PHYTOPHAGY ON FOSSIL FERNS FROM ARGENTINA (PALO PINTADO FORMATION, LATE MIOCENE): A REVIEW OF THEIR FOSSIL RECORD AND ICHNOTAXONOMY

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ABSTRACT – Evidence of insect-fern interactions are described for the first time from late Miocene strata of Salta Province, Argentina. Two ichnospecies are defined to include fossil traces of surface feeding and hole feeding, located between the secondary veins and adjacent with the primary vein of two species of fossil ferns, *Blechnum serrulatiformis* Anzótegui & Horn and *Thelypteris interrupta* (Willd.) Iwatsuki. The first ichnospecies corresponding with surface feeding presents oblong traces and both ends are rounded; occupying the entire intercostal space. This type of phytophagy is found for the first time in the fossil record of ferns. The second ichnospecies is similar in shape and location to the previous ichnotaxon, except that all herbivorized tissues are absent. At last, a review of the fossil record of insect-fern associations is performed.

Key words: insect-fern interactions, fossil traces, surface feeding, hole feeding.

RESUMO – Descreve-se pela primeira vez evidência de interações inseto-samambaia no Mioceno superior da Província de Salta, Argentina. Duas icnoespecies são propostas para incluir rastros fósseis de alimentação superficial e alimentação em orifícios, localizadas entre as veias secundárias e adjacentes à veia primária em duas espécies de samambaias fósseis, *Blechnum serrulatiformis* Anzótegui & Horn e *Thelypteris interrupta* (Willd.) Iwatsuki. A primeira espécie corresponde à alimentação superficial, apresenta rastros oblongos com ambos os extremos arredondados e ocupa todo o espaço intercostal. Este é o primeiro registro de alimentação superficial em samambaias fósseis. A segunda espécie similar na sua forma e localização ao icnotáxon previamente descrito, exceto que todas as camadas de tecido herbivorizado estão ausentes. Finalmente, uma revisão do registro fóssil das associações inseto-samambaia também é realizada.

Palavras-chave: interação inseto-samambaia, traços fósseis, alimentação superficial, alimentação em orifício.

INTRODUCTION

Ferns appeared in the Middle Devonian, about 390 Ma (Scheckler, 1974; Rothwell & Stockey, 2008). Subsequently, they have diversified on all continents (Bancroft, 1932; Herbst, 1977; Rothwell & Stockey, 1989; Van Konijnenburg-Van Cittert, 1989; Tidwell & Ash, 1994; Hill & Jordan, 1998; Wang, 1999; Rößler, 2001), establishing three diversification events during the Carboniferous, the Permian-Jurassic and the Cretaceous (Rothwell, 1987; Tomescu *et al.*, 2006; Schuettpelz & Pryer, 2009).

Despite the ferns and insects occurred in the same past environments, fossil and even extant evidence of insect-fern associations are poorly documented (Table 1). Examples of insect damages on fossils is based on indirect evidence of coprolites that often occur within the rachises, stems and sporangia (Seward, 1923, 1924; Rothwell & Scott, 1983; Scott & Paterson, 1984; Scott *et al.*, 1985; Rex & Galtier, 1986; Labandeira & Beall, 1990; Lesniskowska, 1990; Labandeira *et al.*, 1997; Ash, 2000; Rößler, 2000; Labandeira & Phillips, 2002; Kellogg & Taylor, 2004; D'Rozario *et al.*, 2011; Slater *et al.*, 2012), and to a lesser extent damage inflicted on leaves (Webb, 1982; Hill, 1987; Ash, 1997; Labandeira, 2002b, McLoughlin *et al.*, 2015). Fossil insect-plant interactions in Argentina are poorly documented. Césari *et al.* (2012) described coprolites in *Cuyoxylon* Pujana & Césari, 2008 roots and stem San Ignacio Formation (Late Carboniferous-Early Permian) from, San Juan Province. Possible oviposition or hole feeding

Table 1. Fossil record of insect-fern interactions.

Interaction type	Part of plant	Evidence	Taxa	Age	Author
Marginal excisions	Foliar lamina	Plant damage	Fern sp. indet.	middle Eocene	Labandeira (2002b)
Marginal excisions	Foliar lamina	Plant damage	Filicalean fern sp. indet.	Late Cretaceous	Labandeira *et al.* (2002)
Pith boring	Stem	Coprolites	*Tempskya* sp. (Polypodiales)	Cretaceous	Scott & Paterson (1984)
Root boring	Root	Coprolites	*Tempskya* sp. (Polypodiales)	Cretaceous	Seward (1923)
Pith boring	Stem	Coprolites	*Tempskya wyomingense* (Polypodiales)	Early Cretaceous	Tidwell & Hebbert (1992)
Pith boring	Stem	Coprolites	*Tempskya knowltoni* (Polypodiales)	Early Cretaceous	Seward (1924)
Marginal excisions	Foliar lamina	Plant damage			McLoughlin *et al.* (2015)
Hole feeding	Foliar lamina	Plant damage	*Cladophlebis australis* (Filicales)	Middle Jurassic	
Piercing and sucking	Foliar lamina	Plant damage			
Hole feeding	Foliar lamina	Plant damage	*Angiopteris blackii* (Marattiales)	Middle Jurassic	Hill (1987)
Pith boring	Petioles	Coprolites	*Itopsidema vancleaveii* (Filicales)	Late Triassic	Ash (2000)
Skeletonizations	Foliar lamina	Plant damage	*Dictyophyllum nathorstii* (Gleicheniales)	Late Triassic	Feng *et al.* (2014)
Marginal excisions	Foliar lamina	Plant damage	*Cynepteris lasiophora* (Filicales)	Late Triassic	Ash (1997)
Galls or oviposition?	Foliar lamina	Plant damage	*Dictyophyllum bremerense* (Gleicheniales)	Middle-Late Triassic	Webb (1982)
Pith boring	Petiole	Coprolites	*Antarctipteris* sp. (Gleicheniales)	Middle Triassic	Kellogg & Taylor (2004)
Pith boring	Stem	Coprolites	*Psaronius housuoensis* (Marattiales)	late Permian	D'Rozario *et al.* (2011)
Palynophagy	Sporangium	Coprolites	Fern sp. indet.	middle Permian	Slater *et al.* (2012)
Pith boring	Stem	Coprolites	*Ankyropteris brongniartii* (Filicales)	early Permian	Rößler (2000)
Root boring	Root	Coprolites	*Psaronius* (Marattiales)		
Pith boring	Stem	Coprolites	*Psaronius* (Marattiales)	Early Carboniferous	Labandeira & Phillips (2002)
Galling	Petioles	Plant damage	*Psaronius* (Marattiales)		
Root boring	Root	Coprolites	*Psaronius* sp. (Marattiales)	Late Carboniferous	Labandeira *et al.* (1997)
Piercing and sucking	Rachis	Plant damage	*Psaronius* (Marattiales)	Late Carboniferous	Labandeira & Phillips (1996a)
Galling	Petioles	Plant damage	*Psaronius chasei* (Marattiales)	Late Carboniferous	Labandeira & Phillips (1996b)
Pith boring	Petiole	Coprolites	*Psaronius chasei* (Marattiales)	Late Carboniferous	Lesnikowska (1990)
Pith boring	Stem	Coprolites	*Psaronius* sp. (Marattiales)	Late Carboniferous	Labandeira & Beall (1990)
Pith boring	Stem	Coprolites	*Psaronius magnificus* (Marattiales)	Late Carboniferous	Rothwell & Scott (1983)
Pith boring	Rachis	Coprolites	Zygopterid fern (Zygopteridales)	Early Carboniferous	Rex & Galtier (1986)
Pith boring	Rachis	Coprolites	*Botryopteris* (Ophioglossales)		

