Quereuxia</i> (aquatic angiosperm)	Udurchukan locality, Amur Region, Russia	Late Cretaceous	Vasilenko (2008)
<i>Phyllopteroides laevis</i> (Osmundaceae)	Chunakhal, Rajmahal Basin, India	Early Cretaceous	Banerji (2004)
<i>Acaciaephyllum</i>	Makhtesh Ramon, Negev, Israel	Early Cretaceous (Albian)	Krassilov et al. (2007, 2008); Krassilov and Shuklina (2008)
<i>Pityophyllum</i> and <i>Ginkgoites</i>	Chernovskie Kopi, Chita Region, Russia	Late Jurassic–Early Cretaceous	Vasilenko (2005)
<i>Equisetites foveolatus</i>	Sassendorf, Germany	Liassic (Early Jurassic)	Kräusel (1958)
<i>Schmeissneria microstachys</i> and <i>Podozamites distans</i>	Franconia, Germany	Early Jurassic	van Konijnenburg-van Cittert and Schmeißner (1999)
<i>Neocalamites exornatus</i>	Bayreuth, Germany	Rhaetian–Liassic	Weber (1968)
<i>Equisetites platyodon</i>	Neuwelt, Switzerland	late Middle Triassic (Ladinian), Lettenkohle	Heer (1877)
<i>Equisetites foveolatus</i>	Bedheim, Germany	Lower Keuper (Ladinian)	Roselt (1954); Kelber (1988)
<i>Equisetites arenaceus</i>	Franconia, Germany	Lower Keuper (Ladinian)	Kelber (1988); Geyer and Kelber (1987); Kelber and Geyer (1989); Grauvogel-Stamm and Kelber (1996); Kelber and Hansch (1996); Kelber (1988); Grauvogel-Stamm and Kelber (1996)
<i>Taeniopteris angustifolia</i>	Franconia, Germany/Alsace, France	Lower Keuper (Ladinian)/ Middle Lettenkohle	
<i>Nilssoniopteris angustior</i> and <i>N. haidingeri</i>	Lunz, Austria	Carnian	Pott et al. (2008)
<i>Podozamites distans</i>	Pålsjö, Scania, Sweden	Late Triassic (Rhaetian)	Nathorst (1876, 1878)
<i>Heidiphyllum elongatum</i>	La Ternera Formation, Chile	Late Triassic	Gnaedinger et al. (2007)
<i>Equisetum nuwejaarensis</i> and <i>Heidiphyllum elongatum</i>	Molteno Formation, Karoo Basin, South Africa	Late Triassic	Labandeira (2006a)
Horsetail stems (? <i>Equisetites</i>)	Chinle Fromation, Arizona, USA	Late Triassic	Ash (2005)
<i>Dictyophyllum bremerense</i>	Southeast Queensland, Australia	Middle–Late Triassic	Webb (1982)
<i>Glossopteris bucklandensis</i> / <i>Taeniopteris parvilocus</i>	Stony Creek/Wivenhoe Hill, Australia	Late Permian/Middle Triassic	McLoughlin (2011)
<i>Phyllothea</i>	Belmont, New South Wales, Australia	Late Permian	Beattie (2007)
Glossopterid leaves	KwaZulu-Natal, South Africa	Late Permian	Prevec et al. (2009)
<i>Glossopteris</i> leaves	Wapadsberg Pass, South Africa	Late Permian	Prevec et al. (2010)
<i>Pursongia</i> (Peltaspermales)	Isady, Vologda Region, Russia	Late Permian	Vassilenko (2011)
<i>Glossopteris</i> cf. <i>ampla</i>	La Golondrina, Santa Cruz, Argentina	Middle–Late Permian	Cariglino and Gutiérrez (2011)
Leaves of <i>Glossopteris</i> and <i>Noeggerathiopsis</i>	Raniganj Coalfield, India	Early–Middle Permian	Srivastava (1987); Srivastava and Agnihotri (2011); Shah (2004)
<i>Gangamopteris obovata</i>	Morro do Papaléo Mine, Brazil	Early Permian	Adami-Rodrigues et al. (2004); De Souza-Pinheiro et al. (2012)
Sphenopsid stems	Sachsen, Germany	Pennsylvanian	Geinitz (1855)
<i>Calamites cistii</i>	Graissessac Basin, Hérault, France	Late Pennsylvanian	Béthoux et al. (2004)

place during the Middle–Late Triassic interval (e.g., Sharov, 1970; Dobruskina, 1995; Voigt et al., 2006; Shcherbakov, 2008; Sues and Fraser, 2010; Moisan et al., 2011). However, the early Late Triassic Molteno Formation currently has the greatest documented plant and associational diversity of any documented approximately coeval Lagerstätte, excepting insects (Anderson et al., 1999; Anderson and Anderson, 2003; Labandeira, 2006a, 2006b).

