

# ODONATAN ENDOPHYTIC OVIPOSITION FROM THE EOCENE OF PATAGONIA: THE ICHNOGENUS *PALEOVOIDUS* AND IMPLICATIONS FOR BEHAVIORAL STASIS

LAURA C. SARZETTI,<sup>1</sup> CONRAD C. LABANDEIRA,<sup>2,3</sup> JAVIER MUZÓN,<sup>4</sup> PETER WILF,<sup>5</sup> N. RUBÉN CÚNEO,<sup>1</sup>  
KIRK R. JOHNSON,<sup>6</sup> AND JORGE F. GENISE<sup>1</sup>

<sup>1</sup>CONICET, Museo Paleontológico Egidio Feruglio, Avenida Fontana 140, Trelew, Chubut 9100, Argentina, <lsarzetti@mef.org.ar>, <rcuneo@mef.org.ar> and <jgenise@mef.org.ar>; <sup>2</sup>Department of Paleobiology, National Museum of Natural History,

Smithsonian Institution, 20213-7012; <sup>3</sup>Department of Entomology, University of Maryland, College Park, Maryland 20742, <labandec@si.edu>;

<sup>4</sup>Instituto de Limnología “Dr. Raul A. Ringuelet,” Av. Calchaquí Km 23,5 712, Florencio Varela, Buenos Aires, Argentina, 1888, <muzon@ilpla.edu.ar>;

<sup>5</sup>Department of Geosciences, Pennsylvania State University, University Park, Pennsylvania, 16802, <pwilf@psu.edu>; and <sup>6</sup>Department of Earth Sciences, Denver Museum of Nature and Science, Denver, Colorado 80205, <kirk.johnson@dmns.org>

**ABSTRACT**—We document evidence of endophytic oviposition on fossil compression/impression leaves from the early Eocene Laguna del Hunco and middle Eocene Río Pichileufú floras of Patagonia, Argentina. Based on distinctive morphologies and damage patterns of elongate, ovoid, lens-, or teardrop-shaped scars in the leaves, we assign this insect damage to the ichnogenus *Paleoovoidus*, consisting of an existing ichnospecies, *P. rectus*, and two new ichnospecies, *P. arcuatum* and *P. bifurcatus*. In *P. rectus*, the scars are characteristically arranged in linear rows along the midvein; in *P. bifurcatus*, scars are distributed in double rows along the midvein and parallel to secondary veins; and in *P. arcuatum*, scars are deployed in rectilinear and arcuate rows. In some cases, the narrow, angulate end of individual scars bear a darkened region encompassing a circular hole or similar feature indicating ovipositor tissue penetration. A comparison to the structure and surface pattern of modern ovipositional damage on dicotyledonous leaves suggests considerable similarity to certain zygoteran Odonata. Specifically, members of the Lestidae probably produced *P. rectus* and *P. bifurcatus*, whereas species of Coenagrionidae were responsible for *P. arcuatum*. Both Patagonian localities represent an elevated diversity of potential fern, gymnosperm, and especially angiosperm hosts, the targets of all observed oviposition. However, we did not detect targeting of particular plant families. Our results indicate behavioral stasis for the three ovipositional patterns for at least 50 million years. Nevertheless, synonymy of these oviposition patterns with mid-Mesozoic ichnospecies indicates older origins for these distinctive modes of oviposition.

## INTRODUCTION

OVIPOSITION ON vegetation is a common insect behavior, in which eggs are deposited either on the surfaces of plant organs (exophytic oviposition) or, alternatively, inserted within plant tissues (endophytic oviposition; Corbet, 1999). Endophytic oviposition represents an ancient behavior, based on external ovipositor structure found in some Paleozoic insects (Carpenter, 1971; Labandeira, 1998) and additionally on stereotyped tissue damage occurring within foliage and stems (Labandeira, 2002b; Béthoux et al., 2004; Beattie, 2007). Externally evident, often sawlike ovipositors have been recognized in the Palaeodictyoptera, Protodonata, Dictyoptera, Archaeorthoptera, Hemipteroidea, and early-derived holometabolous clades from the Late Carboniferous through the Triassic (Labandeira, 2006). External ovipositors currently are most prominent in the orders Odonata, Orthoptera, Hemiptera, Coleoptera, Lepidoptera and Hymenoptera (Zeh et al., 1989).

Worldwide, evidence for leaf damage produced by ovipositors is relatively abundant throughout the Phanerozoic. Several Paleozoic examples have been documented on sphenopsis stems from the Late Pennsylvanian of France (Béthoux et al., 2004) and the Middle Permian of Germany (Roselt, 1954), and especially on glossopterid leaves from the Late Permian of Australia (Beattie, 2007), South Africa (Prevec et al., 2009), India (Bunbury, 1861; Banerji, 2004), and Brazil (Adami-Rodrigues et al., 2004). For the Mesozoic, oviposition has been recorded for a variety of sphenopsis and seed plants from the Middle and Late Triassic of Germany and France (Kelber, 1988; Grauvogel-Stamm and Kelber, 1996), Chile (Gnaedinger et al., 2007) and Austria (Pott et al., 2007); the Early Jurassic of Germany (Van Konijnenburg-van Cittert and Schmeißner, 1999); and the early Late Cretaceous of Israel (Krassilov et al., 2007) and Germany (Hellmund and Hellmund, 1996c). Cenozoic occurrences are known from the Eocene for Washington State in the United States (Lewis and Carroll,

1991; Labandeira, 2002a, 2002b) and Spain (Peñalver and Delclòs, 2004), from the Oligocene of Germany (Hellmund and Hellmund, 1991, 1993, 1996a, 1996b, 1998, 2002b; Van Konijnenburg-van Cittert and Schmeißner, 1999), and from the early and late Miocene of Germany (Hellmund and Hellmund, 1996c, 2002a, 2002c).

Complex patterns of ovipositional plant damage frequently allow reliable identification of the producers, particularly when fossil ovipositor structure and egg-laying biology of modern counterparts are well studied. Accordingly, most post-Paleozoic fossil occurrences of oviposition are confidently attributed to the Odonata (Hellmund and Hellmund, 1991; Grauvogel-Stamm and Kelber, 1996; Van Konijnenburg-van Cittert and Schmeißner, 1999; Labandeira, 2002a, 2002b; Adami-Rodrigues et al., 2004; Peñalver and Delclòs, 2004; Gnaedinger et al., 2007), including those described below.

Despite the extensive fossil evidence, as well as autecological knowledge of modern ovipositing insects (Wesenberg-Lund, 1913b; Schiemenz, 1957; Corbet, 1999), formal ichnotaxonomic treatments of these trace fossils were lacking until Vasilenko (2005) established the ichnogenus *Paleoovoidus*, the first ichnotaxon created for ovipositional damage to fossil plants. In a more recent and extensive documentation, Krassilov and Silantieva (2008) defined several new ichnogenera and ichnospecies to include oviposition scars and presumably arthropod eggs from the Late Cretaceous (Turonian) Gerofit locality in Israel. Recently, Vasilenko (2008) redefined their ichnogenus *Paleoovoidus* and also described two new ichnospecies, *P. flabellatus* and *P. arcuatus*, assigning them to endophytic ovipositional traces. He additionally defined a new ichnogenus, *Palaexovoidus*, to refer to exophytic oviposition on plant tissues. Before the establishment of these taxa, trace fossils of oviposition in leaves and stems were described in the literature without formal ichnotaxonomic analyses (e.g., Hellmund and Hellmund, 1998; Labandeira, 2002a), including the damage-type (DT) system of Labandeira et al. (2007),

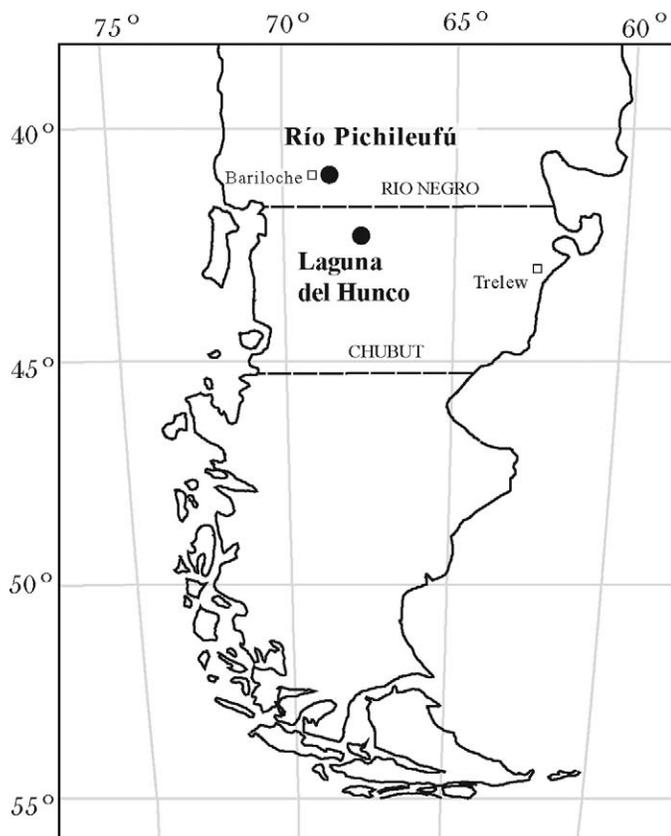


FIGURE 1—Map of central Patagonia showing 50 Ma positions of both localities under study, with modern coastlines: Laguna del Hunco (Chubut Province) and Río Pichileufú (Río Negro Province) (redrawn from Wilf et al., 2005).

used for analyzing the paleoecology of plant-insect associational patterns. Additionally, erection of ichnotaxa for ovipositional trace fossils was not considered in several more encompassing studies (Van Amerom, 1966; Straus, 1977; Givulescu, 1984; Vasilenko, 2006, 2007), whereas in most of those same works, numerous ichnotaxa were established for various other types of foliar damage.