have been reported by Cúneo (1987) in *Ginkgoites* Seward, 1919 leaves from Río Genoa Formation (Lower Permian) in Chubut. Recently, Gallego *et al.* (2014) described plant-insect associations in gymnosperms in the same formation. In La Golondrina Formation (Mid-Late Permian) from Santa Cruz Province, traces on the leaves of *Glossopteris* Brongniart, 1828 species were described by Cariglino & Gutiérrez (2011). The fossil record of insect-plant interactions in angiosperm leaves is more abundant than Paleozoic and Mesozoic records in other host plants. These occurrences come from Chubut (Early Eocene) and Rio Negro (Middle Eocene) provinces (Wilf *et al.*, 2005; Sarzetti *et al.*, 2008, 2009; Sarzetti, 2010; Carvalho *et al.*, 2013). More recently, Horn *et al.* (2011) documented insect-mediated damage from the Middle and Upper Miocene from Tucumán and Salta Provinces. Until now, the only record

known about insect-fern interactions from Argentina, is the one described by Carvalho *et al.* (2013) in the Early Eocene flora from Laguna del Hunco, Chubut Province. The ichnotaxonomy of insect trace fossils on leaves was proposed originally by Vialov (1975), which was later used by other authors (Straus, 1977; Givulescu, 1984; Vasilenko, 2005, 2007a,b; Sarzetti *et al.*, 2008, 2009). Most evidence of surface and hole-feeding damage on fossil leaves were described in the literature but without a formal ichnotaxonomic analysis (Ash, 1997; Zherikhin, 2002; Labandeira, 2002b; Labandeira *et al.*, 2002, 2007; Banerji, 2004; Prevec *et al.*, 2009; Srivastava & Agnihotri, 2011). Givulescu (1984) described the ichnospecies *Phagophytichnus gastropodinus* in fossil angiosperm leaves and showed that some features would allow assignment to surface feeding. The only ichnogenus defined formally for surface feeding is

Cephaloleichnites Wilf, Labandeira, Kress, Staines, Windsor, Allen & Johnson, 2000, assigned as a combination of damage type made by different instars and included larval and adult feeding trails (Wilf *et al.*, 2000). Hole feeding on fossil leaves were defined ichnotaxonomically by Vasilenko (2007a), but he described these traces as windows excisions.

Early studies on the Palo Pintado Formation were focused mostly on plant diversity and taxonomy. The fossil occurrence consists of different plant organs of angiosperms and ferns (leaves, fronds, fruits, woods, pollen and spores) (Herbst *et al.*, 1987, 2000; Anzótegui, 1992, 1998; Lutz & Martinez, 2007; Anzótegui & Horn, 2011). Also, paleoenvironmental reconstructions were performed (Herbst *et al.*, 1987; Galli *et al.*, 2011) and recently trace fossils on leaves were described (Anzótegui *et al.*, 2008; Horn *et al.*, 2011).

The aims of this contribution are twofold. First, trace fossils attributed to phytophagous insects are documented on two species of ferns, *Blechnum serrulatiformis* (Blechnaceae), and *Thelypteris interrupta* (Thelypteridaceae) from Argentina. These new records are placed in a paleontological context that includes other similar insect traces on leaves. Second, two ichnospecies are established to include fossil traces of surface feeding and hole feeding.

GEOLOGICALS ETTING

The fossil impressions were collected from Palo Pintado Formation, at the central southern region of Salta Province, Argentina. The fossil sites are between these two coordinates 25°41'01''S, 66°07'55''W and 25°40'59''S, 66°05'49''W (Galli *et al.*, 2011), with an age constrained between 10.29 + 0.11 Ma (K/Ar) (Galli *et al.*, 2008) and 5.27+ 0.28 Ma (Coutand *et al.*, 2006) at its upper section. This formation is integrated within the Payogastilla Group, which consist of presents a thickness *ca*. 1200 m (Diaz & Malizzia, 1983), and it is bounded by the subjacent Angastaco and the superjacent San Felipe formations (Figure 1). Lithologically Palo Pintado strata consists in cycles of decreasing grains that includes conglomerates at the base and a transition into a sandstone matrix that culminates in a greenish siltstone at top (Herbst *et al.*, 1987; Anzótegui, 1998, Galli *et al.*, 2011). The fossil originate from basal most to middle section of the formation, which crops out at Quebrada del Horno and Peñas Blancas, in Salta Province.

MATERIAL AND METHODS

The impressions of *Blechnum serrulatiformis* and *Thelypteris interrupta* from Quebrada del Horno and Peñas Blancas are found in outcrops of Palo Pintado Formation, from Upper Miocene strata, occurring as intact and fragmented material. Nearly all complete fronds were found with venation and even with sori occurred in a few fronds of *T. interrupta*. The analyzed material is deposited in the Paleobotany (**CTES-PB**) and Ichnology (**CTES-IC**) collections of the Facultad de Ciencias Exactas y Naturales y Agrimensura of the Universidad Nacional del Nordeste, in Corrientes, Argentina. The fossil impressions were compared with extant samples of *Thelypteris interrupta* and *Blechnum serrulatum* Richard 1792, wich are deposited in the CTES herbarium, in Corrientes Province.

Material was observed in a Nikon binocular stereomicroscope, model SMZ-445 and photographed with Nikon mounted camera (model 590CU). Micrometrics software (image processor) was used for measurements, principally of insect damage dimensions.

SYSTEMATIC ICHNOLOGY

Family PHAGOPHYTICHNIDAE Vialov, 1975
Subfamily FOLIFENESTRINAE Vasilenko, 2007a

Folifenestra Vasilenko, 2007a

Type ichnospecies. *Folifenestra dubia* Vasilenko, 2007a (p. 208, pl. 12, figs. 6,7).

Emended diagnosis. Hole feeding damage variable in size and shape, grouped or isolated, occupying part or all the space between two secondary veins. The margin of the perforation range from a fine dark line to a more robust thickened rim.

