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PLANT-INSECT INTERACTIONS IN A *GLOSSOPTERIS* FLORA FROM THE LA GOLONDRINA FORMATION (GUADALUPIAN–LOPINGIAN), SANTA CRUZ PROVINCE, PATAGONIA, ARGENTINA

BÁRBARA CARIGLINO[1,2] AND PEDRO R. GUTIÉRREZ[1,3]

[1]División Paleobotánica y Paleopalinología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Ángel Gallardo 470, C1405DJR, Buenos Aires, Argentina.

[2]Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT).

[3]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

barichi10@gmail.com, prgutiérrez@macn.gov.ar

Abstract. The first description of insect-plant interaction in a *Glossopteris* flora from the Permian of Argentina (La Golondrina Formation, Santa Cruz) is presented. Four specimens are described; these are referred to *Glossopteris browniana* (Brongniart), *G. damudica* (Feistmantel), and *G.* sp. cf. *G. ampla* Archangelsky. Different types of interaction recorded include marginal feeding and oviposition. This is the first evidence of insect-damage in the flora from the La Golondrina Formation, and also presently the only formal description of this kind available for a Paleozoic megaflora in Argentina.

Key words. Plant-insect interaction. La Golondrina Formation. Permian. *Glossopteris.* Santa Cruz. Argentina

Resumen. INTERACCIONES PLANTA-INSECTO EN LA FLORA DE *GLOSSOPTERIS* DE LA FORMACIÓN LA GOLONDRINA (GUADALUPIANO–LOPINGIANO), PROVINCIA DE SANTA CRUZ, PATAGONIA, ARGENTINA. Se presenta aquí la primera descripción de daño de insecto en una flora de *Glossopteris* del Pérmico de Argentina (Formación La Golondrina, Santa Cruz). Se describen 4 ejemplares de hojas de *Glossopteris* referidas a *G. browniana* (Brongniart), *G. damudica* (Feistmantel) y *G.* sp. cf. *G. ampla* Archangelsky. Se registran diferentes tipos de interacción, incluyendo daño marginal y oviposición. Esta es la primera evidencia de daño por insectos en la flora de la Formación La Golondrina, así como la única descripción formal actualmente disponible para una megaflora del Paleozoico en la Argentina.

Palabras clave. Interacción planta-insecto. Formación La Golondrina. Pérmico. *Glossopteris.* Santa Cruz. Argentina.

The fossil record of plant-insect interactions begins in the Late Silurian (Edwards *et al.*, 1995) with the finding of plant matter within insect coprolites. More direct evidence was observed in stems of Devonian *Rhynia*, with apparent injuries produced by piercing-and-sucking caused by arthropods (Kevan *et al.*, 1975; Chaloner *et al.*, 1991). However, it has been questioned whether if these marks had or not a biotic origin (Rolfe, 1985; Scott *et al.*, 1992). Unequivocal evidence of plant-insect interactions comes from the Carboniferous, where a considerable amount of fossil flora and arthropods have been found in association, and observable leaf damage has been identified as the product of insect attacks during life of the plant (Chaloner *et al.*, 1991; Scott *et al.*, 1992; Shear and Selden, 2001).

Phytophagy can occur in two different ways: detritivory, *i.e.*, consumption of dead plant matter; or herbivory or consumption of plant tissue while the plant is still alive. In order to distinguish detritivory and any other form of plant damage (*i.e.*, fungal activity, physical trauma) from biotic damage produced during life of the plant (*i.e.*, herbivory), fossil material must bear an injury reaction, also known as tissue reaction or rim reaction (Chaloner *et al.*, 1991; Labandeira, 1998; Taylor *et al.*, 2009). The presence of necrotic tissue implies that the injury occurred while the plant was alive. However, some fungal attacks can produce necrotic tissue too (Scott *et al.*, 1992). Thus, careful analysis of injury patterns and specific types of damage —sometimes attributable to an identifiable culprit— is also good support to infer insect activity on the plant (Labandeira, 1998).

It has been suggested that during most of the Paleozoic detritivory was a more common feeding mode than herbivory (Chaloner *et al.*, 1991; Scott *et al.*, 1992; Labandeira, 1998). By the Late Pennsylvanian, herbivory became more diverse; this is evidenced by the record of fossil droppings