This contribution has three principal objectives. The first is to formally define new ichnospecies and to provide additional evidence for previously defined ovipositional damage from two diverse Eocene Patagonian paleofloras. Establishment of these new ichnotaxa will be done by comparison with analogous ovipositional damage by modern Odonata. The second is to ascertain whether the ichnotaxa from these Eocene paleofloras have other occurrences in the fossil record, providing a brief review of the relevant fossil record of endophytic oviposition in leaves. The third is to track long-term ovipositional behavior of odonatan lineages inflicted on leaves about 50 million years ago, comparing these oviposition patterns with earlier occurrences of the ichnotaxa.

#### GEOLOGICAL SETTING

Leaves bearing oviposition scars analyzed in this contribution originate from the Laguna del Hunco (early Eocene,  $51.91 \pm 0.22$  Ma) and Río Pichileufú (middle Eocene,  $47.46 \pm 0.05$  Ma) sites in central Patagonia (Fig. 1; Wilf et al., 2005a). These two classic paleobotanical localities (Berry, 1925, 1928, 1935a, 1935b, 1935c; Frenguelli, 1943a, 1943b; Romero and Hickey, 1976; Gandolfo et al., 1988), exhibit very diverse paleofloras (Wilf et al., 2005a) and associated spectra of insect-mediated damage (Wilf et

al., 2005b), including oviposition, which was mentioned but not analyzed by Wilf et al. (2005b).

The Laguna del Hunco (LH) paleoflora comes from a caldera-lake deposit, the Tufolitas Laguna del Hunco (Aragón and Mazzoni, 1997; Aragón et al., 2001), and is located in western Chubut Province, Argentina, 160 km southeast from the Río Pichileufú (RP) locality, along the foothills of the Sierra de Huancache at  $S42.5, W70.0$  degrees (Fig. 1). The fossil material originates from strata consisting of tuffaceous mudstones and sandstones, interpreted as a caldera-collapse lake unit within the expansive middle Chubut River volcanic-pyroclastic complex (Aragón and Romero, 1984; Aragón and Mazzoni, 1997). The entombed plant remains are preserved principally as impressions; angiosperm leaf impressions are the most abundant plant organs, though there are also significant gymnosperm and minor fern components (Wilf et al., 2005a).

Recently, 25 distinct fossil plant localities (known as LH1-25) were intensively collected and placed in a 170 m measured stratigraphic section, from which six paleomagnetic reversals were detected, and three tuffs interbedded with the fossils were dated using the  $^{40}\text{Ar}-^{39}\text{Ar}$  method (Wilf et al., 2003). All Ar-Ar ages were near 52 Ma; and one tuff containing sanidine was reanalyzed, yielding an age of  $51.91 \pm 0.22$  Ma (Wilf et al., 2005a). The combined evidence placed the LH flora within the sustained period of globally warm temperatures known as the early Eocene climatic optimum (Zachos et al., 2001). Leaf-margin and leaf-area analyses indicate local mean-annual paleotemperatures near  $16.6^\circ\text{C}$  and annual rainfall of at least 1140 mm, though certain plant taxa suggest much higher rainfall (Wilf et al., 2005a, 2008). A number of botanical investigations have emerged from the recent collecting effort, which has yielded >210 species, including studies of Myrtaceae (Gandolfo et al., 2006), Casuarinaceae (Zamaloa et al., 2006), Proteaceae (González et al., 2007), and many other groups (Wilf et al., 2007).

Several entomological studies have revealed the presence of a diverse insect fauna, including representatives of the orders Odonata, Blattodea, Orthoptera, Hemiptera, Coleoptera, Mecoptera, Diptera, Hymenoptera and Trichoptera (Rossi de García, 1983; Petrulėvičius and Martins-Neto, 2000; Genise and Petrulėvičius, 2001; Petrulėvičius and Nel, 2003a; Petrulėvičius, 2005). Additionally, pipoid anurans were described by Casamiquela (1961) and Báez and Trüb (1997) and a catfish species by Sáez (1941). Nevertheless, the preserved fauna is less abundant and diverse than the flora of this locality, though insect damage to fossil leaves is abundant and extremely diverse (Wilf et al., 2005b).

The Río Pichileufú (RP) paleoflora originates from a probable caldera-lake facies of the Ventana Formation (Aragón and Romero, 1984) and is located in Río Negro Province of Argentina, approximately 40 km east from the city of San Carlos de Bariloche at  $S41.2, W70.8$  degrees (Fig. 1). The RP flora was the subject of an early monograph (Berry, 1938) that remains the most extensive on Cenozoic macrofloras in South America, though nearly all taxa are in need of revision. More recently, the flora was extensively recollected from three quarries (known as RP1-3), and tuffs immediately associated with the fossil floras produced an Ar-Ar age of  $47.46 \pm 0.05$  Ma (Wilf et al., 2005a). There is much less fossiliferous exposure at RP than at LH, and preservation is not as good, but the floral diversity at RP3 is similar to that of the richest LH quarries (Wilf et al., 2005a). Like LH, the RP flora is dominated by angiosperm leaves but has significant contributions from gymnosperms such as *Araucaria*, Podocarpaceae, and *Ginkgo*, as well as fern species. Early studies of this locality (Berry, 1935a, 1935b, 1938) revealed a great diversity of fossil plant taxa that are only recently being taxonomically updated. Based on preliminary leaf-margin analysis, the RP mean annual paleotemperature is  $19.2 \pm 2.4^\circ\text{C}$  (Wilf et al., 2005a).

Fossil frogs and insects, including large ants, have been noted



FIGURE 2—1, *Paleoovoidus bifurcatus*, isp. nov., holotype specimen (MPEF-IC-1385) on a sapindaceous leaf (LH13, morphotype indeterminate, MPEF-Pb-1607), scale bar: 0.5 cm; 2, specimen MPEF-IC-1385 enlarged from boxed area in A of *Paleoovoidus bifurcatus*, scale bar: 1 mm; 3, *Paleoovoidus rectus* specimen (MPEF-IC-1376) on “*Myrcia*” *chubutensis* (LH13, morphotype TY21, MPEF-Pb-2216), enlarged from boxed area in D, scale bar: 0.5 cm; 4, specimen MPEF-IC showing *P. rectus* (boxed area) and *P. arcuatum* below (MPEF-IC 1392).

from the plant-bearing beds (Wilf et al., 2005a), although *Archimyrmex piatnitzkyi*, reported from the general area (Viana and Haedo-Rossi, 1957; Dlussky and Perfilieva, 2003), can not be correlated stratigraphically to the flora as suggested by those authors, due to local faulting (Wilf and Johnson, personal observation, 2008). Also leaf-cutter bee (Megachilidae) foliar damage was reported from RP (Sarzetti et al., 2008). Interestingly, Berry (1938) figured an extensively insect-damaged leaf from RP he named “*Anona*” *infestans*, one of the earliest explicit illustrations of fossil insect damage from South America. Berry (1938, p.73) reported that the damage “might be the remains of scale insects.” Our updated interpretation of this damage as oviposition scars appears below.

#### SYSTEMATIC ICHNOLOGY

The specimens described here are deposited in the Museo Paleontológico Egidio Feruglio, Trelew, Chubut, under the paleobotanical collections (MPEF-Pb, for the leaf holding the trace), with each trace assigned to a separate suite of ichnological collection numbers (MPEF-IC).

Ichnogenus PALEOVOIDUS Vasilenko, 2005  
Figure 2

*Paleoovoidus* VASILENKO, 2005, p. 630, figs. 1–3.  
*Sertoveon* KRASSILOV, 2008, partim, p. 69, figs. 1–5.  
*Paleoovoidus* VASILENKO, 2008, p. 516, fig. 2, pl. 7.