Remarks. The diagnosis is emended because Vasilenko (2007a) defined the ichnogenus only as "windows feeding", without offering any morphological character for its identification. Moreover, the author restricted the definition of the ichnogenus only for Pteridophyta and Pinophyta, and no potentially applying the designation to other families of plants. According to the illustrated material and their citations (Vasilenko, 2007a, pl. 12, figs. 6,7), the author was probably referring to hole feeding traces. However, Vasilenko (2007a) defined the traces as window feeding traces, which represent another type of feeding behavior, resulting in a misapplied definition.

Folifenestra intervenosa isp. nov.
(Figures 2A-F; 3A,B; 4C,F)

Holotype. CTES-IC 35, traces on pinna of *Thelypteris interrupta* (CTES-PB 14142), (Figure 2A).
Paratype. CTES-IC 34, traces on pinna of *Thelypteris interrupta* (CTES-PB 14141), (Figures 2C,D; 3A; 4F).
Host. *Blechnum serrulatiformis* (Blechnaceae) (CTES-PB 8061, CTES-PB 14064), *Thelypteris interrupta* (Thelypteridaceae).
Other material examined. Specimens CTES-IC 32, CTES-IC 33, CTES-IC 37 (Figure 2B), CTES-IC 62, CTES-IC 64, CTES-IC 65, CTES-IC 66, CTES-IC 67, CTES-IC 68 and CTES-IC 69 occur on pinnules of *Thelypteris interrupta* (CTES-PB 14139, 14140, 14143, 14144, 14145, 14146, 14147, 14148, 14149 and 14150; paleobotanical collection number assigned at fossil plants containing those traces).
Provenance and stratigraphy. Peñas Blancas outcrop, Palo Pintado Formation, Salta Province, Argentina.
Etymology. For the leaf part where the traces are placed. Latin, inter (between) and vena (of the veins).
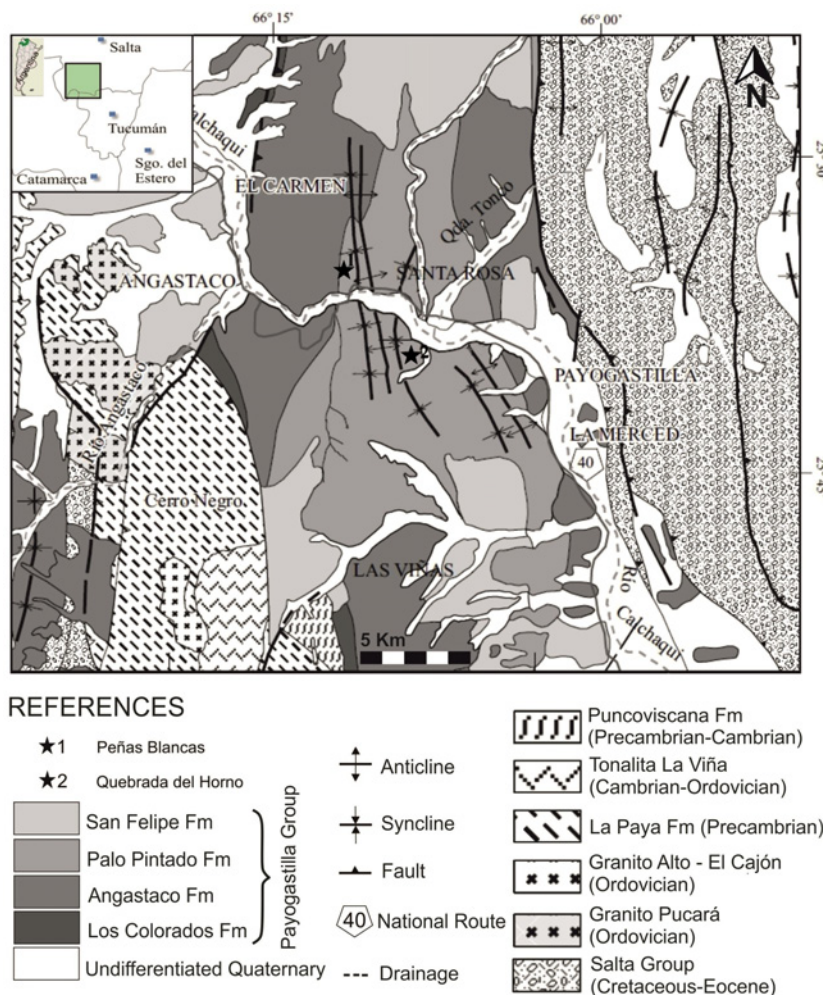
Figure 1. Map of fossiliferous outcrops (edited from Galli *et al.*, 2011).

Diagnosis. Hole feeding traces, oblong in shape and with rounded ends, occupying almost the entire space between two secondary veins. Secondary veins are never removed. The proximal ends of the traces are always in contact with the midvein and distal ends never touch leaf margins. Lateral margins of the traces always touch the secondary veins.
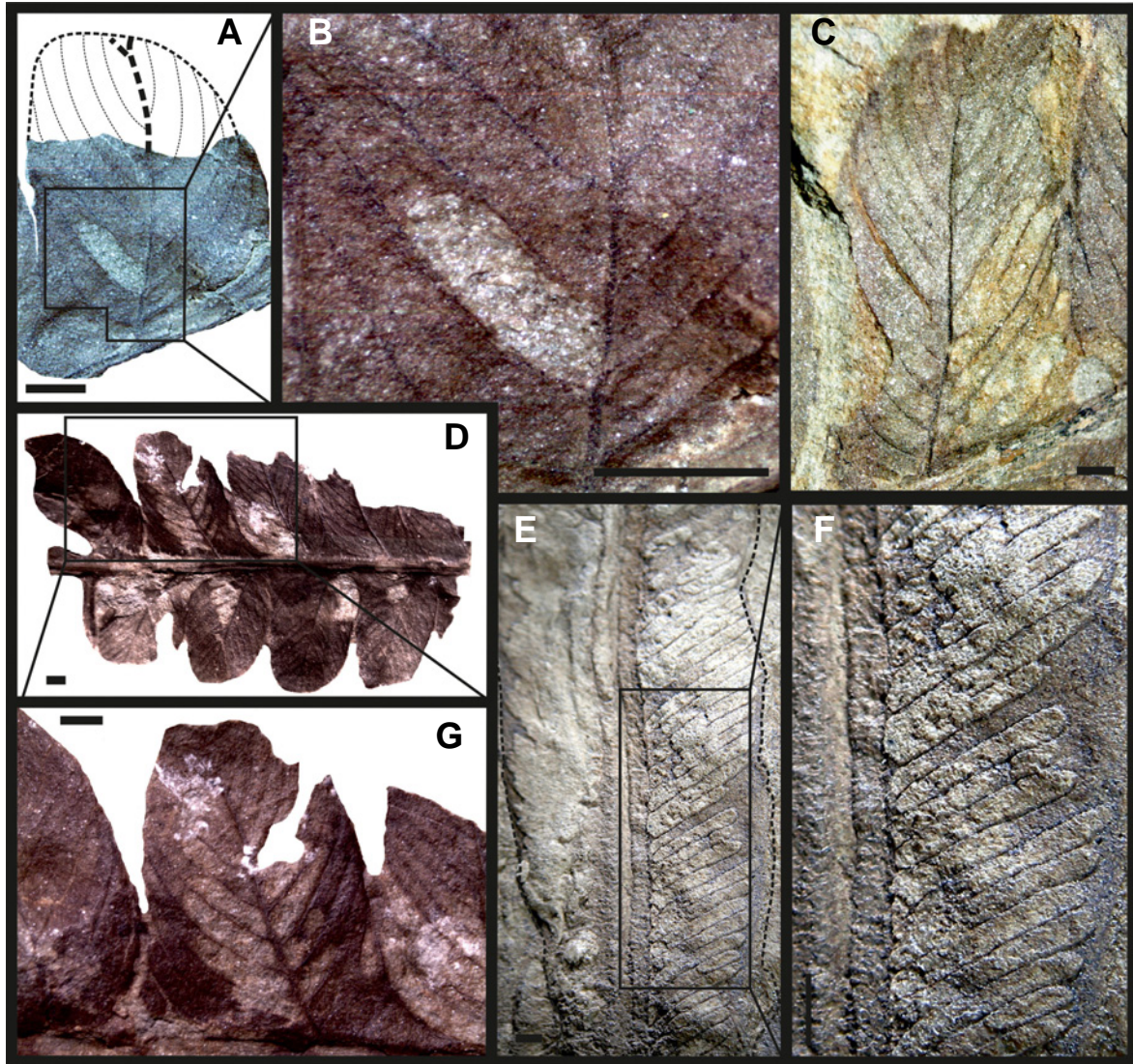
Description. *Folifenestra intervenosa* isp. nov. is found both in pinnae of *Blechnum serrulatiformis* (Figures 2E-F; 4C) and *Thelypteris interrupta* (Figures 2A-D, G; 4F). The traces are deployed to in one or both sides of the midvein (*i.e.* in both hemilaminas). The excisions are distributed either consecutively and separated by secondary veins or otherwise are isolated, but both types are never evident in the same lamina. Usually traces are located at the proximal portion of the fern lamina. The measured lengths varied from 0.45 mm to 4.12 mm. The measured widths vary from 0.26 to 0.93 mm (N= 135). In *Blechnum serrulatiformis* hole feeding excisions reach the margin of the leaf lamina, whereas in *Thelypteris interrupta* traces occupied three-fourths of hemilamina and usually they are located at the base of the leaf.