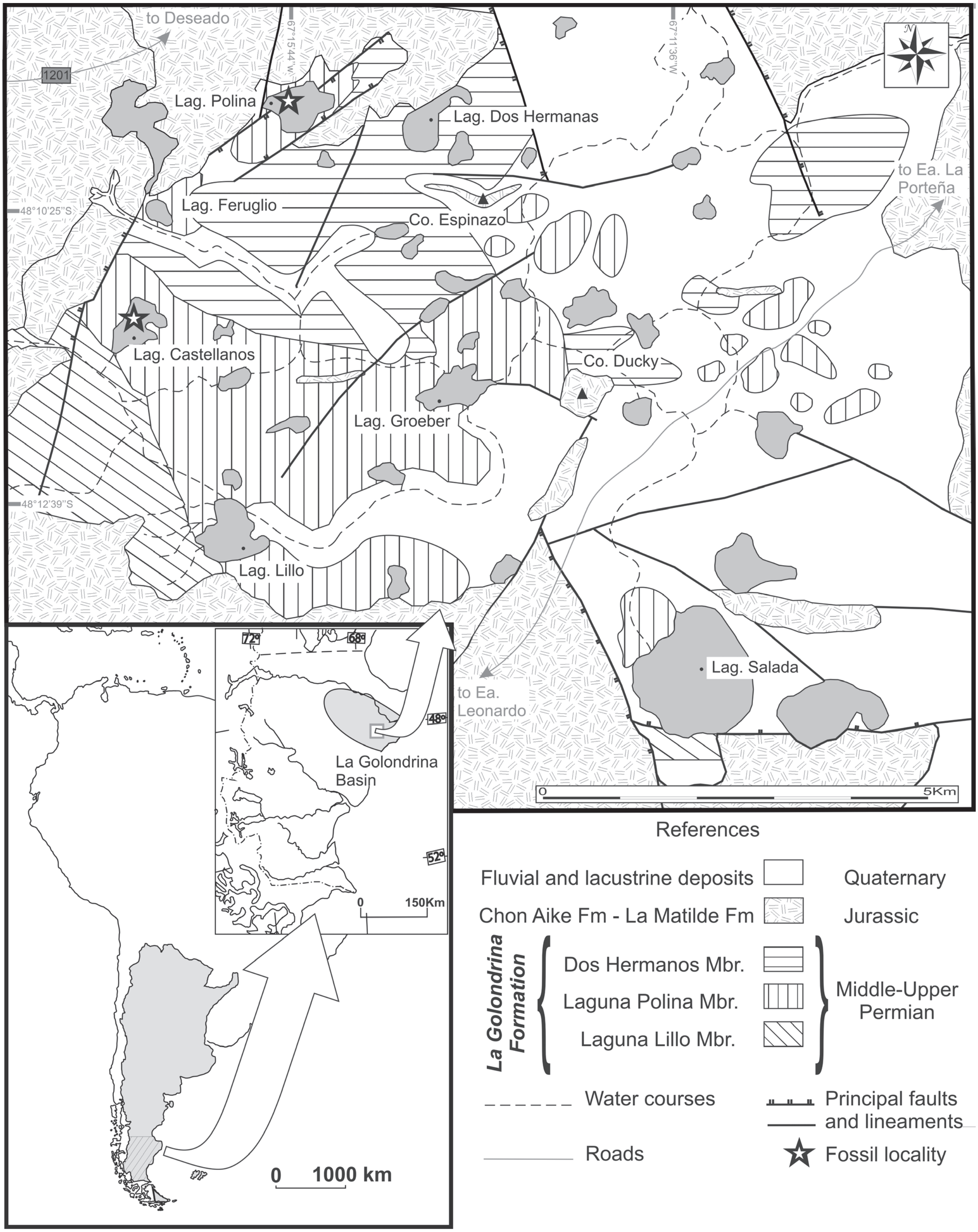

Figure 1. Geological map showing fossil localities (Laguna Polina and Laguna Castellanos) mentioned in this study (modified from Panza, 1995) / *Mapa geológico mostrando las localidades fosilíferas (Laguna Polina y Laguna Castellanos) mencionadas en este estudio (modificado de Panza, 1995).*

(coprolites), arthropod gut contents with spore exines and other plant tissues, wood borings, and leaf damage (Chaloner *et al.*, 1991).

In relation to leaf damage, diverse types of insect-plant interactions have been defined and organized in series of different functional feeding groups, as well as oviposition, and fungal attack (Labandeira *et al.*, 2007).

The aim of this paper is to present the first evidence of insect-plant interaction in fossils from the La Golondrina Formation. It is also the first detailed description of insect damage on a *Glossopteris* flora for the Permian of Argentina, in addition to being the oldest record in the region for both external foliage feeding and oviposition (Sarzetti *et al.*, 2009).

The record of plant-insect interaction in Gondwana is not as well studied as it is for the northern hemisphere. Most of the evidence available comes from South Africa (Prevec *et al.,* 2009), and it is only recently that more in-depth studies have been carried out in South America, namely in Brazil (Guerra-Sommer, 1995; Adami-Rodrigues and Ianuzzi, 2001; Adami-Rodrigues *et al.*, 2004a-b). Thus, the importance of this study lies in the fact that it will allow further comparisons with similar interactions in other areas, and improve our understanding of Late Paleozoic environments in Gondwana, particularly those referred to South American Neopaleozoic biotas.

MATERIAL AND METHODS

The material presented herein is housed in the Paleobotany Collection at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina. While performing a revision of the La Golondrina fossils housed there, one of the authors (B.C.) identified clear herbivory damage on some *Glossopteris* leaves collected by S. Archangelsky and R. Cúneo at Estancia La Golondrina (Santa Cruz, Fig. 1) during a fieldtrip in 1988. The material consists of three fragmented leaves of *Glossopteris*, in which not only the reaction tissue is observed, but also very particular feeding patterns can be identified, in addition to one leaf with oviposition marks on the midrib and lamina.