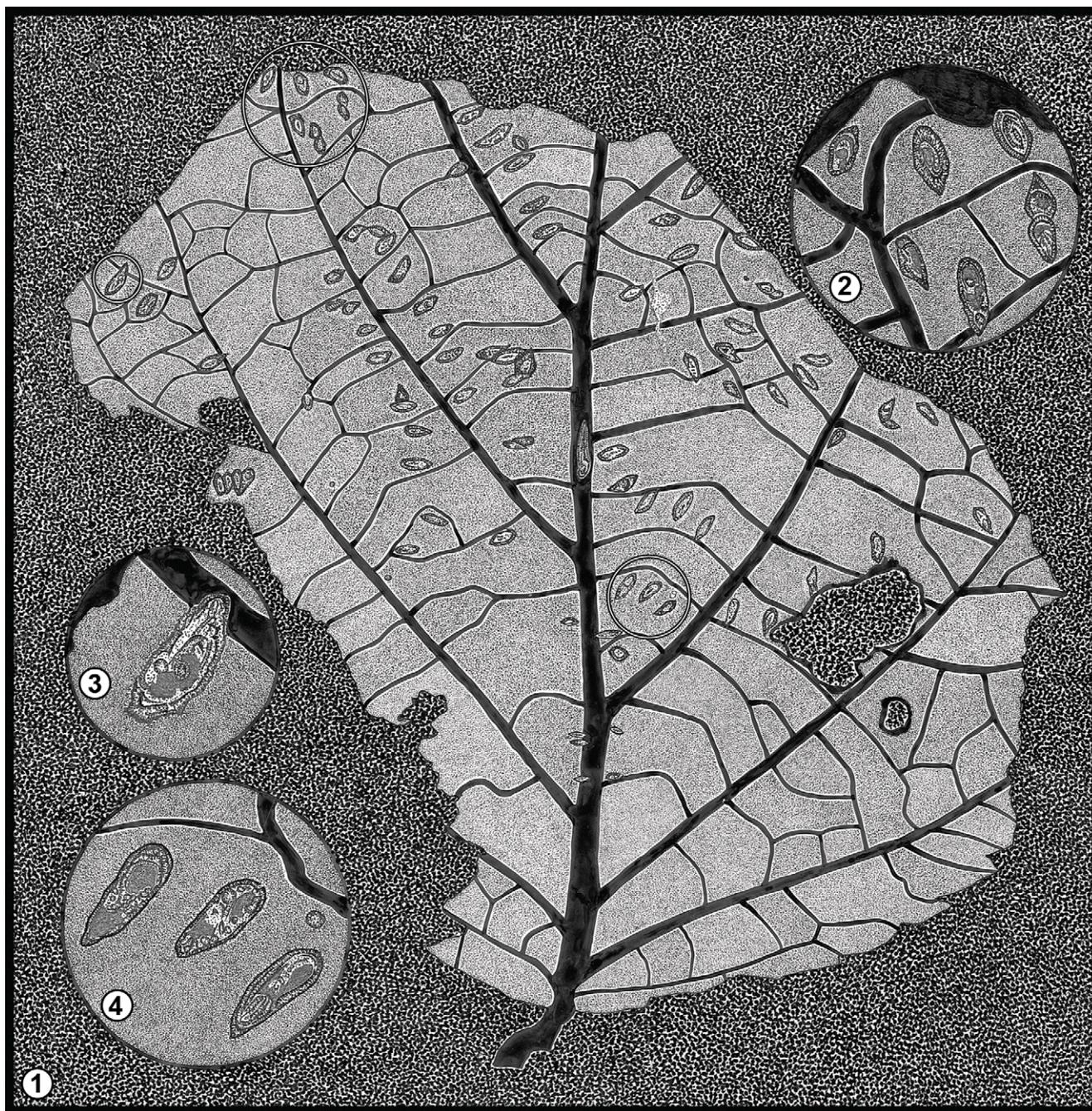
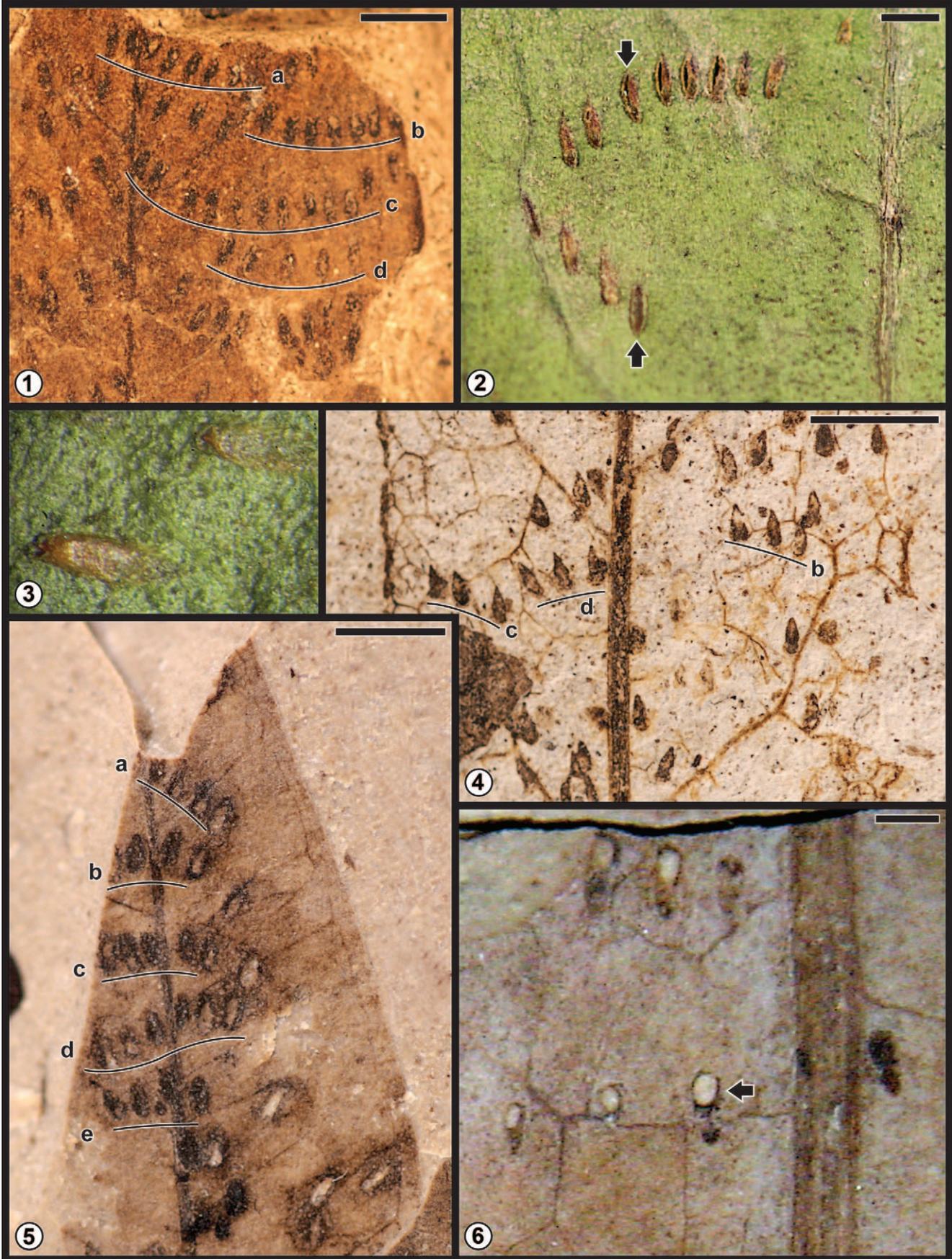


FIGURE 4—Camera lucida drawing of a specimen of *Paleoovoidus arcuatum*, isp. nov. (MPEF-IC-1370), on the dicot "*Celtis*" *ameghenoi* (LH2, morphotype ?TY20, MPEF-Pb-1053), scale bar: 1 cm; 1, entire specimen, show a register of five rows of oviposition scars oriented across the blade from upper-left to the center, and a differently juxtaposed register of perhaps five rows at the upper-right region of the leaf; 2, minor enlargement of six scars with central ovoid depressions from a circled region of the leaf margin at upper-left; 3, major enlargement of callus and emergence hole detail from a single scar, indicated by a circular template from the leaf margin at center-left; 4, similar enlargement of three scars with central emergence holes, from the circled leaf region at center-bottom, axial length of leaf: 4.5 cm, scale bar as in Fig. 3.5.

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FIGURE 3—*Paleoovoidus arcuatum* specimens: 1, MPEF-IC-1380a, MPEF-IC-1380b and MPEF-IC-1380c specimens on an unknown dicot leaf (LH13, morphotype indeterminate, MPEF-Pb-1591), showing a zigzag pattern, lettered arrows point to individual rows or "files" of oviposition marks; 2, MPEF-IC-1371a-c showing consecutive and parallel rows on an indeterminate dicot leaf (LH6, morphotype indeterminate, MPEF-Pb-1054), scale bar: 1 cm; 3, linear oviposition arcs (lettered arrows) covering MPEF-IC-1374a and specimens MPEF-IC-1374b, c on "*Cupania*" *latifolioides* (LH18, ?Cunoniaceae, MPEF-Pb-1585), scale bar: 1 cm; 4, trace-fossil specimens MPEF-IC-1388 a-e (lettered lines) on an indeterminate dicot leaf (RP3, morphotype indeterminate, MPEF-Pb-1611), scale bar: 1 cm; 5, specimens MPEF-IC-1370 a-g (lettered lines) on the dicot "*Celtis*" *ameghenoi* (LH2, morphotype TY20, MPEF-Pb 1053), scale bar: 1 cm.



“Flea beetle egg deposition,” LEWIS AND CARROLL, 1991, p. 335, fig. 2.

“Flea beetle egg deposition,” LEWIS AND CARROLL, 1992, p. 3, fig. 2.

*Emended diagnosis.*—Medium-sized elongate, narrow, ovoid, or lens-shaped structures, characterized by regular arrangement in leaf lamina. These structures, defined by dark, surrounding reaction tissue, are narrow at one end, each of which often bears a dark spot.

*Discussion.*—Vasilenko (2005, p. 629) erected the ichnogenus *Paleoovoidus* originally as “oval or lentiform structures (eggs) with regular distribution over substrate.” More recently, Vasilenko (2008) redefined the ichnogenus, providing a more precise diagnosis. Nevertheless, the diagnosis is emended here because we consider that the term “substrate” should be restricted to leaves, which probably was the original intention of the author. In addition, the mention of “eggs” in the diagnosis is dispensed with herein, as there is no indication for the presence of eggs, thus rendering moot the author’s inference. Alternatively, Krassilov and Silantieva (2008) defined the ichnogenus *Sertoveon* to correspond with a structure and distribution over the leaf lamina very similar to our material. However, according to the current rules of zoological nomenclature, the valid name should be *Paleoovoidus* because of date priority over *Sertoveon*. Other ichnogenes erected by Krassilov and Silantieva (2008), *Costoveon* and *Catenoveon*, are comparable with *Paleoovoidus*, although the disposition of the scars over the leaf are different. In *Costoveon*, all scars are distributed over primary veins. By contrast, *Catenoveon* is similar to *Paleoovoidus* in that the scars are oriented in the direction of stronger veins, but the sets of scars cover the entire surface of the lamina.

PALEOVOIDUS RECTUS Vasilenko, 2005

Figure 2.2, 2.4

“Odonata eggs” VAN KONIJNENBURG-VAN CITTERT AND SCHMEIßNER, 1999, p. 217.

“Egg scars” KRASSILOV, SILANTIEVA, HELLMUND, AND HELLMUND, 2007, p. 806, fig. 3D.

*Emended diagnosis.*—Elongate to lens-shaped scars oriented in a single, linear row, with long axes of scars aligned lengthwise, mostly parallel to the long axis of the leaf and usually occurring along the midrib.