Remarks. Givulescu (1984) described the ichnospecies *Phagophytichnus circumsecans* and *P. nigromarginatus* for hole feeding traces. Originally, Givulescu (1984) included in *P. circumsecans* both marginal excisions and hole feeding damage. *P. circumsecans* differs from *Folifenestra intervenosa* isp. nov. because traces are circular to ovoidal in shape and do not occupy all of the space between the two secondary veins. *P. nigromarginatus* also differs from *F. intervenosa* isp. nov. in that the hole-feeding traces are not adjacent to the primary vein. Examples of hole feeding documented by Labandeira *et al*. (2002 p. 309; figs. 5a-c, e, f, h, i) mostly are circular to ovoidal in shape. Several samples are in contact with a primary vein, but every trace, generally did not contact both adjacent secondary veins. Labandeira *et al*. (2007) recorded "hole feeding traces in intercostal area" (p. 7; DT 78), although the tissue between the veins is not completely removed, in particular two consecutive hole-feeding traces are only separated from each other by a secondary vein. Finally, hole feeding damage documented by Gallego *et al*. (2014) are different from *F. intervenosa* isp. nov. as the hole feeding damages are not in contact with the primary vein (midrib).

Infderefolia igen. nov.

Type ichnospecies. *Infderefolia oblonga*, by monotypy.

Figure 2. A-G, *Folifenestra intervenosa* isp. nov.; **E-F**, *Infderefolia oblonga* isp. nov.; **A-D** and **G**, *Thelypteris interrupta* (CTES-IC 37, 35 holotype and 34); **E-F**, *Blechnum serrulatiformis* (CTES-IC 11 paratype); **C-G**, these samples show grouped excisions (**F** and **G**, details of **E** and **D** respectively); **A-B**, sample showing single trace. Scale bars = 1 mm.

Etymology. In reference to the type of trace. Latin, infmdere (deep cut) and folia (leaves).

Diagnosis. Surface feeding damage variable in size and shape, grouped or isolated, occupying part or all the space between two secondary veins. Only one epidermis remains. The color and hue of the excision is similar to that of the leaf lamina but clearer. Excision margins frequently contain a fine dark line.

Remarks. The diagnosis of the subfamily Folifenestrinae (Vasilenko, 2007a) contemplate both surface feeding as hole feeding damage. Thus, the ichnogenus *Infderefolia* igen. nov. is included in this subfamily together with the ichnogenus *Folifenestra*. The ichnogenus *Infderefolia* igen. nov. is assigned to surface feeding, whereas *Folifenestra* correspond with hole feeding damage.

Infderefolia oblonga igen nov. et isp. nov.
(Figures 3B; 4C)

Holotype. CTES-IC 11, traces on pinna of *Blechnum serrulatiformis* (CTES-PB 8061); (Figure 4C).

Paratype. CTES-IC 17, traces on the pinna of *Blechnum serrulatiformis* (CTES-PB 14064).

**Host.** *Blechnum serrulatiformis* (Blechnaceae).

Other material examined. CTES-IC 12; host plant, *Blechnum serrulatiformis* (CTES-PB 8062).

Provenance and stratigraphy. Quebrada del Horno outcrop; Palo Pintado Formation, Salta Province, Argentina.

Etymology. In reference to the shape of damage.

Diagnosis. Surface feeding, oblong in shape, with both ends of damage rounded. Traces occupy the entire intercostal space between two secondary veins. The primary and secondary veins are always present.

Description. *Infderefolia oblonga* igen nov. et isp. nov. was found on pinnae of *Blechnum serrulatiformis* (Figures 2E-F; 4C) and *Thelypteris interrupta*. Surface feeding occurs on one
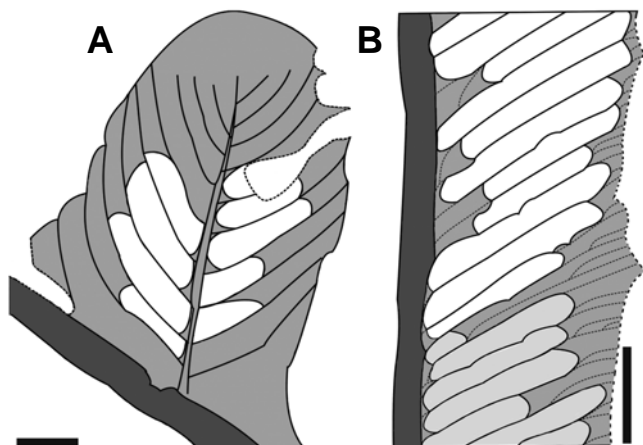
Figure 3. A, Schema showing *Folifenestra intervenosa* isp. nov. in *Thelypteris interrupta* (CTES-IC 34) and **B,** *Infderefolia oblonga* isp. nov. and *Folifenestra intervenosa* isp. nov. in *Blechnum serrulatiformis* (CTES-IC 11 paratype). White: *Folifenestra intervenosa* isp. nov.; light grey: *Infderefolia oblonga* isp. nov.; dark grey: rachis in *Thelypteris interrupta* and midvein in *Blechnum serrulatiformis*; dotted lines: leaf breakage. Scale bars = 1 mm.

or both sides of the primary vein, distributed in a consecutive series between secondary veins or as isolated surface feeding. Both types of distribution are never represented in the same lamina. The measured lengths varied from 0.76 mm to 3.43 mm. The measured widths varied from 0.24 mm to 0.47 mm (N= 32) reaching the margin of the leaf lamina.