Specimens were photographed using a Canon Powershot S5IS (8.0 megapixels) digital camera. A Nikon SMZ800 stereomicroscope and a Nikon DS-Fi1-U2 digital camera were used for detailed analysis and illustration.

GEOLOGICAL SETTING

The La Golondrina Formation is divided into three members, from bottom to top, *i.e.*, the Laguna Lillo, Laguna Polina, and Dos Hermanos members (Jalfin, 1987, 1990; Jalfin *et al.*, 1990; Archangelsky *et al.*, 1996). The total sedimentary sequence is approximately 2200 m thick, and composed mostly of Late Paleozoic continental sandstones and intercalated gravels and shales (Jalfin, 1990; Archangelsky *et al.*, 1996; Andreis, 2002). The stratotype of the La Golondrina Formation was described in the Laguna Polina area (Archangelsky, 1959; Jalfin, 1987; Archangelsky *et al.*, 1996), where only the middle and upper members are present. The sequence consists of greenish-grey, fine to medium-grained sandstone beds (coarser at the top), dominated by wackestones and arkoses, intercalated with rich fossiliferous beds of silt- and claystone containing a flora of *Glossopteris* (Archangelsky, 1959; Panza, 1995; Cariglino *et al.*, 2009). The megaflora of the La Golondrina Formation was assigned to the *Dizeugotheca* Superbiozone (Archangelsky and Cúneo, 1984), and therefore a Middle to Late Permian age was inferred (Archangelsky, 1992; Archangelsky *et al.*, 1996; Archangelsky, 2006).

Fossils were collected along the margins of two dry lagoons, Laguna Polina (300 m South of Km 140.5 on Provincial Highway 1201), and Laguna Castellanos (~3760 m SW from Laguna Polina) (Fig. 1). At these localities there are outcrops with abundant fossils of the middle member of the La Golondrina Formation. Most specifically, the lower section of the sequence is exposed at Laguna Polina, while the upper part appears at Laguna Castellanos (Jalfin, 1987; Archangelsky *et al.*, 1996).

DESCRIPTION OF SPECIMENS

Specimen BA-Pb-13832 (Fig. 2.1–3)

Material. Fragment of a *Glossopteris browniana* Brongniart leaf, 5.5 cm long and 2.5 cm wide. No apex or base preserved. The left side presents an isolated, discontinuous, deep C-shaped excision (~10 mm long), rimmed with a thin, but noticeable reaction tissue, not reaching the midrib. The excision is not continuous, but irregularly scalloped.

Locality. Laguna Polina, Estancia La Golondrina, Santa Cruz (Fig. 1).

Formation and Age. La Golondrina Formation, lower part of the Laguna Polina Member, Permian.

Specimen BA-Pb-13833 (Fig. 3.1–4)

Material. Middle to apical fragment of *Glossopteris damudica* Feistmantel leaf showing both the left and right mar-

gins damaged by discontinuous external feeding. Irregularly shaped excisions rimmed by a thin reaction tissue. Excisions do not reach the midrib.
Locality. Laguna Polina, Estancia La Golondrina, Santa Cruz (Fig. 1).
Formation and Age. La Golondrina Formation, lower part of the Laguna Polina Member, Permian.

Specimen BA-Pb-13874 (Fig. 4.1–3)
Material. Fragment of a medial part of *Glossopteris* sp. cf. *G. ampla* Archangelsky leaf, 5 cm wide. No apex and base preserved. Left margin with circular excisions, ~2.5 mm in diameter, vertically aligned, with a distance of 2–2.5 mm between each excision, sometimes arranged closer. Excisions are bordered by a thin rim of reaction tissue. There are circular to subcircular marks on the blade, 2.5 to 2.8 mm in diameter, also vertically aligned.
Locality. Laguna Castellanos, Estancia La Golondrina, Santa Cruz (Fig. 1).
Formation and Age. La Golondrina Formation, upper part of Laguna Polina Member, Permian.

Specimen BA-Pb-13876 (Fig. 5.1–4)
Material. A very fragmented leaf of *Glossopteris* cf. *G. ampla* Archangelsky with only the left part of lamina preserved. No apex or base. Ovoidal marks (less than 1 mm in diameter)