*Description.*—The specimen of *Paleoovoidus rectus* (Fig. 2.3) occurs in a leaf of “*Myrcia*” *chubutensis* (Myrtaceae, MPEF-Pb 2216). This leaf has two sets of leaf scars; those corresponding to *C. rectus* are indicated by the inset box in Figure. 2.4. There are twelve scars arranged rectilinearly near the leaf apex, aligned approximately along the primary vein, with the scar long axis parallel or subparallel to the vein. Two scars are on the primary vein, whereas the other ten are closely adjacent to it in a single row along the intersection of the laminar and veinal tissue, except for the two closest scars at the tip of the leaf that appear on the opposite side of the primary vein. The individual length of the scars ranges from 1.0 to 1.2 mm, and the width ranges from 0.4 to 0.5 mm. The distance between adjacent scars varies from 0.7 to 1.4 mm. All scars have an ovoidal shape and rounded ends,

and they lack the dark spot observed in other specimens. In addition, we note that in this leaf a distinctive occurrence of *Paleoovoidus arcuatum* (MPEF-IC 1392) (Fig. 2.3) appears basal to the *P. rectus* trace, indicating that both patterns can occur on the same leaf.

The *P. rectus* holotype described by Vasilenko (2005) exhibits minor differences from the material presented here. Vasilenko’s (2005) oviposition damage has a similar arrangement, orientation, and measurements compared with the LH specimen, but the scars are distributed in two linear rows adjacent to the central vein in *Pityophyllum* sp. leaves (Coniferales: Pinaceae), and in up to four subparallel rows on *Ginkgoites* (Ginkgoales: Ginkgoaceae), which lack a midvein. None of these scars occurs within veins. Our LH specimen also resembles the Lower Jurassic scar pattern documented by Van Konijnenburg-van Cittert and Schmeißner (1999) in leaves of *Schmeissneria microstachys* (Ginkgoales: Schmeissneriaceae) and *Podozamites distans* (Coniferales: Podocarpaceae); both species lack midveins. These authors described two types of row arrangement, but in both cases, the scars are slightly longer than the Patagonian material, with major-axis values approximating 3 mm. These multiple rows provide the most important difference from the pattern described here, where scars are distributed along a single row.

*Material examined.*—One specimen (MPEF-IC-1376) occurs on a “*Myrcia*” *chubutensis* (MPEF-Pb-2216, from locality LH13 of Wilf et al., 2003), from the early Eocene Tufolitas Laguna del Hunco, Chubut Province, Argentina (Fig. 2.3).

*Discussion.*—Vasilenko (2005) defined this ichnospecies as “oval or lentiform relief structures, individual eggs oriented in chain on leaf blades.” The diagnosis is emended here to avoid the use of an interpretative concept, such as “eggs” and to provide a more accurate description of the oviposition pattern. However, Pott et al. (2008) have described Late Triassic oviposition scars from Austria with preserved ovoidal egg cuticles in bennettitalean leaves, arranged in a near-circular pattern but lacking the linearity of *P. rectus*. These early Mesozoic ichnospecies can be distinguished from the ichnospecies *P. rectus* because of the arrangement of scars in a single row. Krassilov and Silantieva (2008) defined a similar ichnospecies, *Catenoveon undulatum*. However, their definition included “elliptical to fusiform egg pits” (page 68) distributed nearly parallel or oblique to veins but distributed over most of the leaf. The principal difference between *C. undulatum* and *P. rectus* is that oviposition scars cover most of the laminar surface, whereas in *P. rectus* a single linear row is present along the primary vein. We consider Vasilenko’s ichnospecies *Paleoovoidus rectus* (2005) more germane for understanding the pattern in the Patagonian specimen. Other similar evidence of *P. rectus* comes from the Mesozoic (Van Konijnenburg-van Cittert, 1999; Vasilenko, 2005). These occurrences appear to be associated with the great diversity of parallel-veined, broadleaved gymnosperms from floras of Late Triassic to Early Cretaceous age. Older documentation comes from Late Permian floras, typically occurring in or adjacent to the robust midribs of *Glossopteris* leaves. Paleozoic occurrences were probably produced by protodonatan dragonflies and related paleodictyopteroid lineages (Labandeira, 2006).

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FIGURE 5—Fossil and extant specimens of *Paleoovoidus arcuatum* isp. nov.: 1, specimen MPEF-IC-1390 a-d (lettered lines) in an indeterminate dicot leaf (RP3, morphotype indeterminate, MPEF-Pb-1612) with a consecutive and parallel pattern of rows, scale bar: 0.5 cm; 2, extant oviposition of *Acantagrion oblutum* (Coenagrionidae) on *Cynoglossum amabile* (Boraginaceae) showing a zigzag pattern and probably the immature aperture observed as a dark lineal in the centre of the scar; 3, two individual eggs and associated callus tissue of *Acantagrion oblutum*, scale bar: 0.5 cm; 4, specimens MPEF-IC 1393b-d (lettered lines) on an indeterminate dicot (RP3, morphotype indeterminate, MPEF-Pb-2407); scale bar: 0.5 cm; 5, specimens MPEF-IC-1368a-e (lettered lines) showing a distinct zigzag pattern on “*Myrcia*” *deltoidea* (LH4, Myrtaceae, MPEF-Pb-1052), scale bar: 0.5 cm; 6, specimen MPEF-IC-1389d, a scar with a circular breached area probably representing the emergence portion of the naiad (arrow) on *Lomatia occidentalis* (LH2, morphotype TY44, MPEF-Pb-988), scale bar: 1 mm.

## PALEOVOIDUS BIFURCATUS new ichnospecies

Figure 2.1, 2.2

“Galle *Aceria nervesqua fagina*” STRAUS, 1977, p. 74, fig. 2, p. 78, fig. 50.

“Lestiden-Typ” HELLMUND AND HELLMUND, 1991, p. 4, figs. 1, 2; HELLMUND AND HELLMUND, 1996c, p. 160, fig. 16; HELLMUND AND HELLMUND, 2002b, p. 49, figs. 1, 2.

“Oviposition damage on secondary veins” LABANDEIRA, WILF, JOHNSON, AND MARSH, 2007, p. 10.

**Diagnosis.**—Elongate to lens-shaped scars arranged in pairs along both sides of a primary vein, forming double rows and sometimes a V-shaped configuration, with the arms of the V parallel to secondary veins and the vertex embedded in the midvein. Oviposition scars may continue as a single row of scars located in an acute angle along and parallel to one side of the vein. A dark spot at one extremity of an individual scar very frequently touches the primary vein.

**Description.**—The holotype occurs in a leaflet of “*Schmidelia*” *proedulis*, MPEF-Pb-1607. This specimen shows an upper pair of scars arranged symmetrically about the midvein and parallel to secondary veins characterized by a V-shaped configuration along the primary vein. Another pair of scars occurs with a similar V configuration, but their arrangement is less clear than for the upper pair. Two additional isolated scars occur at one side of the vein in a more basal position with respect to the preceding two pairs. The axial length of the scars ranges from 1.7 mm to 2.6 mm, and their width ranges from 0.5 mm to 0.7 mm. The preservation of the specimen is poor, and individual scars are only partially preserved. The first scar occurs at the upper left side of the lamina and is the best preserved; it has a length of 2.6 mm that may indicate that the remaining scars were probably longer than the values measured. The minimum distance between the scars of the first pair is 0.8 mm and for the second pair is 1.3 mm. The longitudinal distance between two adjacent pairs ranges from 5.5 mm to 10.7 mm. The greatest distance occurs between the second pair of scars and the first scar of the single row.

The scars often occur in pairs or are isolated and oriented at an acute angle with respect to the vein; their prominence is attributable to the thickened scar tissue surrounding and probably elicited by the inclined, secondary veins. Paired scars do not occur at the same level on each side of opposite veins, or at the same transverse position in the case of alternate veined leaves. MPEF-IC 1385 (Fig. 2.2) is an example in which the upper pair of scars is characterized by the left scar being slightly nearer the tip of the leaf than the right one; by contrast, the lower pair shows the opposite arrangement.

The specimens described by Hellmund and Hellmund (1991, 2002b) on *Cinnamomum* sp. (“*Daphnogene*”; Rott locality, Germany, late Oligocene) and on a fragment of an unidentified leaf (Geiseltal locality, Germany, middle Eocene) show a scarring arrangement similar to that described above. In both examples, double rows and single rows were found; in several instances, these patterns appeared on the same leaf. In all cases for which a single row was present, there was the continuation of a double row. However, the double rows show some differences from the Patagonian specimen. These European specimens were composed of 12 to 16 scars that are separated for short longitudinal distances between 0.1 to 1 mm, some of which are oriented 90° with respect to the vein. Moreover, the average length, 1.20 mm, is shorter than that of the LH specimen.

**Etymology.**—From the Latin noun, *bifurcatus*, the condition of having two prongs or forks; masculine.

**Types.**—Holotype specimen MPEF-IC-1385 on the leaflet specimen of “*Schmidelia*” *proedulis* (Sapindaceae) MPEF-Pb-1607 (Fig. 2.1, 2.2).

**Examined material.**—The same as the holotype.

**Occurrence.**—From the early Eocene Tufolitas Laguna del Hunco, Chubut Province, Argentina, locality LH13.

**Discussion.**—This ichnospecies is comparable with *Paleoovoidus rectus*, as in both cases scars are located in relation to the primary veins. However, in *P. rectus* there is a single row of scars, their long axes approximately parallel with the long axis of the leaf and consequently with the midrib or other major vein. The combination of scar structure and position on the leaf separates *P. bifurcatus* from *P. rectus* and *P. arcuatum*. This distinctive ovipositional pattern corresponds to the damage type DT102 of Labandeira et al. (2007). Patterns similar to *P. bifurcatus* described here occur throughout the Cenozoic (Hellmund and Hellmund, 1991, 1996c, 2002b); this damage has a sporadic presence on Mesozoic gymnospermous vegetation (Labandeira, pers. observation.), but is common on *Glossopteris* leaves from certain Late Permian floras of South Africa (Prevec et al., 2009). Preservation of *P. bifurcatus* is variable across a broad range of compression/impression floras, but all occurrences have the signature ovoidal, ellipsoidal, or teardrop-shaped oviposition scars oriented along or within the secondary venation and can occur at variable distance from the midrib.

## PALEOVOIDUS ARCUATUM (Krassilov, 2008)

Figures 3, 4, 5.1, 5.4–5.6, 6, 7

“Coenagrioniden-Typ” HELLMUND AND HELLMUND, 1991, p. 7, fig. 3; HELLMUND AND HELLMUND, 1993, p. 349, fig. 1, p. 350, fig. 2; HELLMUND AND HELLMUND, 1996a, p. 109, fig. 1a, b; HELLMUND AND HELLMUND, 2002a, p. 255, fig. 1a.