2. Geological setting, material and methods

The specimens were collected from the Madygen fossil site, situated about 50 km to the west of Batken, in the northern foothills of the

Turkestan Mountains in southwestern Kyrgyzstan, Central Asia (Fig. 1). The Madygen lake system represents an upland, intramontane basin (Voigt et al., 2006), and is one of the very few truly continental Triassic deposits in Central Asia. The Madygen Formation consists of a ca. 580 m thick succession of complexly interbedded conglomerates, sandstones and siltstones representing deposits of alluvial fans, alluvial plains and freshwater lakes. The specimens of *Isoetes madygensis* and *I. sixteliae* that exhibit evidence of oviposition come from lacustrine deposits in the lowermost part of the Brown-Grey Member (T5), described by Dobruskina (1995). The specimens are housed in the paleontological collection of the Geologisches Institut, Technische Universität Bergakademie Freiberg, Germany (FG).

Table 2

Taxonomic diversity and wing size of the fossil dragonflies from the Madygen Formation (after Pritykina, 1981; Nel et al., 2001, 2002, 2005). Taxonomy is given after the original descriptions of species. Those species representatives of which characterized by small wing length (up to 3 cm) are typed in bold.

Species	Family	Wing length (in cm)
<i>Triadotypus sogdianus</i> Pritykina, 1981	Triadotypidae	>8.2
<i>Triadophlebia madygenica</i> Pritykina, 1981	Triadophlebiidae	7.4
<i>Triadophlebia distincta</i> Pritykina, 1981	Triadophlebiidae	>4.5
<i>Triadophlebia minuta</i> Pritykina, 1981	Triadophlebiidae	>2.6
<i>Triadophlebia magna</i> Pritykina, 1981	Triadophlebiidae	c. 12–13
<i>Triadophlebia honesta</i> Pritykina, 1981	Triadophlebiidae	>6.5
<i>Triadophlebia modica</i> Pritykina, 1981	Triadophlebiidae	>2.7
<i>Neritophlebia elegans</i> Pritykina, 1981	Triadophlebiidae	7.2
<i>Neritophlebia vicina</i> Pritykina, 1981	Triadophlebiidae	>7.1
<i>Neritophlebia longa</i> Pritykina, 1981	Triadophlebiidae	12–12.5
<i>Cladophlebia parvula</i> Pritykina, 1981	Triadophlebiidae	2.6
<i>Cladophlebia brevis</i> Pritykina, 1981	Triadophlebiidae	2.2
<i>Paurophlebia lepida</i> Pritykina, 1981	Triadophlebiidae	2.6–2.9
<i>Paurophlebia angusta</i> Pritykina, 1981	Triadophlebiidae	2.6–2.8
<i>Nonymophlebia venosa</i> Pritykina, 1981	Triadophlebiidae	3.9–4.3
<i>Mitophlebia enormis</i> Pritykina, 1981	Mitophlebiidae	4.3
<i>Zygophlebia ramosa</i> Pritykina, 1981	Zygophlebiidae	3.9–4.2
<i>Zygophlebiella curta</i> Pritykina, 1981	Zygophlebiidae	>4.0
<i>Myxophlebia mixta</i> Pritykina, 1981	Zygophlebiidae	5.7
<i>Cyrtophlebia sinuosa</i> Pritykina, 1981	Zygophlebiidae	>2.3
<i>Xamenophlebia ornata</i> Pritykina, 1981	Xamenophlebiidae	>3.7
<i>Kennedyia carpenteri</i> Pritykina, 1981	Kennedyidae	2.9–3.1
<i>Kennedyia gracilis</i> Pritykina, 1981	Kennedyidae	2.4
<i>Terskeja paula</i> Pritykina, 1981	Protomyrmeleontidae	1.2–1.4
<i>Terskeja pumilio</i> Pritykina, 1981	Protomyrmeleontidae	1.2
<i>Terskeja tenuis</i> Pritykina, 1981	Protomyrmeleontidae	1.9
<i>Ferganagrion kirghiziensis</i> Nel et al. 2005	Protomyrmeleontidae	>1.8
<i>Batkenia pusilla</i> Pritykina, 1981	Batkeniidae	>0.8–1.5
<i>Triassolestodes asiaticus</i> Pritykina, 1981	Triassolestidae	3
<i>Triassoneura primitiva</i> Pritykina, 1981	?Triassolestidae	>1.5

3. Results

The Ladinian–Carnian Madygen Formation contains a diverse and rich assemblage of fossil lycopsids, including endemic subarborescent and herbaceous forms (Moisan, 2012). Of this assemblage, two specimens belong to the herbaceous lycopsid taxa *Isoetites madygensis* and

Isoetites sixteliae (Isoëtaceae), and show unequivocal evidence of ovipositional scars on their leaf surfaces. The leaves of both *Isoetites* host species are very elongate and lanceolate; have a midvein; and numerous intervening, parallel, miniscule surface striae. The species are distinguishable by the type of leaf margin, which is serrated in *I. sixteliae* and entire in *I. madygensis*.