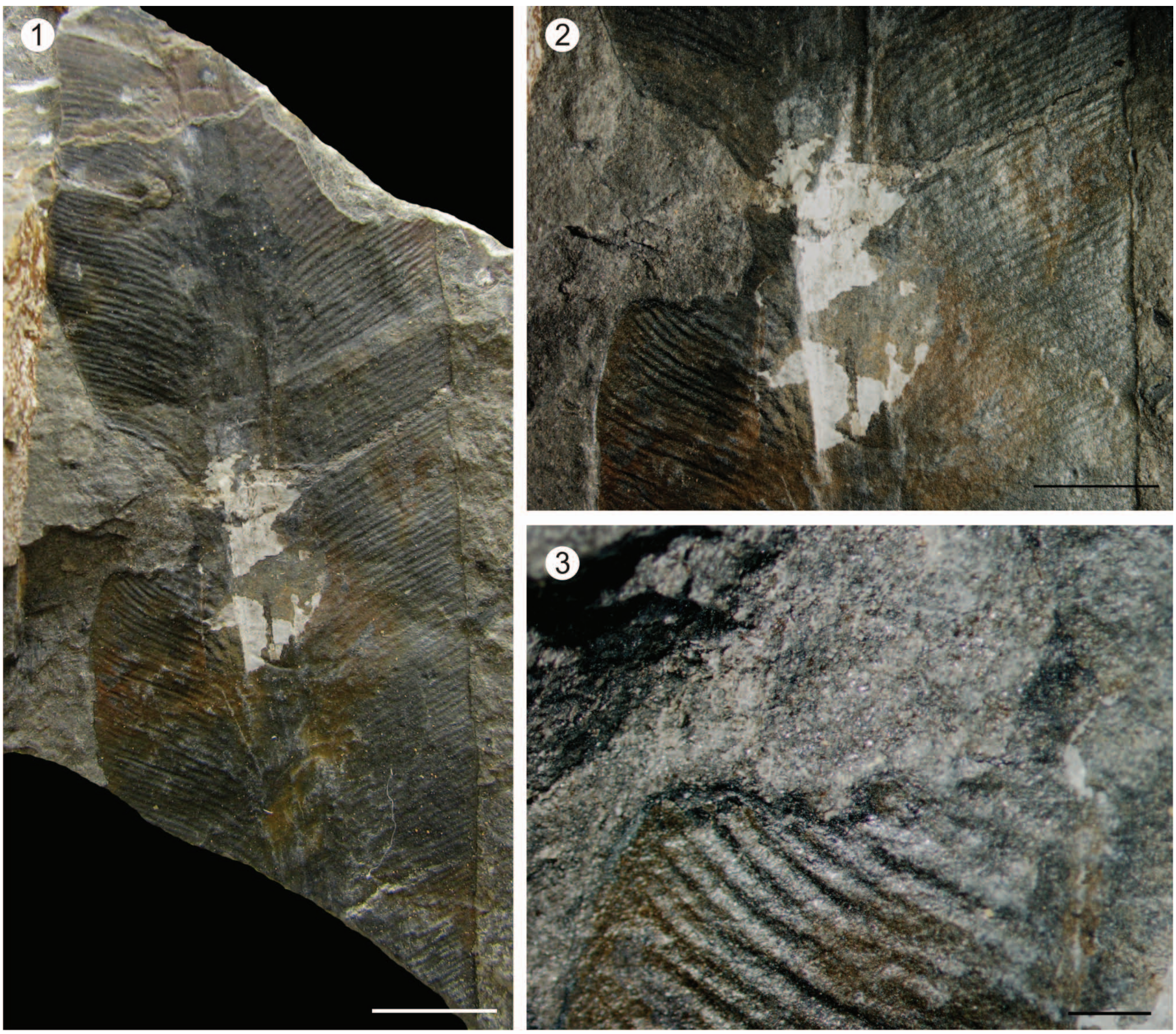

Figure 2.1–3, BA Pb-13832, ***Glossopteris browniana*** Brongniart 1828, discontinuous marginal damage / **Glossopteris browniana** *Brongniart 1828, daño marginal discontínuo*; **2–3**, Detail of scalloped marginal damage / *Detalle de daño marginal festoneado.*

present on midrib, and apparently on blade too. Marks are randomly scattered, not following a defined pattern of oviposition.

Locality. Laguna Castellanos, Estancia La Golondrina, Santa Cruz (Fig. 1).

Formation and Age. La Golondrina, upper part of Laguna Polina Member, Permian.

DISCUSSION

This is the first evidence of insect-plant interactions in the flora from the La Golondrina Formation, Santa Cruz Province, Argentina. Furthermore, it is the first description of detailed insect damage on *Glossopteris* leaves from Argentina. Some authors (Labandeira, 1998; Ianuzzi and Labandeira, 2008) have mentioned insect-plant interactions in Ginkgoales from the Lower Permian of the Río Genoa Formation (Cúneo, 1987); however, no formal descriptions were provided. In any case, these insect-plant interactions on Ginkgoales would be the oldest record of insect-plant interaction known from Argentina.