“Träufelspitze” HELLMUND AND HELLMUND, 1991, p. 291, pl. 1, fig. 2.

“Coenagrioniden-Typ vom Bogenmodus” HELLMUND AND HELLMUND, 1998, p. 282, fig. 1.

“Concentric oviposition tracks” LABANDEIRA, 2002a, p. 41.

“Radially oriented oviposition scars” LABANDEIRA, JOHNSON, AND LANG, 2002, p. 312, fig. 8o.

“Ovoposiciones de la Familia Coenagrionidae” PEÑALVER AND DELCLÒS, 2004, p. 74, fig. 2.

“Zygopteran egg sets” KRASSILOV, SILANTIEVA, HELLMUND, AND HELLMUND, 2007, p. 806, fig. 3a, b, c.

“Endophytic oviposition probably of Calopterygina” VASILENKO AND RASNITSYN, 2007, p. 1156, figs. 4–6.

*Sertoveon arcuatum* KRASSILOV, 2008, p. 69, fig. 5.

*Paleoovoidus arcuatus*, VASILENKO, 2008 (new syn.), p. 516, fig. 2c, pl. 7, figs. 2, 3.

**Emended diagnosis.**—Elongate, lens-shaped to teardrop-shaped scars arranged with the short axes aligned horizontally to each other, either as straight rows or as arcs. Frequently the long axes of scars are subparallel to each other. Occasionally, successive rows are parallel or exhibit zigzag patterns.

**Description.**—The shape of the scars ranges from elongate (Fig. 5.5), lens-shaped (Figs. 4.1, 4.2, 5.1, 6.5), to teardrop-shaped (Figs. 4.1, 4.3, 4.4, 5.4). The specimens are from 0.9 to 1.6 mm in length but only two specimens represent the highest values (Fig. 3.5); widths range from 0.4 to 0.6 mm. The scars in the rows are variously oriented within the leaves, with the long axis parallel to subparallel to the primary vein (Figs. 3.4, 5.1, 5.4–5.6), perpendicular to it (Figs. 3.1, 3.3), at a highly inclined angle (Fig. 3.3), or at other inclinations (Fig. 6.1–6.3). The distance between each scar within a row often is a relatively constant value of 1 mm, but in some cases (e.g., Figs. 3.5, 4.1) the scars are variably separated, with values that range from 0.4 to 2 mm (Fig. 6.3–6.5). Some leaves present distinct and well-defined arcuate rows from three to 13 scars (Figs. 3.1, 3.2, 4.1, 5.1, 5.6, 6.1–6.3, and 7.2–7.5), in which the acute end of the scar always is orientated in the same direction (Figs. 3.1, 4.4, 5.4). In other cases the arcuate rows are parallel to each other and are arranged en echelon (Figs. 3.4, 3.5, 4.1, 5.1, 5.5, 6.2), with scars of each

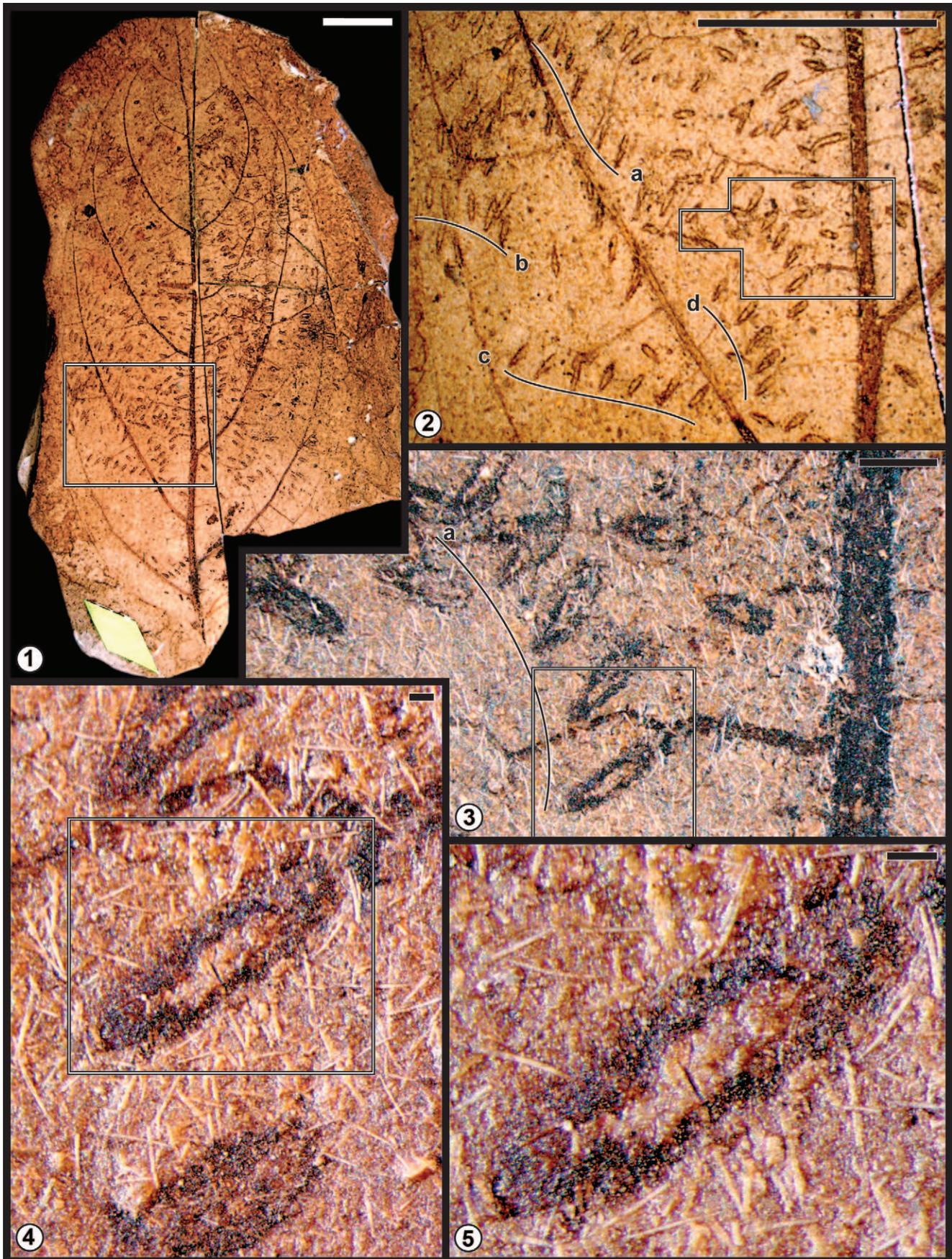


FIGURE 6—Specimen of *Paleovoidus arcuatum* on the holotype of “*Anona*” *infestans* from Río Pichileufú (Berry, 1938) (morphotype unknown, type material, USNM 40389a,b): 1, entire leaf fossil showing the distributions of scars over the lamina, scale: 1 cm; 2, specimens USNM 40389a-b (lettered lines) 6.3–6.5, details of individual scars, scales: 1 cm (Fig. 6.1, 6.2), 1 mm (Fig. 6.3, 6.4), and 0.1 mm (Fig. 6.5).



FIGURE 7—Additional specimens of *Paleovoidius arcuatum* isp. nov. exhibiting an overlapping distribution of oviposition scars (Fig. 7.1, 7.2, 7.4) and clearly demarcated rows (Fig. 7.3, 7.5): 1, MPEF-IC-1367 in an unknown dicot leaf (LH4, morphotype TY122, MPEF-Pb-1051) [note continuous linear file of oviposition marks at bottom of leaf (arrow)], scale bar: 1 cm; 2, MPEF-IC-1391 in an unknown dicot leaf (RP2, morphotype indeterminate, MPEF-Pb-1613); 3, MPEF-IC-1375 in an unknown dicot leaf (LH2, morphotype indeterminate, MPEF-Pb-1588), scale bar: 1 cm; 4, enlargement from rectangular template in Figure. 7.1, showing detail of oviposition scars exhibiting dark spots (arrows) at the narrow end of each ovoidal scar; 5, MPEF-IC-1377 on “*Cassia*” *argentinensis* (LH4, morphotype TY117, MPEF-Pb-1589); scale bar: 0.5 cm.

consecutive row arranged regularly with minimal deviation of scars within a row. These rows may be subparallel to each other (Figs. 4.1, 6.2) or convergent in one or more points that result from projected lines drawn perpendicular to the multiply oriented oviposition rows (Fig. 3.4) (Hellmund and Hellmund, 1991, fig. 6). In other cases (Figs. 3.1, 5.5) the arcuate rows are not parallel to each other, the terminus of one approaching the terminus of the next one, resulting in a zigzag pattern. In some specimens the

leaf tissue between two adjacent scars is broken or removed (Fig. 5.5). In other specimens (Figs. 3.2, 4.3, 4.4, 5.6, 6.4), the blunt end of the scars displays a rounded hole, indicating the absence of plant tissue, resulting in a whitish area. In these same specimens, and in others (Figs. 5.6, 6.4), a dark spot at one end is observed, which is most clearly distinguished at the acute ends of teardrop-shaped scars (Figs. 3.5, 4.1).

Chaotic ovipositional patterns on leaves as in Figure. 7.1 may

result in uninterpretable behavior. However, closer examination reveals that rows of distinctive oviposition scars have been overprinted (Fig. 7.1, 7.4), with individual scars having an elongate-to lens-shaped structure with an enveloping raised rim and a central depression, often housing a dark circular region at one angulated end (Fig. 7.4). There is discernible alignment of scars into particular rows and arcs. Targeted host plants typically are robustly constructed pinnate leaves with prominent midveins.