3.1. Ovipositional scars on *Isoetites madygensis* (Fig. 2A–E)

The specimen FG 596/X/1009 represents a leaf fragment, 5 cm long by 6 mm wide, of the lycopsid *I. madygensis*, which exhibits thirty-five ovipositional scars on the leaf surface (Fig. 2A). The ovipositional scars are elliptical to fusiform (spindle-shaped), longitudinally elongated, and faithfully oriented parallel to but avoiding the midvein (Fig. 2B–E). The ovipositional scars are between 1.0 and 1.2 mm long and 0.35–0.45 mm wide, and are arranged in longitudinal parallel rows (Fig. 2A, D). The scars are separated longitudinally by 0.6–1.2 mm and horizontally by 0.3–0.5 mm. Although the ovipositional scars are mostly solitary, a few adjacent scars overlap slightly on their ends (Fig. 2C–E).

3.2. Ovipositional scars on *Isoetites sixteliae* (Fig. 3A–F)

A leaf fragment of *I. sixteliae* (specimen FG 596/X/675), 3.7 cm long by 5 mm wide, contains approximately 13–14 ovipositional scars (Fig. 3A). The ovipositional scars are between 0.9 and 1.4 mm long by 0.4–0.8 mm wide, longitudinally elliptical to slightly fusiform (Fig. 3B–F). The pattern of ovipositional scars is almost exclusively positioned in a solitary manner, although in some portions of the leaf surface they are more or less aggregated (Fig. 3B). However, it is not possible to distinguish with clarity whether any ovipositional scars are partially overlapping as in *I. madygensis*.

4. Discussion

Our discovery of dragonfly-induced ovipositional damage on *Isoetites* at Madygen can be contextualized by four considerations that provide a better understanding of our find. First, what is the relationship, if any, of the *Isoetites* damage to other types of ovipositional

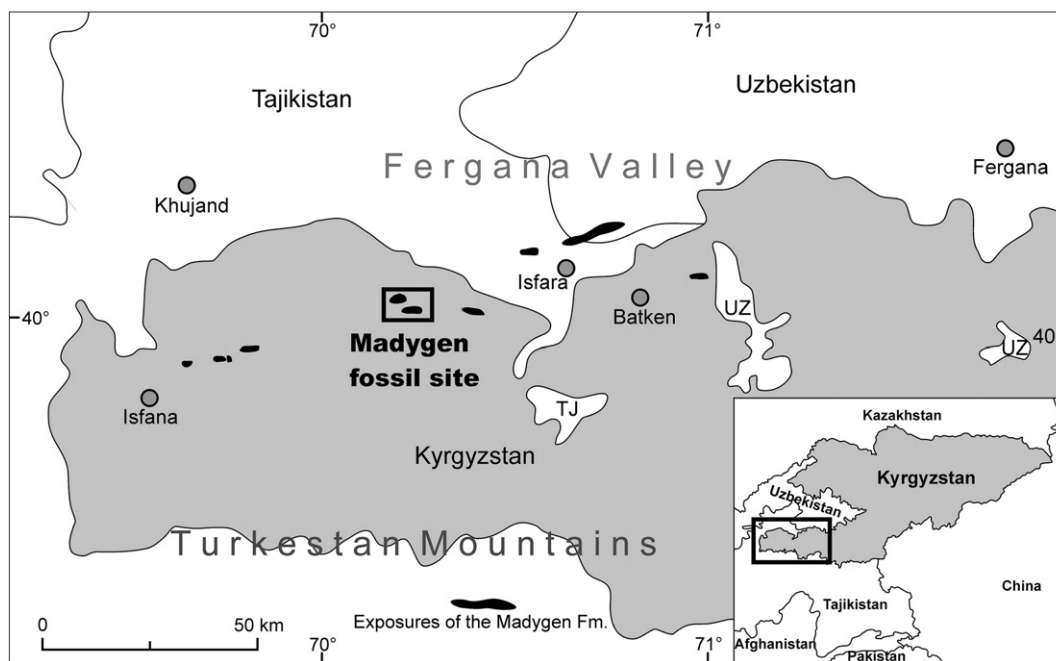


Fig. 1. Map showing exposures of the Madygen Formation in southwestern Kyrgyzstan and neighboring countries in Central Asia. The polylobate areas in white represent geopolitical enclaves within Kyrgyzstan: TJ: Tajikistan; UZ: Uzbekistan.