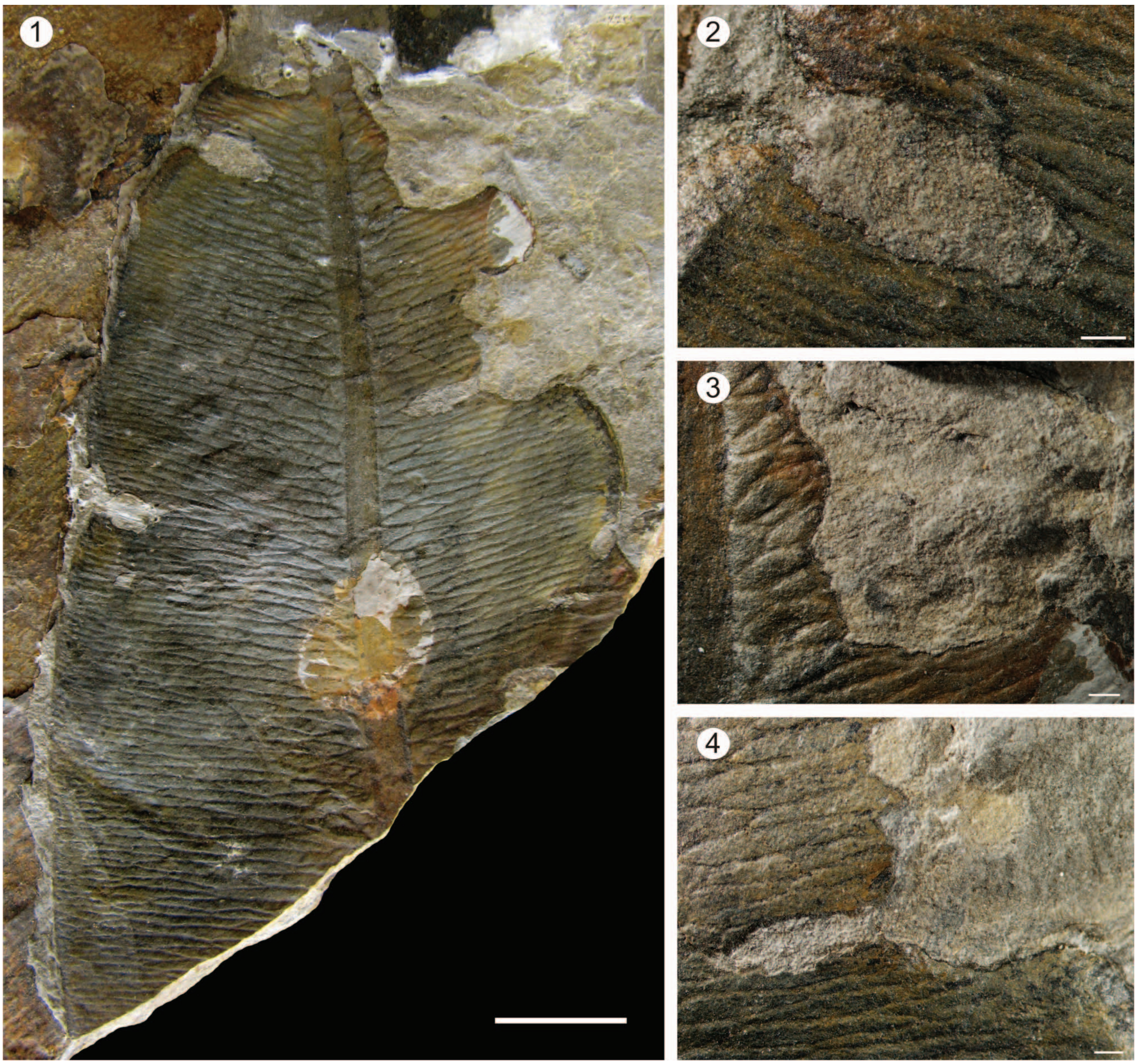

Figure 3.1–4, BA Pb-13833, ***Glossopteris damudica*** Feistmantel 1879, discontinuous marginal damage / **Glossopteris damudica** *Feistmantel 1879, daño marginal discontínuo*; **2–4,** Detail showing thin reaction tissue of irregularly shaped excisions / *Detalle mostrando el fino tejido de reacción en excisiones de formas irregulares.*

The fossil record of external foliage feeding has shown a leaf-eating behavior trend from continuous marginal feeding —which prevailed during the Paleozoic and early Mesozoic— to interrupted marginal feeding and non-marginal feeding, which became more common from the Cretaceous onwards (Chaloner *et al.*, 1991; Scott *et al.*, 1992). The record of eaten leaves previous to the Upper Carboniferous is not abundant. According to Scott *et al.* (1992), the reason for this could be that pre-Carboniferous times had mostly small lamina leaves, and arthropods did not develop a taste for leaves until they could get enough nutrients out of them, quantitatively and qualitatively speaking. However, there is certainly a collection bias towards the more complete undamaged leaves too, so potential study-objects from pre-Carboniferous rocks are excluded. The earliest evidence for external foliage feeding comes from the Late Mississippian of Australia, where the ichnotaxon *Phagophytichnus ekowskii* van Ameron 1966, was recognized in *Triphyllopteris austrina* leaves (Ianuzzi and Labandeira, 2008).