Remarks. *Infderefolia oblonga* igen. nov. et isp. nov. differs from *Phagophytichnus gastropodinus* Givulescu (1984) as the latter ichnospecies presents an irregular arrangement on the leaf, semicircular shape and occurring in a consecutive and parallel series. *Infderefolia oblonga* igen. nov. et isp. nov. differs from window feeding traces documented by Ash (1997, p. 239, fig. 2E; p. 241, 3c,f) as the traces of the damaged leaf are arranged in a group and not isolated. By contrast, other surface feeding documented by Ash reveals an oval shape and breach the secondary veins. Wilf *et al.* (2000) described the ichnospecies *Cephaloleichnites strongi* (Wilf, Labandeira, Kress, Staines, Windsor, Allen & Johnson, 2000), which are elongated with rounded lateral borders and located between parallel veins of third-order rank. The surface feeding of *Cephaloleichnites strongi* is not adjacent to the midvein and thus, differs from *Infderefolia oblonga* igen. nov. et isp. nov.

DISCUSSION

One type of insect phytophagy on ferns (Table 1) consists principally of galleries that containing coprolites in the rachises, stems and petioles of tree ferns. These occurrences are recorded from the Lower Carboniferous to Cretaceous, mostly from the Northern Hemisphere (Seward, 1923, 1924; Rothwell & Scott, 1983; Scott & Taylor, 1983; Scott & Paterson, 1984; Rex & Galtier, 1986; Labandeira & Beall, 1990; Lesnikowska, 1990; Tidwell & Hebbert, 1992; Labandeira *et al.*, 1997; Ash, 2000; Labandeira &

Phillips, 2002; Rößler, 2000; D'Rozario *et al.*, 2011). These occurrences were reported mostly in the stems of *Psaronius* Cotta, 1832 a marattialean tree fern (Rothwell & Scott, 1983; Labandeira & Beall, 1990; Lesnikowska, 1990; Labandeira & Phillips 1996a,b; Labandeira *et al.*, 1997; Labandeira & Phillips, 2002; Rößler, 2000; D'Rozario *et al.*, 2011) and *Tempskya* Corda, 1845 a probable filicalean tree fern (Seward, 1923, 1924; Scott & Paterson, 1984; Tidwell & Hebbert, 1992). Less common occurrences of insect damage are galls (Labandeira & Phillips, 1996b; Labandeira & Phillips, 2002), piercing and sucking (Scott & Taylor, 1983; Labandeira & Phillips, 1996a) and marginal excisions (Ash, 1997; Labandeira, 2002b) which have been recorded from the Carboniferous to the Eocene of the USA. In the Southern Hemisphere, there are few records of coprolites occurring in tissues of ferns from Permian and Triassic deposits of Antarctica (Kellogg & Taylor, 2004; Slater *et al.*, 2012). Only three reports of folivory are known on Jurassic fossil ferns from Australia (Hill, 1987; McLoughlin *et al.*, 2015) and early Eocene from Argentina (Carvalho *et al.*, 2013) and one record of piercing-and-sucking on filicalean fern from Jurassic of Australia (McLoughlin *et al.*, 2015). The first evidences of folivory in ferns appeared in the Late Triassic from USA and China. These traces correspond with marginal excisions on *Cynepteris lasiophora* Ash, 1969 (Ash, 1997), and skeletonizations on *Dictyophyllum nathorstii* Zeiller, 1903 (Feng *et al.*, 2014). In Middle Jurassic from Australia have been documented hole feeding traces on *Angiopteris blackii* van Cittert, 1975 (Hill, 1987) and marginal and hole feeding damages on *Cladophlebis australis* Morris, 1845 (McLoughlin *et al.*, 2015).