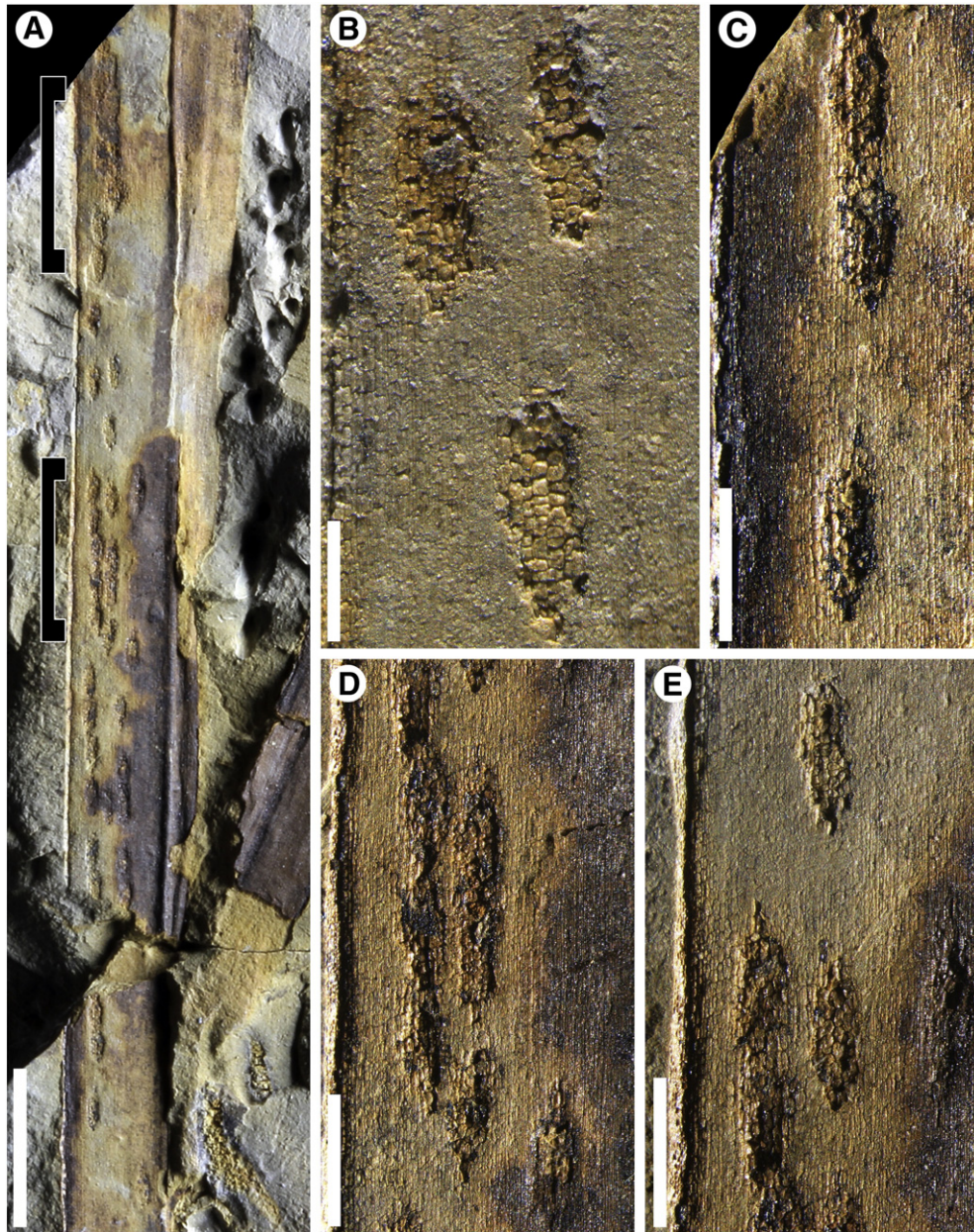


Fig. 2. Ovipositional scars on an *Isoetites madygensis* leaf from the Middle–Late Triassic Madygen Formation, Kyrgyzstan. Specimen FG 596/X/1009. A. Portion of the leaf showing an endophytic ovipositional scar arranged parallel to the midvein. Scale bar = 5 mm. Square brackets indicate the regularly patterned scars, which are redrawn in Fig. 4. B. Detail of solitary and elliptical scars on the leaf surface. Scale bar = 500 μ m. C–E. Details of endophytic elliptical to fusiform scars, including forms that are solitary or overlapping at their ends. Scale bars = 1 mm.

associations in the fossil record? Second, how does the *Isoetites* ovipositional damage compare with analogous modern damage? Third, can the fossil record of Odonata at Madygen or modern related associations provide any clues to the identity of the culprit? And fourth, what is the broader importance of the *Isoetites* and other insect damage at Madygen to the evolution of plant host and plant–arthropod associational diversity in deep time?