External foliage feeding became more common by the Permian. Medullosan pteridosperms were most attacked by insects in Euramerica, while in Gondwana the preferred targets were glossopterid pteridosperms (Adami-Rodrigues *et al.*, 2004a; Labandeira, 2006; Prevec *et al.*, 2009).

Insect damage on Glossopterids was observed on leaves from Australia (McLoughlin and Nedlands, 1994a, b; Holmes, 1995), South Africa (Plumstead, 1963; Van Dijk *et al.*, 1978; Anderson and Anderson, 1985; Prevec *et al.*, 2009), India (Srivastava, 1987, 1996; Pant and Srivastava, 1995; Banerjee and Bera, 1998), and Brazil (Guerra-Sommer 1995; Adami-Rodrigues and Ianuzzi, 2001; Adami-Rodrigues *et al.*, 2004a, b). Australian Late Permian fossils show clear insect-plant interactions; Holmes (1995) described a partly eaten leaf, with continuous marginal feeding traces. McLoughlin and Nedlands (1994a, b) illustrated several specimens from the Late Permian Bowen Basin with damaged, scalloped margins. Many South African Permian fossil plants carry different types of insect damage (Prevec *et*

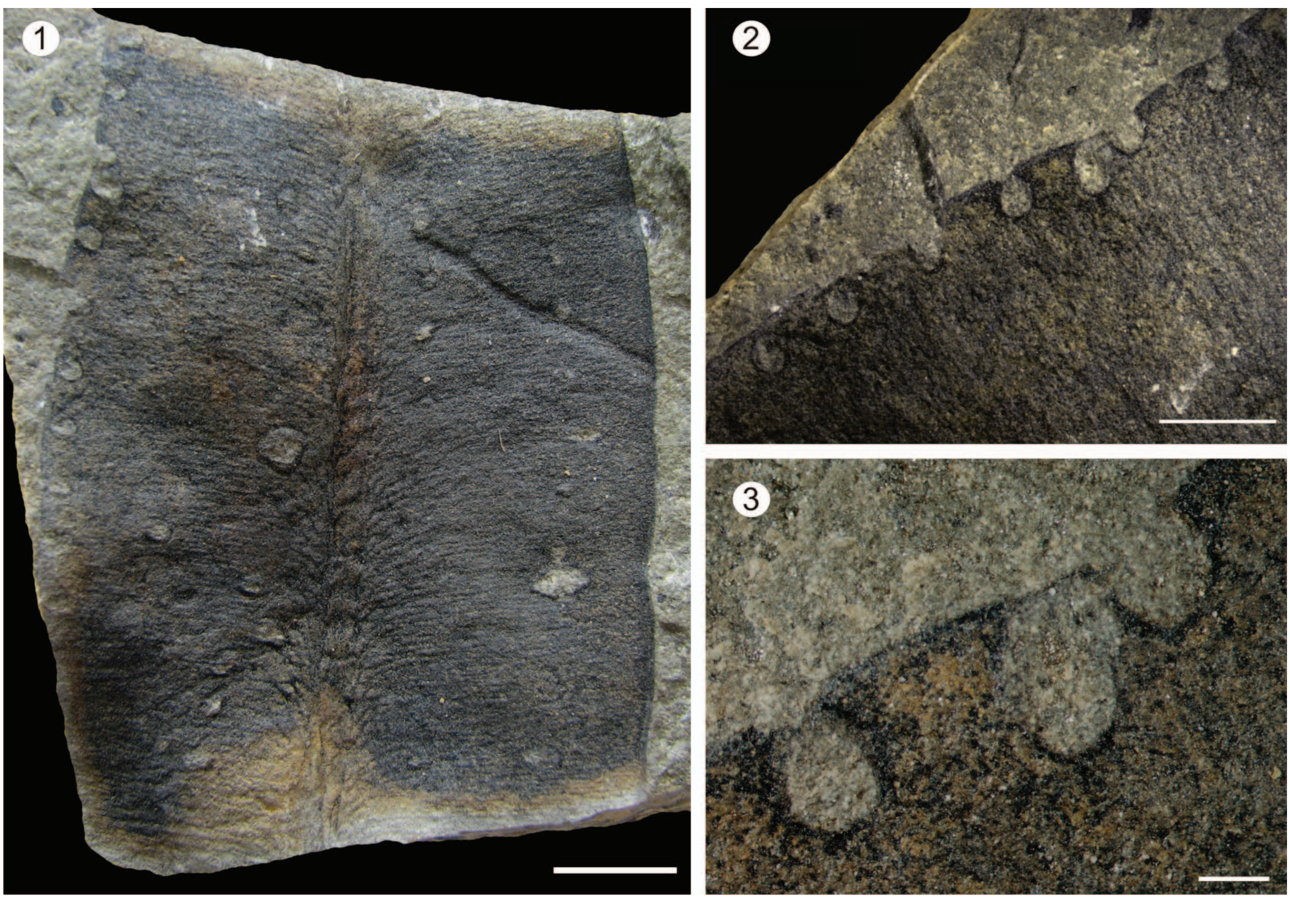

Figure 4.1–3, BA Pb-13874 ***Glossopteris*** sp. cf. ***G. ampla*** Archangelsky 1958; **2–3,** Detail showing circular excisions, vertically aligned. Observe thin, but well defined reaction tissue / *Detalle mostrando excisiones circulares, verticalmente alineadas. Observar el delgado, pero bien definido margen de reacción.*