**Material examined.**—Specimen MPEF-IC 1367, on an unaffiliated dicot (LH4-1213, morphotype TY122 of Wilf et al., 2005a), specimen MPEF-IC-1368a–e, on “*Myrcia*” *deltoides*, (LH4, Myrtaceae, MPEF-Pb-1052); specimen MPEF-IC-1369, on “*Myrcia*” *chubutensis*, (LH13, Myrtaceae, MPEF-Pb-2217); specimen MPEF-IC-1370a–f, on “*Celtis*” *ameghenoi* (LH2, MPEF-Pb-1053); specimen MPEF-IC-1371a–c, on an unaffiliated dicot (LH6, MPEF-Pb-1054, morphotype indeterminate); specimen MPEF-IC-1372a–e, on an unaffiliated dicot (LH2, MPEF-Pb-1584); specimen MPEF-IC-1373a–f, on “*Myrcia*” *chubutensis* (LH13, Myrtaceae, MPEF-Pb-2215); specimen MPEF-IC-1374a–c, on “*Cupania latifolioides*” (LH18, ?Cunoniaceae, MPEF-Pb-1585); specimen MPEF-IC-1375, in an unaffiliated dicot (LH2, morphotype indeterminate, MPEF-Pb-1588); specimen MPEF-IC-1377, on “*Cassia*” *argentinensis* (LH4, morphotype TY117, MPEF-Pb-1589); specimen MPEF-IC-1378a–e, on *Lomatia occidentalis*, (LH4, Proteaceae, MPEF-Pb-998); specimen MPEF-IC 1380a–c, on an unaffiliated dicot leaf (LH13, MPEF-Pb 1591); specimen MPEF-IC-1381, on Malvaceae (LH6, morphotype TY23, MPEF-Pb-1592); specimen MPEF-IC-1383, on an unaffiliated dicot (LH4, morphotype TY170 of Wilf et al., 2005a, MPEF-Pb-1605); specimen MPEF-IC-1384a,b, on an unaffiliated dicot (LH17, morphotype indeterminate, MPEF-Pb-1606); specimen MPEF-IC-1386a–c, on an unaffiliated dicot (RP3, morphotype indeterminate, MPEF-Pb-1608); specimen MPEF-IC-1388a–f, on an unaffiliated dicot (RP3, morphotype indeterminate, MPEF-Pb-1611); specimen MPEF-IC-1389a–f, on *Lomatia occidentalis* (LH2, Proteaceae, MPEF-Pb-988); specimen MPEF-IC-1390a–f, on an unaffiliated dicot (RP3, morphotype indeterminate, MPEF-Pb-1612); specimen MPEF-IC-1391, on an unaffiliated dicot (RP2, morphotype indeterminate, MPEF-Pb-1613); specimen MPEF-IC-1392, on “*Myrcia*” *chubutensis* (LH13, morphotype TY21, MPEF-Pb-2406); specimen MPEF-IC-1393a–e, on an unaffiliated dicot (RP3, morphotype indeterminate, MPEF-Pb-2407); and specimen USNM 40389a,b on the holotype of “*Anona*” *infestans* (type material).

**Occurrences.**—From the early Eocene Tufolitas Laguna del Hunco Formation, Chubut Province, and from the middle Eocene Río Pichileufú locality, Río Negro Province, Argentina.

**Discussion.**—In his recent contribution, Vasilenko (2008) included in the ichnogenus *Paleoovoidus* two new ichnospecies, *P. flavellatus* and *P. arcuatus*. The former ichnospecies was described as “arched oviposition distributed in rows and separated by distance about a maximum width of the eggs or somewhat larger.” This differs from *P. arcuatus* in having shorter distances between scars. By contrast, *P. arcuatus* has slightly arched oviposition scars, with the eggs set in rows at considerable distance from each other parallel to their long axes. This ichnospecies is more similar to the patterns observed in the Patagonian leaves. However, a few months prior to Vasilenko’s paper, Krassilov (2008) established a similar ichnogenus named *Sertoveon* which he described as “egg scars in transverse rows or arches, inserted at about right angles to the direction of the row.” Likewise, he erected two new ichnospecies, *S. cribellum* and *S. arcuatum*. These two ichnospecies also resemble closely the pattern described in our material. We consider that both ichnospecies, *P. arcuatus* and *S. arcuatum*, represent the same oviposition pattern. However, according to the ISCN rules, *Paleoovoidus* has nomenclatorial priority and is the valid ichnogenus; *P. arcuatum* is the correct ichnospecies.

The diagnosis is emended herein to include scars of a broader range of shape (elongate, lens-shaped and teardrop-shaped) that are distributed both in linear rows and in arcs, which in some cases can exhibit a zigzag trajectory. Oviposition specimens that exhibited a zigzag pattern were referred by Krassilov and Silantjeva (2008) to a similar ichnospecies, *Catenoveon undulatum*. Nevertheless, the principal difference between *C. undulatum* and *P. arcuatum* is the relationship with the primary vein, which is absent in the later. Moreover, *P. undulatum* is the only ichnospecies with scars distributed in the leaf lamina without any apparent relation to the primary vein, a feature that differentiates it from *P. bifurcatus* scars that are inclined to the primary vein and from *P. rectus* scars that occur along major veins. Several authors have documented scars exhibiting patterns similar to the material described here under *P. arcuatum*. Hellmund and Hellmund (1991, 1993, 1996c, 1998, 2002a), in particular have described and figured numerous specimens with identifiable scar patterns, including examples from Kounice and Vyšehořovice (both Upper Cretaceous) in Bohemia, Czech Republic; and from Messel (middle Eocene), Salzhausen (middle Miocene), Rott (upper Oligocene), Hammerunterwiesenthal (upper Oligocene), and Berzdorf and Randecker Maar (both lower Miocene) in Germany. They distinguished between smaller scars, 1.3 to 1.4 mm in length, present as an arcuate, parallel pattern, versus larger scars, 1.6 to 1.8 mm long, deployed in a zigzag pattern. The material documented by Peñalver and Delclòs (2004) from the “La Rincoñada” site at the Ribesalbes locality (early Eocene, in Castellón, Spain) also show parallel rows occurring in a zigzag pattern from different species composed of ovoidal-oblong scars, with values that range from 0.9 to 1.1 mm in length and from 0.2 to 0.3 mm in width. Moreover, the traces documented by Labandeira (2002a), from the middle Eocene Republic Flora of eastern Washington, USA, show similar patterns that were defined as separated, equal-sized, lenticular scars, arranged in semicircular arcs. Scars from the latest Cretaceous Hell Creek Formation of North Dakota, USA, show similar morphologies to the ones described here but lack a clear pattern of arrangement (Labandeira et al., 2002). Recently, Vasilenko (2007, 2008) described specimens on the floating leaves of *Quereuxia* possessing elongate oviposition scars of 0.75 to 0.85 mm in length and 0.13 mm in width, distributed in parallel rows. The *Quereuxia* material is from the Maastrichtian age and originates from the Udurchukan locality of the Amur Region, Russia.

Berry (1938) described scars on the holotype of “*Anona*” *infestans* from the Río Pichileufú paleoflora that clearly represent *P. arcuatum* ovipositional damage (Fig. 6.1–6.5). However, he suggested that these marks could represent the bodies of scale insects (Hemiptera: Coccoidea). This leaf (Fig. 6) shows many arcuate rows, either parallel or in a zigzag pattern, of lenticular to teardrop scars distributed over most of the lamina. The temporal occurrence of distinctive *Paleoovoidus arcuatum*, unlike *P. rectus*, and *P. bifurcatus*, probably is confined to the Cenozoic and Late Cretaceous; no known occurrences antedate the appearance of angiosperms during the mid Early Cretaceous.

#### DISCUSSION

Endophytic oviposition has considerable potential for the study of dragonfly host-plant use and behavioral evolution. This is attributable to the fact that the insertion of the ovipositor into plant tissue results in a persistent, fossilizable scar of callus tissue that surrounds inserted, typically nonpreserved eggs. This distinctive, convex, ovoidal damage has an extensive fossil record on various plant tissues, displaying a characteristic pattern of linear, curvilinear or arcuate rows that occur in plant organs as dark, oval, to teardrop-shaped scars (Labandeira, 2002a, 2006). In many cases, ovipositional patterns occur in a parallel or zigzag fashion, or alternatively, in no pattern at all. By contrast, in exophytic oviposition, eggs often are distributed in tight packets or as looser

clusters on the leaf surface (Corbet, 1999; Labandeira, 2002a; Labandeira et al., 2007; Vasilenko and Rasnitsyn, 2007; Krassilov and Silantjeva, 2008; Vasilenko, 2008). Moreover, exophytic oviposition is done by insects either lacking an external ovipositor or possessing a modified, nonslicing ovipositor (Labandeira, 2006), and any resulting effects on plant surface features rarely preserve as fossils. In addition, egg morphology also can be useful to distinguish the type of oviposition, when infrequently present (e.g., Sahlén, 1995; Vasilenko and Rasnitsyn, 2007; Vasilenko, 2008; Pott et al., 2008; Krassilov and Silantjeva, 2008). Corbet (1999) characterized endophytic odonatan eggs as rather elongate, often flattened, and several times longer than wide, whereas exophytic eggs are more ellipsoidal to subspherical.

*Fossil record of insect oviposition.*—Ichnofossils of ovipositional traces have been recognized principally in sphenopsid stems and seed-plant leaves (Roselt, 1954; Kelber, 1988; Schaarschmidt, 1992; Johnston, 1993; Grauvogel-Stamm and Kelber, 1996; Zherikhin, 2002; Banerji, 2004; Beattie, 2007). The oldest record of oviposition is from an arborescent Pennsylvanian age sphenopsid, *Calamites cistii*, bearing pronounced, ellipsoidal scars that were attributed to the Archaeorthoptera or Palaeodictyoptera (Béthoux et al., 2004). The oldest trace fossils assigned to odonatan oviposition, referred to the Protodonata, comes from the Lower Permian flora of the Río Bonito Formation, Brazil (Adami-Rodrigues et al., 2004). Later Paleozoic endophytic oviposition, such as that from the Upper Permian of Australia, is recognizable but difficult to assign to a particular producer. For example, an upper Permian flora from southeastern Australia reveals small circular insertion scars grouped into several clusters in the foliage of the extinct sphenopsid cladode *Phyllothea* (Beatty, 2007). Presumably, these scars were induced by a member of the Protodonata or Palaeodictyopteroidea, paleopterous clades that largely became extinct at the end Permian (Labandeira, 2006).