4.1. Ovipositional and other damage in the fossil record attributed to Odonata

Fossil records of insect oviposition from the Late Pennsylvanian to early Miocene are relatively abundant (Table 1). Evidence for the earliest occurrence of oviposition during the Middle Pennsylvanian has been found in sphenopsids (Béthoux et al., 2004); later Paleozoic associations involve principally seed plants such as the glossopterids *Glossopteris*

and *Gangamopteris* in Gondwana (Srivastava, 1987; Adami-Rodrigues et al., 2004; Prevec et al., 2009, 2010; Carigino and Gutiérrez, 2011; Srivastava and Agnihotri, 2011; De Souza-Pinheiro et al., 2012). In these cases, ovipositional scars are elongated and oval in shape, often with an encircling rim of raised callus tissue, and typically oriented parallel to the long axis of the stem in sphenopsids or midrib in glossopterid leaves. Beattie (2007) described small, circular and clustered ovipositional scars on sphenopsid vegetation. One exception to this pattern is ovipositional scars on a leaf of the peltaspermalean seed fern, *Pursongia*, as the ovipositional scars are deployed in transverse rows (Vassilenko, 2011), an arrangement typically not seen until much later in the fossil record (Sarzetti et al., 2009). For the Mesozoic, ovipositional damage has been recorded from numerous Mesozoic localities worldwide, demonstrating that almost all of the dominant plant lineages were used presumably by odonatans as a substrate for oviposition, including sphenopsids, ferns, conifers, bennettitaleans, ginkgoaleans and angiosperms (Table 1). Pott et

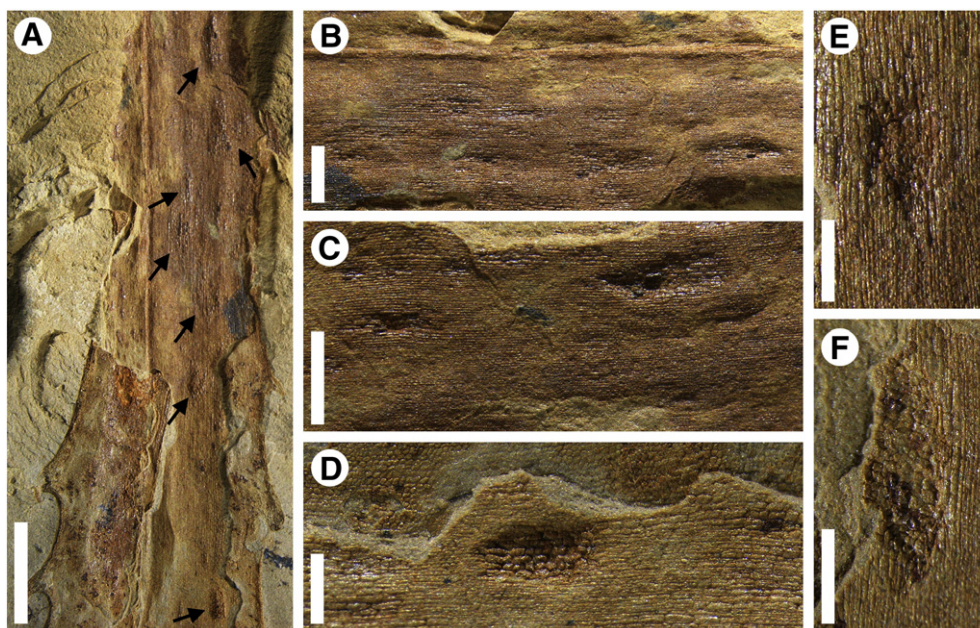


Fig. 3. Ovipositional scars on an *Isoetites sixteliae* leaf from the Middle–Late Triassic Madygen Formation, Kyrgyzstan. Specimen FG 596/X/675. A. Portion of the leaf showing the position of presumed underlying endophytic eggs (arrows), arranged parallel to the midvein. Scale bar = 2.5 mm. B–C. Several oval to fusiform ovipositional scars vary in size, probably due to differential preservation of the material. Scale bar = 1 mm. D–F. Details of endophytic ovipositional scars on the leaf surface. Scale bars = 500 μ m.

al. (2008) described from the Carnian of Austria two types of oviposition in foliage of the bennettitalean *Nilssoniopteris*, the first consisting of oval scars arranged in circles, and the second comprised of lenticular scars oriented parallel to the lateral veins and perpendicular to the rachis. The arcuate ovipositional patterns found on bennettitalean foliage are rare for the Mesozoic, and principally do not reappear until the Late Cretaceous in aquatic angiosperms (Vasilenko, 2008). The most common ovipositional pattern, at least during the early Mesozoic, corresponds to elliptical and oval scars arranged in linear rows along longitudinal axes of leaves. In this regard there is remarkable similarity of the ovipositional scars described in *Equisetites arenaceus* from Ladinian localities in Central Europe (Kelber, 1988; Grauvogel-Stamm and Kelber, 1996; Kelber and Hansch, 1996) with those documented herein for both *Isoetites* species. This similarity extends to the arrangement of the scars in linear, longitudinal rows along the leaf edge, scar shape, the end-to-end overlap of adjacent scars. Grauvogel-Stamm and Kelber (1996) attributed these scars to endophytically inserted eggs by the Odonatoptera. Accordingly, modern species of Odonata have two ovipositional strategies to lay eggs (Corbet, 1999). In exophytic oviposition, the eggs are completely visible and normally clustered and on the surface, while in endophytic oviposition the eggs are solitary (Vasilenko, 2005), normally long and cylindrical in shape, and they are inserted directly into plant tissue where they are completely or partially hidden. It is the latter type of oviposition that typifies the Madygen ovipositional damage on lycopsid tissues.