Surface feeding and hole feeding damages on other groups of vascular plants, particularly seed plants are more abundant compared with those recorded on ferns (Table 2). The oldest surface feeding was described in leaves of *Comia* sp. from the Lower Permian of USA (Beck & Labandeira, 1998). De Souza Pinheiro *et al.* (2012) described surface feeding on *Glossopteris indica* Schimper, 1869 and *G. communis* Feistmantel, 1876 leaves from Lower Permian of Brazil and Gallego *et al.* (2014) also documented those damage types on *Glossopteris*, *Ginkgoites* and *Cordaites* Unger, 1850 leaves from approximately the same age in Argentina. Ash (1997) described elongate surface feeding in pinnae of *Zamites* sp. (Bennettitales) from the Upper Triassic of USA. Other occurrence bennettitaleans was reported by Banerji (2004), who documented a circular window excision on *Ptilophyllum* sp. from the Lower Cretaceous of India. Labandeira *et al.* (2002) found surface feeding with elongated shape located between secondary veins on a leaf of *Nilssonia yukonensis* Hollick, 1930 (Nilssoniales) from the latest Cretaceous of the USA. Surface feeding occurring on angiosperms were the described on two species of Zingiberales from the Upper Cretaceous and Lower Eocene of the USA (Wilf *et al.*, 2000) and those reported by Givulescu (1984) on *Acer integerrimum* Viviani, 1833 from Upper Miocene of Romania. Hole feeding damage is more abundant in the fossil record and older comparing with surface feeding. The fossil record of hole feeding is
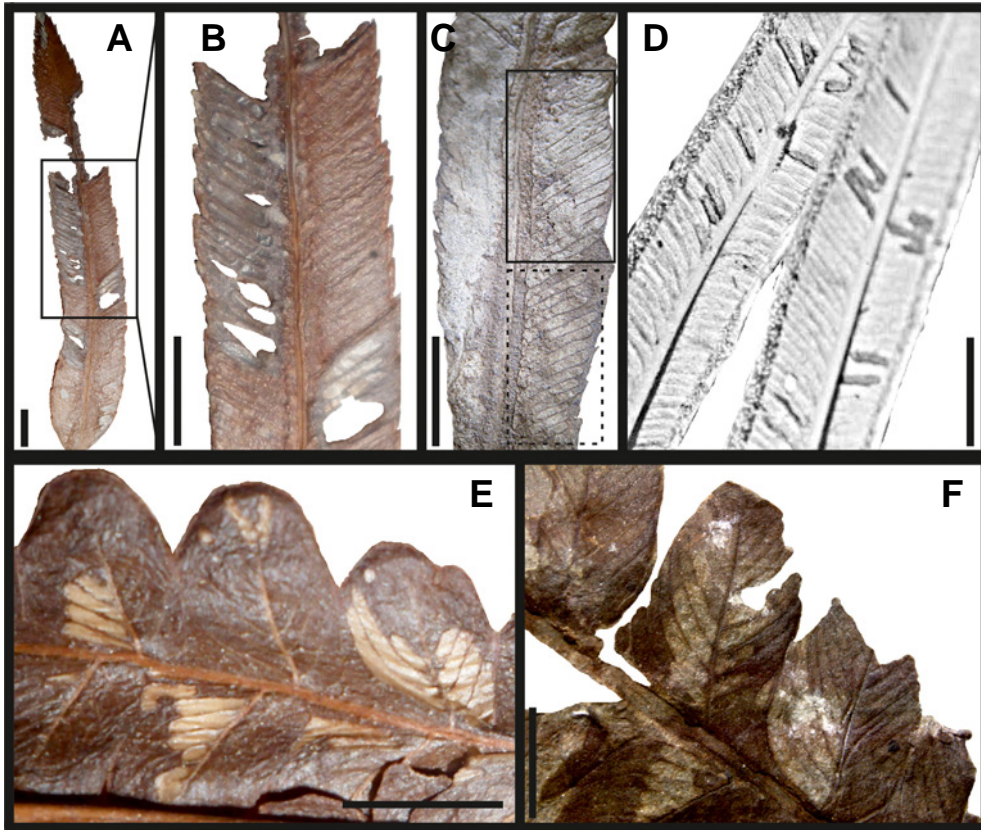
Figure 4. Comparison of traces identified in fossil plants with extant samples. **A**, *Blechnum serrulatum*, the image shows surface feeding and hole feeding between the secondary veins; **B**, Detail of traces in **A**; **C**, *Blechnum serrulatiformis* (CTES-IC 11 paratype), surface feeding and hole feeding identical at those observed in **A** and **B**. Dotted line corresponds with surface feeding (*Infderefolia oblonga* isp. nov.) and continuous line with hole feeding (*Folifenestra intervenosa* isp. nov.). **D,** image edited from Patra & Bera (2007), it can to observe surface feeding on pinna of *Pteris vittata*; **E** and **F**, *Thelypteris interrupta*; **E,** an extant sample that presents surface feeding; **F**, fossil sample (CTES-IC 34) showing the same traces that in **E**. Scale bars = 5 mm.

almost continuous since Upper Carboniferous (Castro, 1997; Trout *et al*., 2000) and extends to Pliocene (Straus, 1977). Until the Mid-Lower Cretaceous these traces were described on gymnosperms (Medullosales, Gingantopteridales, Cordaitales, Cycadales, Peltaspermales, Glossopteridales, Ginkgoales) and Sphenopsids, predominately from the Northern Hemisphere (North America and Europe), by Ash (1972, 1997), Castro (1997), Grauvogel-Stamm & Kelber (1996), Beck & Labandeira (1998), Labandeira (2006), Trout *et al*. (2000), Glasspool *et al*. (2003), Labandeira & Allen (2007), Vasilenko (2007a). Moreover, there are a few pre-Cretaceous records in South America that include circular to slot holes on *Cordaites*, *Gangamopteris* McCoy, 1875 and *Glossopteris* leaves from the Lower Permian of Brazil (Adami-Rodrigues *et al*., 2004; De Souza Pinheiro *et al.,* 2012); circular to elliptical hole feeding traces in *Glossopteris wilsonii* Seward, 1914 and *Ginkgoites eximia* Feruglio, 1942 from the Early Permian of Argentina (Gallego *et al*., 2014); hole and marginal feeding, leaf-mines and skeletonizations in different plant species from Middle-Late Triassic of Argentina (Adami-Rodrigues *et al*., 2012) and hole feeding on leaves of *Taeniopteris* sp. from Upper Triassic of Chile (Gallego *et al*., 2003). From the mid-Cretaceous to Neogene, hole-feeding damages were described exclusively on angiosperms from the

Northern Hemisphere (Straus, 1977; Givulescu, 1984; Scott *et al*., 1992; Stephenson & Scott, 1992; Labandeira, 1998; Wilf *et al*., 2000; Labandeira, 2002a,b; Labandeira *et al*., 2002; Krassilov, 2008; Krassilov & Shuklina, 2008; Wappler, 2010; Wappler & Denk, 2011). For the Southern Hemisphere, the only for circular hole feeding is on *Nectandra saltensis* Anzótegui, 1988 and *Sapium haematospermoide* Anzótegui & Horn, 2011 from the Late Miocene of Argentina (Horn *et al*., 2011). The extensive record of hole feeding in angiosperms during the mid-Cretaceous, is coincident with the extinction of most gymnosperms (Niklas *et al*., 1983; Taylor *et al*., 2009), which could demonstrate a variation and shift in the preferences of insects to alternative host plants.

Currently, the predominant type of fern-insect interaction is herbivory (Cooper-Driver, 1985a; Mehltreter, 2010), although mutualism are also know (Auerbach & Hendrix, 1980; Cooper-Driver, 1985b; Tryon, 1985). Some studies revealed that phytophagous insects prefer to feed on angiosperms more than on ferns (Brues, 1920; Soo Hoo & Fraenkel, 1964; Hendrix, 1980), which would explain the scanty record of these associations in both in extant and fossil ferns. Two opposite explanations about the preference of insects to angiosperm compared with ferns were proposed. One explanation is that ferns are poorly attacked by insects,

Table 2. Fossil record of surface feeding (**SF**) and hole feeding (**HF**), on sphenopsids and seed plants.