Pre-Cretaceous, Mesozoic evidence for odonatan ovipositional damage predominantly originates from biogeographically disparate Middle and Upper Triassic sites worldwide, and from the European Lower Jurassic. The most important odonatan oviposition occurrences, unaffiliated to family, are from the Middle and Upper Triassic of France and Germany (Grauvogel-Stamm and Kelber, 1996). In particular, Pott and colleagues (2008) documented spectacular material, replete with microstructural details of insect egg and adjacent plant cuticle, from the Upper Triassic of Austria. Gondwanan occurrences from the Upper Triassic of Chile (Gnaedinger et al., 2007) and especially the Molteno Formation of South Africa (Labandeira, 2006), have documented several distinctive ovipositional types (Labandeira et al., 2007). Van Konijnenburg-van Cittert and Schemießner (1999) have documented younger, new types of ovipositional damage from the Lower Jurassic of Bavaria (Germany) that may represent an expansion of dragonfly egg-laying strategies from the earlier Triassic.

More recent, better-defined, endophytic oviposition damage, attributable to particular modern lineages, becomes abundant during the Cretaceous and especially the Cenozoic (Hellmund and Hellmund, 1991, 1993, 1996a, 1996b, 1996c, 1998, 2002a; Lewis, 1992; Labandeira, 2002a, 2002b; Labandeira et al., 2002; Peñalver and Declòs, 2004; Vasilenko, 2005, 2008; Vasilenko and Rasnitsyn, 2007; Krassilov et al., 2007; Krassilov and Silantjeva, 2008). As in Triassic and Jurassic examples of oviposition, Cretaceous and Cenozoic material is attributed commonly to the Odonata, or occasionally to other groups such as the Diptera, Lepidoptera, Coleoptera, Hymenoptera and Hemiptera (Krassilov and Silantjeva, 2008). Specimens referred originally as coleopterous eggs in *Alnus* (Betulaceae) leaves (Lewis and Carroll, 1991, 1992; Lewis, 1992), later were reidentified as odonatan ovipositional damage (Labandeira, 2002a). Many of these documented descriptions come from the Cenozoic of Germany and were evaluated by Hellmund and Hellmund (1991, 1993, 1996a,

1996b, 1996c, 1998, 2002a), and typically involve damselfly oviposition. The German mid-Cenozoic occurrences reveal considerable behavioral information and are directly comparable with extant oviposition patterns and associated behaviors.

*The biology and paleobiology of odonatan oviposition.*—Odonatan oviposition patterns have received considerable attention in ecological studies, particularly those emphasizing endophytic placement and behavior (Wesenberg-Lund, 1913a, 1913b, 1943; Schiemenz, 1957; Jurzitza, 1974; Grunert, 1995; Hellmund and Hellmund, 1998; Corbet, 1999). Matushkina and Gorb (2007) have emphasized that females of most odonate species deposit their eggs into a plant substrate. Females use the two sets of valves of the ovipositor to penetrate and cut leaf tissue, inserting eggs within surface or deep tissue (Matushkina and Gorb, 2007; Corbet, 1999; Miller and Miller, 1988; Labandeira, 2006). Typically, one egg is deposited for each insertion (Tillyard, 1917; Ando, 1962; Hellmund and Hellmund, 2002a; Sahlén, 1995; Lutz and Pittman, 1968).

The Anisoptera (dragonflies) display a wide variety of ovipositional modes, involving both exophytic and endophytic egg placement (Corbet, 1999). However, patterns of endophytic plant damage are poorly described in the literature for this group, and the behaviors and mechanisms of egg insertion within leaves or other plant organs are largely unknown. Considerably more is known of extant zygopteran ovipositional behavior, in which scars typically are narrow and have an oval to ellipsoidal surface expression. For example, the eggs of *Lestes eurinus* were described by Lutz and Pittman (1968) as elongate, cylindrical, and uniform in size. Modern field and laboratory observations at Horco Molle, in Tucumán Province, Argentina, were made for oviposition of *Acanthagrion ablutum* (Zygoptera: Coenagrionidae) (Calvert, 1909) on *Cynoglossum amabile* (Boraginaceae) leaves and for oviposition of the same zygopteran species on *Polygonum punctatum* (Polygonaceae) at Dique Escaba, in southern area of Tucumán Province. Both of these modern examples display eggs with a general ellipsoidal shape, whose ends are acute, rounded, or blunt in shape. The egg structure is characterized by a yellowish to brownish region, which in a few cases bears a small, linear aperture (Fig. 5.2, 5.3). However, in some cases a white aperture at one end also is observed. This last pattern matches the ovipositional scars in the fossils (Fig. 5.6).

Fossil ovipositional scars described herein and in the literature share with extant odonatan egg insertions a similar general shape. This similarity ranges from scars with two similar extreme, rounded, or more tapering points, but in other cases with a blunt and acute end resulting in a teardrop shape. Hellmund and Hellmund (2002a) noted that several scars possess raised encircling rims and have a smooth concavity in the central area. They also argued that small protrusions in the interior depression of the scars could be the remnants of egg envelopes. These features were not observed on our material. In some specimens (Figs. 3.3, 5.5), a visible dark spot was observed at the angulate scar end. The same feature was observed by Krassilov et al. (2007) but described as preserved callus tissue. By contrast, Krassilov and Silantjeva (2008) show a slender dark band inside the egg impression that was interpreted as a dried yolk sac or an exuvium of an embryonic larva.

In other cases (Figs. 4, 5.2, 5.6), scars display a blunt end cradling a more centrally positioned, rounded or more linear hole that is distinguishable as a clear zone because of the absence of plant tissue. This distinctive zone, observed both in the fossils and in one leaf from the Dique Escaba locality, may represent an emergence aperture, indicating that the immature nymph had abandoned the foliar microenvironment for life in water (Fig. 5.6).

Ovipositional behavior varies among the major groups of Odonata, resulting in a diversity of patterns that characterize extant and fossil damage on leaf surfaces. Observations of extant

Zygoptera show that there are differences in ovipositional behavior, for example between Coenagrionidae and Lestidae (Gower and Kormondy, 1963; Lutz and Pittman, 1968; Hellmund, 1991, 2002b; Matushkina and Gorb, 2007). The endophytic oviposition of Coenagrionidae includes more-or-less a 1 mm spaced distance between the oviposition scars that form linear rows, which are either slightly crescentic, semicircular, or parallel, or alternatively deployed as a zigzag pattern (Wesenburg-Lung, 1913a, 1913b; Grunert, 1995; Hellmund and Hellmund, 1991, 1998). *Paleoovoidus arcuatum* clearly resembles this range of pattern. Hellmund and Hellmund (1991) were the first to attribute similar patterns in fossil leaves to ovipositional traces of Odonata from the upper Oligocene of Rott, Germany. These authors originally named the arcuate and parallel rows as *Bogenmodus*, and the zigzag rows as *Zickzackmodus*. These alternative styles were compared to extant ovipositional damage in leaves made by damselflies, particularly the Coenagrionidae, and this clade was determined to be the producer of this pattern. Later, new fossil evidence from the Hell Creek Formation (Upper Cretaceous) of North Dakota, U.S.A., attributed oviposition damage on leaves of *Marmarthia pearsonii* (Laurales) and *Erlingdorfia montana* (Platanaceae) to the Coenagrionidae (Labandeira et al., 2002). Moreover, Peñalver and Delclòs (2004) documented Miocene oviposition trace fossils of Coenagrionidae from La Rincoñada, Spain, on leaves of *Laurophyllum* (Lauraceae), *Caesalpinia* (Fabaceae), and *Populus* (Salicaceae). Similar ovipositional patterns from the Eocene of Washington were observed by Labandeira (2002a) for *Betula* (Betulaceae), *Crataegus*, *Paracrataegus*, *Sorbus* (all Rosaceae), and *Ginkgo* (Ginkgoaceae), some of which initially and incorrectly were attributed to beetles (Chrysomelidae) by Lewis and Carroll (1991, 1992). Likewise, Vasilenko and Rasnitsyn (2007) and Vasilenko (2008) described several examples of elongate and oval endophytic oviposition on leaves of *Quereuxia* that were assigned to the ichnotaxonomic group, Paleooovoididae, from the Maastrichtian of the Udurchukan locality in the Amur Region of Russia.

Body fossils of Coenagrionidae are known from several Early Cretaceous localities (Jarzembowski, 1990; Jarzembowski et al., 1998; Jell, 2004). It is unclear if *Paleoovoidus arcuatum* originated within the Coenagrionidae or possibly from an earlier Mesozoic ancestor shared with the sister-clade Platynemidae (Bechley, 1996), which generates a similar pattern of oviposition (Watanabe and Atachi, 1987). A similar pattern of damage, found in *Agriion* (Wesenberg-Lund, 1943, fig. 57), a member of the distant zygopteran clade Calopterygidae, may represent behavioral convergence.

A different mode of oviposition is represented by species of Lestidae that lay eggs in double rows at both sides of a primary vein or occasionally in a single row along one side of the vein. At insertion, lestid eggs normally are oriented from an acute to a perpendicular angle relative to a major vein. Structural details of the ovipositional process were provided by Matushkina and Gorb (2007), including the ovipositional behavior of *Lestes sponsa* and *L. barbarus*, indicating that the major axis of paired or single eggs is parallel to plant fibers. Similarly, the fossil oviposition pattern described here and assigned to *Paleoovoidus bifurcatus* probably was produced by damselflies of the family Lestidae. Hellmund and Hellmund (1991, 1996c, 2002b) described the same type of oviposition that we attribute to *P. bifurcatus* in a leaf of *Cinnamomum* sp. ("*Daphnogene*," Lauraceae) from the late Oligocene and in a unidentified leaf from the middle Eocene of Germany, a pattern they named *Doppelreihenmodus*.