4.2. Ovipositional behavior in recent Odonata

Recent Odonata are subdivided into three groups, the Zygoptera (damselflies), Anisoptera (dragonflies) and Anisozygoptera. Odonatan naiads occupy a wide spectrum of aquatic habitats ranging from fast flowing, slowly moving or standing fresh water, to bogs and brackish water (Corbet, 1980). Most zygopteran naiads have affinities for plants and occur among submerged plants in the water column. However, certain forest-dwelling zygopterans develop in phytotelmata such as water-containing leaf bases, bromeliads and tree holes (Machado, 1977; Hadrys et al., 2005). By contrast, anisopteran naiads inhabit diverse habitats, frequently living epibenthically among silt and plant debris at the bottom of ponds and lakes or as burrowers into bottom

sediments. The degree of plant association of anisopteran naiads is variable across naiad instars, a pattern that occurs in the Aeshnidae. Some anisopteran naiads, such as the Petaluridae and some Aeshnidae, are semiterrestrial, inhabiting burrows or leaf litter.

The Odonata fundamentally have two types of egg-laying strategies (Corbet, 1980). In endophytic oviposition, the females penetrate a live plant substrate in an iterative manner, using a well-developed, slicing ovipositor and sequentially inserting an egg into each laceration. The eggs are inserted into living or dead plant tissues, and above or below water level. This strategy occurs in the Zygoptera, Anisozygoptera and the anisopteran Aeshnidae. Alternatively, the majority of other Odonata lay eggs exophytically, upon or above the water surface, and on a variety of substrates, including the surfaces of live and dead aquatic plants, plant debris, rocks or the ground. Females with exophytic behavior lack a well-developed ovipositor and produce ovoid to rounded eggs whereas those with an endophytic behavior have prominent, slicing ovipositors and bear eggs of elliptical-elongate shapes.

Recent Odonata lay their eggs on pleustophytes (free-floating plants), hydrophytes (adapted to subaquatic environments), and terrestrial plants near water bodies. Several Odonata are generalists, laying their eggs on floating plants as well as other plants (Matushkina and Gorb, 2002a). For example, the generalist zygopteran *Lestes* lays eggs in narrow, vertical stems, flower stalks, and hydrophyte leaves, typically horsetails (*Equisetum*) and a wide variety of aquatic monocots, including *Carex*, *Butomus*, *Glyceria*, *Juncus*, *Phalaris*, *Scirpus* and *Typha* (Matushkina and Gorb, 2002a). Conversely, other odonatans show a clear ovipositional host-plant preference (Bick and Bick, 1970; Martens, 1992, 1993, 1994; Wildermuth, 1993; Grunert, 1995). For example, Schoor (1990) reported that *Aeshna viridis* oviposits exclusively on the floating plant *Stratiotes alooides* (Hydrocharitaceae) and that *Coenagrion mercuriale* almost exclusively oviposits on *Siella erecta* (Apiaceae). Evidence indicates that ovipositional preference is determined by visual appearance, location, architecture, and chemical signatures of the host plants (Martens, 1992; Grunert, 1995; Matushkina and Gorb, 2002b).

Odonatan eggs are inserted in host tissues leaving characteristic rows that form spirals, concentric circles, zigzags or straight lines. In some damselflies, the pattern of oviposition is strongly dependent on substrate features, and consequently variability is present, exemplified