Interaction type	Taxa	Age	Author
HF	*Laburnum* sp. (Fabales)	Pliocene	Straus (1977)
HF	*Parrotia persica* (Saxifragales)		
HF	*Sapium* sp. (Malpighiales)	late Miocene	Horn *et al.* (2011)
HF	*Nectandra saltensis* (Laurales)		
HF	*Acer integerrimum* (Sapindales)	late Miocene	Givulescu (1984)
HF	*Alnus* sp. (Fagales)		
HF	*Tremophyllum tenerrimum* (Urticales)	late Oligocene	Wappler (2010)
HF	*Alnus menzelii* (Fagales)		
HF	*Betula leopoldae* (Fagales)		
HF	Angiosperm sp. indet.		
HF	*Alnus parvifolia* (Fagales)	middle Eocene	Labandeira (2002b)
HF	*Rhus malloryi* (Sapindales)		
HF	*Ulmus* sp. (Urticales)		
HF	*Sassafras hesperia* (Laurales)		
HF	Angiosperm sp. indet.	middle Eocene	Labandeira (2002a)
SF	*Zingiberopsis isonervosa* (Zingiberales)	early Eocene	Wilf *et al.* (2000)
HF	Angiosperm sp. indet.	Eocene	Stephenson & Scott (1992)
HF	'*Corylites*' *hebridicus*	Paleogene	Wappler & Denk (2011)
HF	*Ptemspermites cordata* (Dilleniidae)	Paleocene	Labandeira *et al.* (2002)
HF	Angiosperm sp. indet.		
HF	Ulmaceae sp. Indet.		
HF	*Liriodendrites bradacii* (Magnoliales)		
HF	"*Dryophyllum*" *subfulcatum* (Magnoliales)		
HF	"*Dryophyllum*" *tennesseensis* (Magnoliales)		
HF	*Grewiopsis saponaria* (Platanaceae)	Late Cretaceous	Labandeira *et al.* (2002)
HF	*Erlingdorfia montana* (Platanaceae)		
HF	"*Rhamnus*" *cleburni* (Rhamnaceae)		
HF	*Bisonia niemi* (Laurales)		
HF	*Marmarthia trivialis* (Laurales)		
SF	*Nilssonia yukonensis* (Nilsssoniales)		
SF	*Zingiberopsis attenuata* (Zingiberales)	Late Cretaceous	Wilf *et al.* (2000)
HF	Angiosperm sp. Indet.	Late Cretaceous	Scott *et al.* (1992)
HF	*Eocercidiphyllites glandulosus* (Cercidiphyllales)	middle Cretaceous	Krassilov & Shuklina (2008)
HF	*Dewalquea gerofitica* (proangiosperm)	middle Cretaceous	Krassilov (2008)
HF	*Crassidenticulum* sp. (Laurales)	middle Cretaceous	Labandeira (1998)
HF	*Pandemophyllum* (Laurales)		
SF	*Ptilophyllum* sp. (Bennettitales)	Early Cretaceous	Banerji (2004)
SF?	*Otozamites feistmanteli* (Gnetopsid)	Jurassic	McLoughlin *et al.* (2015)
HF	*Gontriglossa verticilliata* ("Gnetopsid")	Late Triassic	Labandeira (2006)
HF	*Yabiella mareyesiaca* ("Gnetopsid")		
HF	*Zamites* sp. (Bennettitales)	Late Triassic	Ash (1997)
SF	*Zamites* sp. (Bennettitales)		
HF	*Schizoneura paradoxa* (Sphenopsid)	Late Triassic	Grauvogel-Stamm & Kelber (1996)
HF	*Marcouia neuropteroides* (uncertain affinity)	Late Triassic	Ash (1972)
HF	*Glossopteris* cf. *G. ampla* (Glossopteridales)	late Permian	Cariglino & Gutiérrez (2011)
HF	*Pursongia* sp. (Peltaspermales)	late Permian	Vasilenko (2007a)
HF	*Gigantonoclea hallei* (Gigantopteridales)	late Permian	Glasspool *et al.* (2003)
HF	*Gigantonoclea lagrelii* (Gigantopteridales)		
SF	*Ginkgoites feruglioi* (Ginkgoales)		
SF	*Ginkgoites eximia* (Ginkgoales)		
SF	*Glossopteris wilsonii* (Glossopteridales)	early Permian	Gallego *et al.* (2014)
SF	*Cordaites* sp. (Cordaitales)		
HF	*Glossopteris wilsonii* (Glossopteridales)		
HF	*Ginkgoites eximia* (Ginkgoales)		

Continues.

Table 2. Continuation.

Interaction type	Taxa	Age	Author
SF	*Glossopteris indica* (Glossopteridales)		
SF	*Glossopteris communis* (Glossopteridales)		
HF	*Cordaites hislopii* (Cordaitales)		
HF	*Gangamopteris obovata* (Glossopteridales)		
HF	*Gangamopteris buriadica* (Glossopteridales)	early Permian	De Souza Pinheiro *et al.* (2012)
HF	*Glossopteris occidentalis* (Glossopteridales)		
HF	*Glossopteris indica* (Glossopteridales)		
HF	*Glossopteris communis* (Glossopteridales)		
HF	*Glossopteris* sp. (Glossopteridales)		
HF	*Autunia* cf. *A. conferta* (Peltaspermales)	early Permian	Labandeira & Allen (2007)
HF	*Russellites taeniata* (Cycadophyta)		
HF	*Cordaites hislopii* (Cordaitales)	early Permian	Adami-Rodrigues *et al.* (2004)
SF	*Comia* sp. (Peltaspermales?)		
HF	*Gigantopteridium americanum* (Gigantopteridales)	early Permian	Beck & Labandeira (1998)
HF	*Cathaysiopteris yochelsonii* (Gigantopteridales)		
HF	*Taeniopteris* sp. (Ginkgoales?)		
HF?	*Ginkgoites eximia* (Ginkgoales)	early Permian	Cúneo (1987)
HF	*Macroneuropteris* sp. (Medullosales)	Late Carboniferous	Trout *et al.* (2000)
HF	*Mixoneura wagneri* (Medullosales)	Late Carboniferous	Castro (1997)

probably because of their low nutritional value (Coe *et al.*, 1987), the presence of anti-herbivore chemical compounds (Swain & Cooper-Driver, 1973; Hendrix, 1977, 1980; Cooper-Driver, 1978, 1990; Rowell *et al.*, 1983), and the absence of nutritionally attractive like fruits, seeds and flowers (Mehltreter, 2010). A complementary explanation proposes that many extant groups of insects have had a close evolutionary history with angiosperms that would be reflected in the higher phytophagy levels on angiosperms (Zwölfer, 1978; Strong *et al.*, 1984). Some authors suggest that ferns reached the peak diversity in the Carboniferous and subsequently declined, which would explain the low number of interactions recorded, both in post-Carboniferous fossil ferns as extant species, if these are compared with angiosperms (Niklas *et al.*, 1983; Tahvanainen & Niemelä, 1987). In contrast, other authors have proposed a hypothesis that ferns exhibit the similar levels of insect phytophagy to angiosperms (Balick *et al.*, 1978; Auerbach & Hendrix, 1980; Hendrix & Marquis, 1983). For instance, ferns present proportions of leaf damage (5% to 15%) (Balick *et al.*, 1978; Hendrix & Marquis, 1983; Mehltreter & Tolome, 2003; Mehltreter *et al.*, 2006) that are similar to those reported for angiosperms in tropical forests (Lowman, 1984, 1985; Coley & Aide, 1991; Williams-Linera & Baltazar, 2001). In addition, Hummel *et al.* (2008) demonstrated that leaf tissues of ferns and seed plants provide similar amounts and types of nutrients.