Ovipositional damage distributed in a single row, assigned here to *Paleoovoidus rectus*, also has been attributed to the Lestidae based on extant foliar damage patterns. Modern lestid ovipositional scars have been observed to occur within major veins forming a single concatenated row, characterized by parallel alignment of long axes of the elongate scars (Gower and Kormondy, 1963).

The same pattern has been observed by Hellmund and Hellmund (1991, 1996a) in various dicot leaves. Some specimens (Fig. 2.2, 2.3) display subparallel ovipositional insertion in a single row, of which individual scars may occur in both midrib vascular tissue and in the leaf-blade. This pattern also consists of scars that appear in a single, straight row described by Vasilenko (2005) and herein, but it has not been documented extensively in modern foliar material.

Some of our specimens (Fig. 7.1–7.5), included under *Paleoovoidus arcuatum*, show some disorder in the distribution of scars in contrast to the distinctive patterns described previously. This more chaotic distribution may be related to the high density of scars, which would preclude identification of individual rows, possibly because of superimposed, multiple ovipositional events by one or several females in the same leaf. Alternatively, elevated scar density may be attributable to the normal reproductive behavior of an unknown, ovipositing odonatan. This latter alternative is less likely because distinct linear files of scars were detectable and apparently were overprinted with subsequent waves of oviposition.

Analyses of the distribution of oviposition scars on fossil leaves and their comparison to patterns obtained from extant autecological studies is important for the interpretation of these ichnofossils. This allows for an understanding of the ovipositional behavior that produced the original damage. Especially in *Paleoovoidus arcuatum*, the orientation of each scar in an arcuate or zigzag trajectory can indicate the position of the female on the leaf during oviposition (Hellmund and Hellmund, 1991). Accordingly, if lines are drawn perpendicular to each linear file of scars, the point where these lines converge, through triangulation, should be the abdominal pivot point represented by an anchored thorax. When the scars are teardrop-shaped, the abdominal pivot point is more precisely identifiable because the shape of eggs allows a sharper definition of the perpendicular lines. From this pivot point, the female lays eggs by swinging her abdomen from one side to the other, depositing from three to fifteen eggs during each swipe. The next row likewise is produced after she moves a single step forward and inscribes another swinging movement of her abdomen (Hellmund and Hellmund, 1991; Peñalver and Delclòs, 2004). The abdominal pivot point potentially is moved along the same axis when producing different arcs of scars, resulting in a distinctive and successive series of en echelon files (Hellmund and Hellmund, 2002a). These parallel and zigzag patterns may be combined in the same ovipositional behavior, as shown by field observations at Horco Molle and Escaba in northwestern Argentina. Oviposition begins with well-defined and independent curved rows, continues with increasingly arcuate files, and results finally in a zigzag configuration. This observation indicates that the same female can produce both types of patterns, *Bogenmodus* and *Zickzackmodus*, from the same ovipositional pivot point, which should discourage the possibility of separating ichnospecies based on this modern behavioral character.

Other behavioral traits are reflected in the ichnospecies described herein. Some members of the Lestidae insert their eggs on plant stems near water, instead of leaves. Hellmund and Hellmund (1991) mentioned that Lestidae lay eggs at the sides of a primary leaf vein, usually a midrib, and inferred that they used this anatomic structure as a guide. (The use of a prominent vein as a guide may have an evolutionary relationship with linear oviposition on stems, extending to the late Paleozoic.) The eggs are inserted into foliar tissue by moving the abdomen once to the right and then to the left for each oviposition point, producing often paired files along the vein (Hellmund, 1991, 2002a). Observations made on the reproductive habits of extant *Lestes rectangularis* Say 1839 on leaves of *Rumex* (Polygonaceae), *Typha* (Typhaceae) and *Scirpus* (Cyperaceae), from Pennsylvania, U.S.A., showed that females rotate the last eight to ten abdominal

segments 90 degrees to produce this pattern (Gower and Kormondy, 1963). By contrast, coenagrionid oviposition appears not to be influenced by vein architecture during selection of the foliar area for egg insertion. This type of oviposition targets different regions of the leaf without restriction and produces canted orientations of scar files.

*Host-plant preferences.*—Observations regarding host-plant preferences for endophytic oviposition have been made for several extant zygopteran species (Gower and Kormondy, 1963; Bick and Hornuff, 1965). Corbet (1963) showed that some zygopteran species chose one type of plant for oviposition among several available alternatives. Similar results were obtained by Lutz and Pittman (1968) who concluded that *Lestes eurinus* Say, 1839 oviposited only in *Sparganium americanus* (Sparganiaceae). However, Kumar and Prasad (1977) did not note any host-plant preference in their study of the reproductive behavior of *Neurobasis chinensis* (Calopterygidae), which oviposited endophytically in several species of riparian plants.

Only a few of our leaf specimens, each with oviposition scars at LH or RP, represent the ichnospecies *Paleoovoidus rectus* and *P. bifurcatus*. Given the paucity of occurrences, it is impossible to determine if ovipositional specialization was present for *P. rectus* and *P. bifurcatus*. By contrast, comparatively abundant *Paleoovoidus arcuatum* is represented by ovipositional damage on a wide variety of foliage, including specimens of Lauraceae, Proteaceae, Fabaceae, Malvaceae, Cunoniaceae, and Myrtaceae. Supporting this broad spectrum of plant hosts, *P. arcuatum* only occurs more than once per species in two specimens each of “*Myrcia*” *chubutensis* and *Lomatia occidentalis*. These observations indicate that no preferential host-plant preference was present for damselflies in their selection of oviposition leaf substrates.

*The South American odonatan body fossil record.*—South America has a significant body-fossil record of Odonatoptera, particularly because the wings of dragonflies and damselflies preserve well. From the Paleozoic and Mesozoic of Brazil, several families are known (Martins-Neto, 2005; Moura et al., 2006), particularly from the Early Permian of the Paraná Basin and the Early Cretaceous of the Araripe Basin. By contrast, in Argentina odonatan body-fossil specimens overwhelmingly originate from Cenozoic deposits (Petrulevičius, 2001; Petrulevičius et al., 1999; Petrulevičius and Nel, 2002a, 2002b, 2003a, 2003b, 2004a, 2004b, 2005, 2007). There are a few records from the Paleozoic of Argentina, including two members of the Geroptera in the Early Pennsylvanian (Riek and Kukalová-Peck, 1984; Wootton et al., 1998; Gutierrez et al., 2000), and multiple occurrences of the Odonata from the Middle and Late Triassic (Carpenter, 1960; Martins-Neto et al., 2003). Additionally, Petrulevičius and Nel (2003a, 2005, 2007) previously documented body fossils (wings) of Odonata from the Laguna del Hunco locality. One zygopteran specimen was assigned to the extinct family Austroperilestidae (*Austroperilestes hunco*) and possibly is related to the extant family Perilestidae. The other specimen was assigned to the new extinct family Frenguelliidae (*Frenguella patagonica*). The Austroperilestidae and Frenguelliidae records currently represent the only body-fossil evidence for Odonata from LH; neither family has been documented at RP. These taxa conceivably could have produced any of the ichnotaxa observed on LH leaves, but there is no evidence for or against this other than the presence of the body fossils. It bears re-emphasis that neither the Coenagrionidae nor Lestidae are known from body fossils at either locality.

Currently the oldest reliable evidence worldwide of Lestidae is ovipositional traces from the middle Eocene of Germany (Hellmund and Hellmund, 2002b). Additionally, Coenagrionidae ovipositional patterns have been documented from the upper Oligocene and upper Miocene of Germany (Hellmund and Hellmund, 1996a, 1998). By contrast, specimens of *Paleoovoidus bifurcatus* and *P. arcuatum* from the LH and RP localities of Patagonia represent the oldest records of ovipositional damage for lineages

likely to be Lestidae and Coenagrionidae. Based on these Patagonian occurrences and evidence for distinctive damselfly ovipositional damage, we infer that, by the early to middle Eocene boundary interval, species of the Lestidae and Coenagrionidae and their ovipositional behaviors probably were present at the LH and RP localities.

#### CONCLUSIONS

1. Evidence of endophytic odonatan oviposition is documented from the Laguna del Hunco (LH, early Eocene) and Río Pichi-leufú (RP, middle Eocene) floras of Patagonia, Argentina. Three types of oviposition are described from LH, assigned to the three newly defined ichnospecies *Paleoovoidus rectus* and *Paleoovoidus bifurcatus*, as well as the previously established *Paleoovoidus arcuatum* of Krassilov and Silantjeva (2008). By contrast, only *P. arcuatum* is recorded from the RP paleoflora. Ichnospecies of *Paleoovoidus* include elongate to lens-shaped or teardrop-shaped scars expressed on the surfaces of foliar tissue that are arranged in distinctively regular or otherwise random patterns. In some cases, the narrow end of the scar bears a dark spot, but in other instances, there is a broader, circular, small depression lodged at the wider end. Both of these features suggest apertures for the emergence of dragonfly (odonatan) immatures.

2. By comparison with similarities in morphology with extant oviposition patterns, ichnospecies of *Paleoovoidus* are attributable to recognizably modern types, specifically to the Suborder Zygoptera. *Paleoovoidus rectus* and *P. bifurcatus* probably were produced by members of the Family Lestidae; *P. arcuatum* was produced by members of the Family Coenagrionidae.

3. The same patterns of egg insertion, particularly for the more abundant *Paleoovoidus arcuatum*, were present for several leaf morphotypes, but no host-plant specificities were observed.

4. Evidence from the Eocene of South America demonstrate that certain odonatan taxa have maintained similar patterns and behaviors of endophytic oviposition, represented by scars distributed in linear, zigzag, or otherwise parallel traces over leaf laminae for approximately a 50 million-year interval. These behaviors, by virtue of their ichnotaxonomic synonymy with earlier Early Jurassic to Late Cretaceous occurrences, considerably antedate the mid Paleogene, and extend deeper into the Mesozoic.

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