by the calopterygid *Phaon iridipennis* (Miller and Miller, 1988). Other species show a distinctive ovipositional pattern with minimal variability (Hellmund and Hellmund, 1991; Matushkina and Gorb, 2000). Inserted odonatan eggs resulting in rectilinear patterns of scars are considered stereotypical for the zygopteran genera *Lestes* and *Chalcolestes* (Lestidae) (Matushkina and Gorb, 2000, 2002b), consisting of a simple, linear row of ovipositional lacerations, arranged in parallel fashion and separated from each other by c. 2.4 mm gap (Matushkina, 2007). A complex linear pattern was described for *Lestes sponsa* and *Chalcolestes parvidens*, which consists of a row of 2–8 ovipositional scars per set and separated from each other by a 1.1–1.4 mm wide space (Matushkina, 2007). Representatives of several other zygopteran clades, such as the Calopterygidae, Platynemididae, Coenagrionidae, the lestid genus *Sympecma*, the anisozygopteran *Epiophlebia* and some anisopteran Aeshnidae, insert their eggs in distinctive zigzag-like sets (Hellmund and Hellmund, 2002a; Matushkina, 2007). Usually, the scars in zigzag pattern are arranged in linear rows and consist of several egg rows, which are slightly crescentic, semicircular, or parallel (a broad zigzag pattern). The pattern of some sets is formed by a single scar in the angle of the zigzag, with the set appearing to contain two parallel lines (the double row) of scars. Such a positioning of egg insertions is described as a simple zigzag-pattern and was described for *Calopteryx splendens* (Lindeboom, 1996), *Platynemis latipes* (Heymer, 1966) and an unidentified aeshnid species (Matushkina, 2007). This pattern also can be discerned in Late Jurassic to Early Cretaceous *Paleoovoidus rectus* damage on a leaf of the conifer *Pityophyllum* sp. (Vasilenko, 2005) and herein as scars on the lycopsid *Isoetites madygensis*. In recent Odonata, distances between adjacent scars in zigzag clutches vary from 0.6 to 1.1 mm (Matushkina, 2007), which is identical to those of the fossil oviposition scars described herein for *I. madygensis* and *I. sixteliae*. The length of recent odonatan endophytic eggs varies from 0.8 mm (in zygopteran Coenagrionidae), to 1.9 mm (in anisopteran Aeshnidae). However, in some of the most gracile representatives of the zygopteran family Protoneuridae, eggs are likely even smaller. The fossil oviposition scars described here in herbaceous lycopsids are almost identical in length and shape to the endophytic eggs of some recent dragonflies. This assessment of size and shape takes into account that distinct, gall-like reaction rims, often as bulbous callus tissue, can form around

an inserted egg and scar, affecting the ovipositional scar size through enlargement and, for fossils, suggesting that some ovipositional scars could have been created by relatively small dragonflies.

4.3. Odonata ovipositional damage at Madygen and circumscription of the culprit

Since the first expedition investigating the Triassic Madygen Formation, more than 16,000 insect specimens have been collected, and assigned to twenty orders, approximately one hundred families, and in excess of five hundred species. The Triassic Madygen localities represent the most diverse and rich insect fauna during the Mesozoic (see Shcherbakov, 2008). Aquatic and amphibiotic insects such as the Odonata were not as dominant in the Madygen biota as compared to terrestrial Coleoptera, Blattodea, and homopterous Hemiptera (Shcherbakov, 2008). Among entirely amphibiotic orders, the fossil record of Odonata was the most diverse and abundant, represented by well-preserved isolated wings of about one hundred specimens distributed across ten families and thirty species, with many endemic forms (Table 2) (Pritykina, 1981; Nel et al., 2001, 2002, 2005; Shcherbakov, 2008, but see Nel et al., 1999). The fossil record of Odonata from the Madygen Formation consists primarily of well-preserved wings of protozygopteran insects (Pritykina, 1981; Nel et al., 2001, 2002, 2005; Shcherbakov, 2008). Based on the most recent taxonomic re-evaluation of the order Odonatoptera proposed by Nel et al. (2012), fossil dragonflies from Madygen are part of the extinct suborder Archizygoptera Handlirsch 1908. They were mainly represented by gracile, damselfly-like insects with petiolate wings (Nel et al., 2012), which are associated with relatively small egg sizes, such as the fossils described here. Moreover, some ovipositional scars on the leaves of *Isoetites madygensis* (Fig. 2A) and *I. sixteliae* (Fig. 3A, B) exhibit a typical, simple zigzag-pattern indicating the striking antiquity of this ovipositional behavior in dragonflies (Fig. 4). Nevertheless, little is known about ovipositor structure in the Archizygoptera, indicating that a more complete and better preserved body-fossil record of this clade would provide needed data to better associated insect damage patterns with a known culprit lineage.