al., 2009). Most of the damage types are oviposition marks and external foliage feeding, including shallow to deep cuspate margin feeding, trenched feeding, and hole feeding (see Labandeira *et al.*, 2007), especially on *Glossopteris* leaves (Plumstead, 1963; Anderson and Anderson, 1985; Prevec *et al.*, 2009). Plant-insect interactions on *Glossopteris* leaves have also been found in the Upper Permian of India (Pant and Srivastava, 1995). Galls in *Glossopteris browniana* leaves have been recorded from the Mohuda Basin (Banerjee and Bera, 1998), and oviposition marks and external foliage damage on leaves from the Barakar Formation in India (Srivastava, 1987). Lastly, evidence of plant-insect interaction during the Permian in South America has been only known from the Paraná Basin, Brazil. *Glossopteris* leaves were found to have marginal damage, mining, skeletonisation, piercing and sucking, and possible oviposition scars and galling (Guerra-Sommer, 1995; Adami-Rodrigues and Ianuzzi, 2001; Adami-Rodrigues *et al.*, 2004a, 2004b).

As was the case for most of the Permian *Glossopteris* floras from other parts of Gondwana, our material also presents clear external foliage feeding, most specifically discontinuous marginal feeding (Fig. 2). On the other hand, the type of insect damage present on BA-Pb-13874 (Fig. 3) has not been recognized in other *Glossopteris* specimens. Nevertheless, oviposition seems to be rather common, as it has been noticed in *Glossopteris* leaves from India (Srivastava, 1987),