Despite their abundant fossil record, the ichnotaxonomy of hole feeding, was poorly treated in the literature. The few records that have documented hole feeding damages were included in the ichnogenus *Phagophytichnus* van Amerom, 1966 (Straus, 1977; Givulescu, 1984), for which several morphologies of hole feeding were described from the early Pliocene of Germany Straus (1977). Following Straus

(1977), Givulescu (1984) documented examples of hole feeding in the same ichnospecies and established additional icnotaxa from the late Miocene of Romania. Nevertheless, the ichnogenus *Phagophytichnus* was created originally by van Amerom (1966) for marginal excisions. Sarzetti *et al.* (2008) proposed to restrict *Phagophytichnus* only for margin-feeding traces as defined originally by van Amerom (1966). This restriction is because marginal and hole feeding damage involves two distinct morphological patterns which are the result of two different feeding behaviors, related to particular insect mouthparts design and strategies for energy conservation (Edwards & Wratten, 1980). With hole feeding, few studies that have documented surface feeding provided formal ichnotaxonomic assignments. The first ichnospecies of surface feeding was described by Givulescu (1984), who defined *Phagophytichnus gastropodinus* in *Acer integerrimum* (Sapindales). Although the author did not mention this ichnospecies as surface feeding, the characters showed by the author in the figures (p. 130, pl. VI, fig. 1) demonstrated that P. *gastropodinus* represented a surface feeding. Later, Wilf *et al.* (2000) described the ichnospecies *Cephaloleichnites strongi*, assigned to beetles, which consisted in surface feeding that formed as linear strips along parallel veins. More recently, Vasilenko (2007a) defined the ichnogenus *Folifenestra*, assigned to the single ichnospecies dubia, to include traces he called "window feeding". However, the illustrated material suggests that the author was referring most likely to hole feeding instead surface feeding excisions. It is proposed here to emend the diagnosis of *Folifenestra* to include only hole feeding excisions and define the new ichnogenus *Infderefolia* igen. nov. for surface feeding.

Based on shape, pattern and arrangement on the leaf, *Folifenestra intervenosa* and *Infderefolia oblonga* igen. nov.

et isp. nov., may be produced by leaf beetles (Coleoptera: Chrysomelidae). Several studies documenting the feeding behavior of leaf beetles on extant plants showed similar patterns to the new ichnospecies described here. For example, Patra & Bera (2007) demonstrated that adults of at least one species of Chrysomelidae, *Schenklingia bhaumiki* Basu & Sen Gupta, 1982 (Tribe Alticini) feeds on ten fern species of the families Adiantaceae, Thelypteridaceae, Polypodiaceae, Nephrolepidaceae and Pteridaceae. The adults *Schenklingia bhaumiki* produce window excisions in *Pteris vittata* Linné, 1753 (Figure 4D) consuming selectively the tissues between veins. The beetles move on the adaxial or abaxial surface of the fronds, initially exploring the central region of the pinnule, removing all tissues except the epidermis that later can be consumed, creating holes in the lamina. This evidence could indicate that both *F. intervenosa* isp. nov. and *I. oblonga* igen. nov. et isp. nov. are the result of the same species, a phenomenon recently recognized in a study of herbivory of lowland modern tropical forest (Carvalho *et al.*, 2014). Window excisions similar to *I. oblonga* igen. nov. et isp. nov. also were recorded on extant angiosperms. Strong (1977) described four different types of feeding behaviors of beetles in Zingiberales monocotyledon angiosperms. One type consisted in scraping across the plant surface, which was called "strip mining" (Strong, 1977). These traces were attributed to four species of chrysomelids, *Chelobasis perplexa* Baly, 1858, *Xenarescus monocerus* Olivier, 1808, *Nympharescus separatus* Baly, 1858 (all Tribe Arescini) and *Cephaloleia consanguinea* Baly, 1885 (Tribe Cephaloliini). Magalhães *et al*. (2012) identified traces which are comparable with *I. oblonga* igen. nov. et isp. nov. on leaves of *Aechmea blanchetiana* Baker, 1955 (Bromeliaceae) produced by *Acentroptera pulchella* Guérin-Méneville, 1830 (Chrysomelidae, Hispinae). Beetles scrape the lamina of *A. pulchella* leaving only few layers of cells of mesophyll and epidermis. Wilf *et al*. (2000) described the ichnospecies *Cephaloleichnites strongi* that represent surface feeding in fossil leaves of Zingiberales. These authors attributed this ichnospecies to members of the Tribe Cephaloliini (Coleoptera: Chrysomelidae). However, García-Robledo *et al*. (2007) and García-Robledo & Staines (2008) described surface feeding with a similar morphology as *C. strongi* in extant Zingiberales species caused by the Curculionidae (Coleoptera) and larval stages of Pyralidae and Choreutidae (Lepidoptera). These authors proposed these insects as potential producers of *C. strongi*. Chrysomelidae also are recorded as body fossils since the Late Jurassic (Ponomarenko, 2002), mainly from the Northern Hemisphere (Santiago-Blay, 1994), although a few records occur in South America. In Argentina, there is a description of a chrysomelid from the Paleogene (Cockerell, 1926). Currently, this family is recorded in the central and northern part of Argentina (Blackwelder, 1957; Cabrera *et al*., 1997; Defagó *et al*., 2010; Cabrera & Rocca, 2012).

Extant samples of *Blechnum serrulatum* (Blechnaceae) and *Thelypteris interrupta* (Thelypteridaceae) housed in the CTES Herbarium were investigated for insect damage and were analyzed to compare their morphology with *F. intervenosa*

isp. nov. and *I. oblonga* igen. nov. et isp. nov.. The insect damage either on *B. serrulatum* and *T. interrupta* are similar to *I. oblonga* igen. nov. et isp. nov.. Traces are oblong excisions with both ends very rounded and arranged faithfully between two secondary veins (Figures 4A). They are grouped, without remove the upper epidermis and resulting in window excisions. As in *I. oblonga* igen. nov. et isp. nov., extant excisions occupy the entire intercostal area. In *T. interrupta* hole-feeding traces were also recorded, but these traces are not as comparable to *F. intervenosa* isp. nov. because both the secondary veins and the primary vein of the pinnae are consumed. Unfortunately, the producer of the traces in extant ferns was not identified because there are no current records of insects associated with extant species of *T. interrupta* and *B. serrulatum* (Farias, pers. comm. 2013). More work on extant fern species is needed in order to assess the potential producer of *I. oblonga* igen. nov. et isp. nov. and *F. intervenosa* isp. nov..

CONCLUSIONS

This study reports the second fossil record of fern-insect interactions from Argentina and the first record of window excisions on fossil ferns. Despite that the producer of the new ichnospecies *Infderefolia oblonga* igen. nov. et isp. nov. and *Folifenestra intervenosa* isp. nov. remains unclear, both ichnogenera reveal a Neogene fern-insect interaction and is a contribution to sparse record of fern-insect relationships. Moreover, the Palo Pintado Formation offers a potential opportunity to study novel insect interactions of the past. Further exploration is needed to achieve greater understanding of the trophic interaction of this biota from the Miocene of Argentina.

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