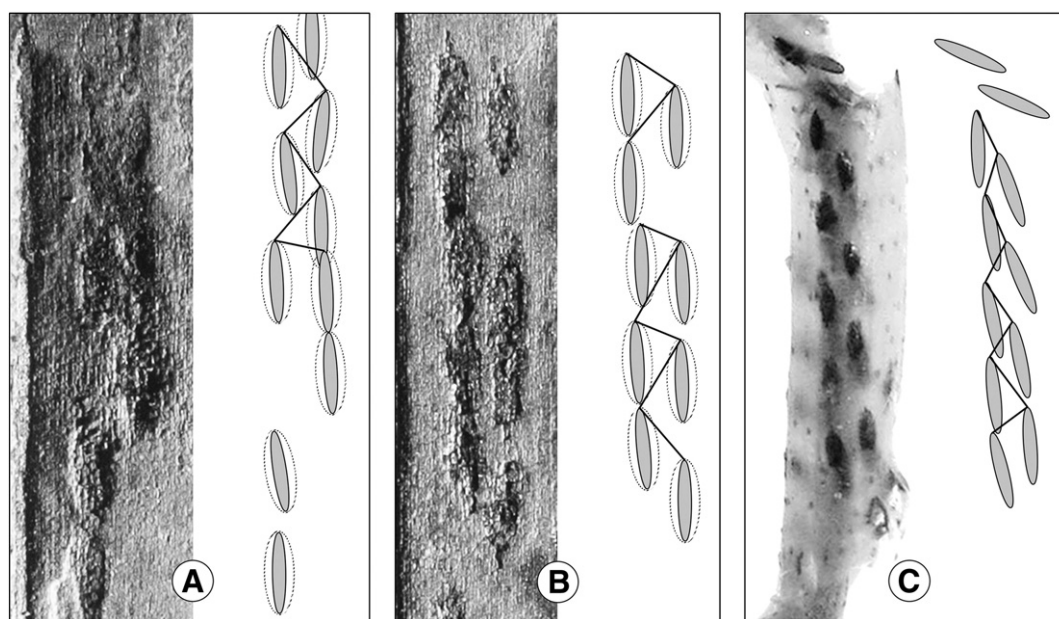


Fig. 4. Photographs (left) and related diagrammatic drawings (right) of the fossil ovipositional scars on a *Isoetites madygensis* leaf (A, B) and of regularly arranged eggs in a clutch of recent Odonatoptera (C) representing an unidentified member of the Anisoptera–Aeshnidae (after Matushkina, 2007).

4.4. The broader significance of Madygen plant–arthropod associations

Based on mostly preliminary data from the past 25 years from the Middle Permian to Late Triassic interval of the Karoo Basin in South Africa (Labandeira, 2006a; Anderson et al., 2007; Prevec et al., 2009), the Late Triassic of Arizona (Walker, 1938; Ash, 1997, 1999), and the Late Permian to Late Triassic of Western Europe (Kelber, 1988; Kelber and Geyer, 1989; Goth and Wilde, 1992; Grauvogel-Stamm and Kelber, 1996), there appears to be a two-phased recovery of ecosystems after the ecological crises at the end of the Permian. Based mostly on early floral and plant–arthropod associational data from the Karoo Basin, there initially was a modest diversification of an almost entirely different suite of major plant lineages following the end-Permian aftermath (Labandeira, 2006a; Prevec et al., 2009, 2010), including isoetalean lycopods. This initial lag of diversifying major plant lineages probably commenced in the Early Triassic, accelerated during the Middle Triassic, and was completed by or at the beginning of the Late Triassic (Anderson et al., 1999; Anderson and Anderson, 2003). Importantly, this primary lag of plant–host lineages was followed by a second, longer lag of more intense herbivory that modestly colonized newly emerging plant lineages during the Middle Triassic, associations which increased in intensity, diversity and specialization during the early Late Triassic (Labandeira, 2006a, 2006b; personal observation). The unique dragonfly–*Isoetites* ovipositional association and co-preservation of the body fossils of these groups at Madygen (Shcherbakov, 2008) are examples of this increasing level of associations and constitute the beginning of the third phase of plant–arthropod associations in the fossil record (Labandeira, 2006b).

5. Conclusions

From this documentation of dragonfly oviposition on two species of the lycopsid *Isoetites* from the late Middle to Upper Triassic Madygen deposit of Kyrgyzstan, and an assessment of the fossil and modern lycopsid–arthropod associations, we present five conclusions.

1. Evidence from fossil and modern plant–insect associations indicate that lycopsids have been the least herbivorized major vascular plant group in time and space.
2. A distinctive oviposition pattern has been identified on two lycopsid plant hosts, the quillworts *Isoetites madygensis* and *Isoetites sixteliae* (Isoëtaceae) from the Middle–Late Triassic of Madygen, in south-western Kyrgyzstan.
3. Based on stereotypical zigzag oviposition patterns made by several extant dragonfly lineages that strongly resemble the Madygen damage pattern and the presence of gracile damselfly-like insect fossils at Madygen, we conclude that the culprit likely was a member of any of the ten families of the Archizygoptera occurring at Madygen.
4. Oviposition on Mesozoic lycopsid taxa is not exceptional, as almost every major vascular plant group – lycopods, horsetails, ferns and seed plants – was a target for ovipositing insects, particularly dragonflies.
5. At least some ovipositional behavior is complex and particularly conservative, indicating that modern, stereotypical ovipositional patterns may extend minimally to the early Mesozoic.

Acknowledgments

This research was supported in part by the Deutscher Akademischer Austausch Dienst (DAAD grant A/06/27956 to P.M.) and the Deutsche Forschungsgemeinschaft (DFG grant VO 1466/1–1 to S.V.). The first author thanks Christian Pott (Stockholm) for providing relevant literature. This is contribution 248 of the Evolution of Terrestrial Ecosystems Consortium at the National Museum of Natural History, in Washington

D.C. The comments and suggestions by two anonymous reviewers greatly improved this manuscript.

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