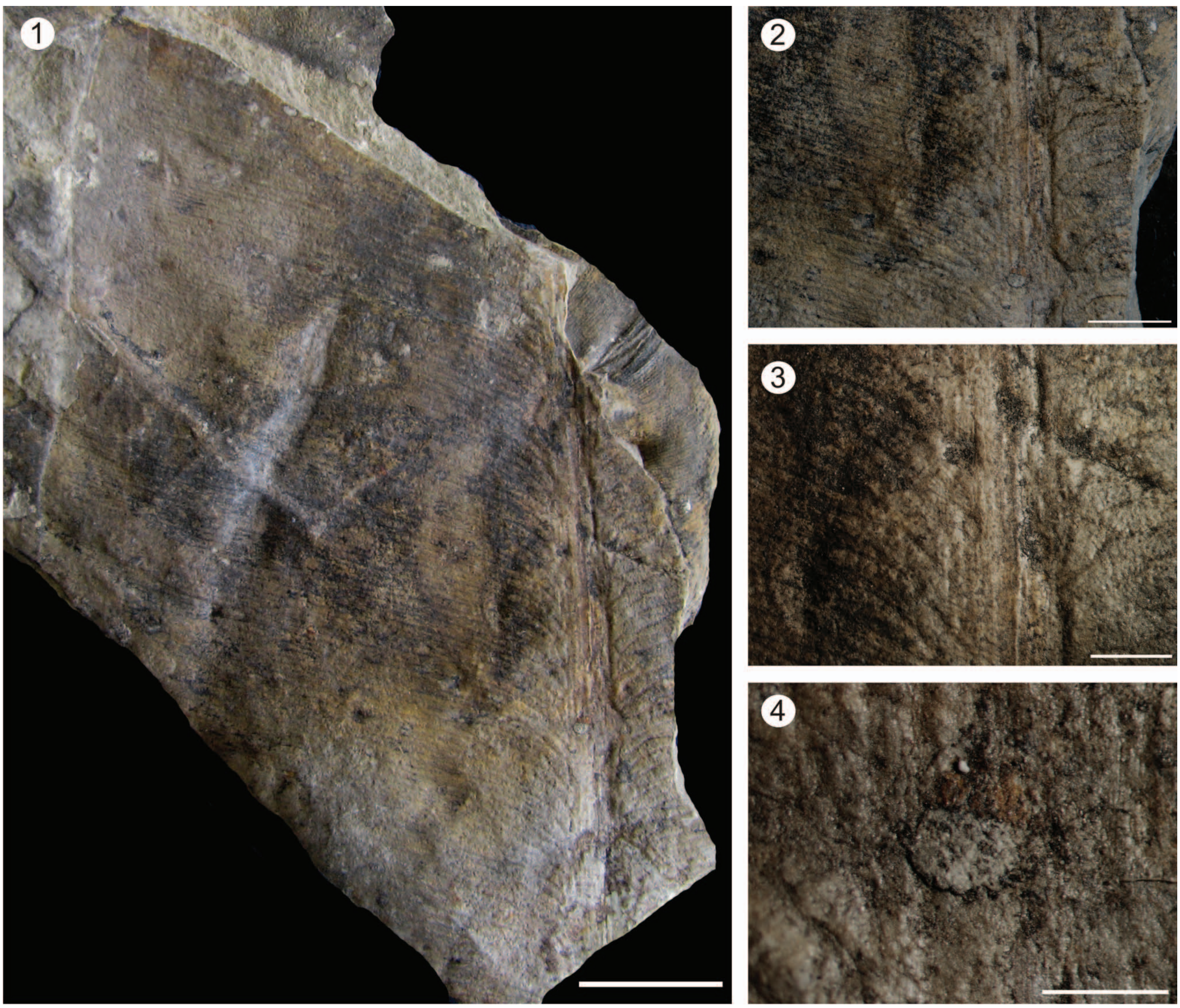

Figure 5.1–4, BA Pb-13876 ***Glossopteris*** cf. ***G. ampla*** Archangelsky 1958; **2–3,** Close-up of oviposition scars on midrib and scatterly on left side of the blade / *Detalle de las marcas de oviposición en la vena media y aleatoriamente distribuidas en la hemilámina izquierda*; **4,** Close-up of circular herbivory damage on midrib, showing scalloped marks / *Detalle mostrando la marca de herbivoría circular en la vena media, con marcas festoneadas.*

Brazil (Adami-Rodrigues *et al.*, 2004a), and South Africa (Prevec *et al.*, 2009), as well as in our material (Fig. 4).

Recognizing insect-damage on *Glossopteris* leaves is less problematic than in other typical elements of a *Glossopteris* flora, such as lycophytes, ferns, sphenophytes, and cordaitaleans. This is in part due to the fact that *Glossopteris* leaves are broad, spatulate, and with entire margins; thus, identification of potential biotic damage is easier than in, for example, small fern pinnules (Scott *et al.*, 1992). In this way, the different possible patterns and damage types are also simpler to identify. By the Permian, several distinctive herbivory damage types (see Labandeira *et al.*, 2007) were present on *Glossopteris* leaves, *i.e.*, external foliage feeding, piercing-and-sucking, galling, and oviposition (the latter is functionally treated as a type of feeding analogous to piercing-and-sucking, see Prevec *et al.*, 2009). The ichnotaxon *Phagophytichnus* (Van Ameron, 1966) is used to indicate the presence of biting marks of an unknown culprit on the margin of leaves from the Paleozoic to the Tertiary. Most *Glossopteris* leaves from the Permian of Gondwana show *Phagophytichnus*-type of marginal feeding, but it is not possible to accurately define the producer of such marks. Labandeira (1998) suggested potential external foliage feeders in the Early to Late Permian, including taxa referable to Protorhtoptera, Orthoptera, and Caloneurodea. Guerra-Sommer (1995) mentioned Coleoptera, Homoptera, and Protorthoptera as insect groups with a phytophagous diet for the Parana Basin, Brazil. In an attempt to assign culprits to the different foliar damage types on *Glossopteris* leaves from the same basin, Adami-Rodrigues *et al.* (2004a) suggested possible inducing insect groups, mostly based on the foliar damage patterns and the known insect record for similar horizons (albeit not the same horizons where the flora is found). Consequently, orthopteroid insects are considered as potential culprits for foliar margin feeding, although primitive Coleoptera may be candidates too (Adami-Rodrigues and Ianuzzi, 2001, Adami- Rodrigues *et al.*, 2004a). With regard to the oviposition scars, evidence from the Parana Basin is scarce. These authors interpreted the lenticular-shaped structures on a *Gangamopteris* leaf as produced by (proto) odonatan dragonflies, since this group is found in Paleozoic deposits of the same basin.

Unfortunately, no insect body-fossils are known to have been recovered from the La Golondrina Formation, so it is not possible to confirm the presence of any of these taxa, but only to infer it from the damage marks they left. However, fossil insects have been recovered from other Permian basins in Argentina. Several wings of Protorthoptera were found in the Bajo de Véliz Formation (San Luis, latest Carboniferous/earliest Permian) and later described (Fossa-Manzini, 1941; Pinto 1992, 1994, 1996; Gutiérrez *et al.*, 2000; Schlüter, 2003). Rocks from the Piedra Shotle Formation (Chubut, latest Carboniferous–earliest Permian) have yielded Palaeodyctioptera insects (Pinto 1992, 1994; Gutiérrez *et al.*, 2000; Schlüter, 2003).

Patterns of distinctive insect-plant interaction have been classified under a series of damage types (DT), and sorted on the basis of defined functional feeding groups (Beck and Labandeira, 1998; Labandeira and Phillips, 2002; Labandeira *et al.*, 2007; Adami-Rodrigues *et al.*, 2004a; Labandeira and Allen, 2007; Prevec *et al.*, 2009). According to this classification, the fossil specimens from the La Golondrina Formation would fall under the hole feeding, margin feeding, and oviposition categories of Labandeira *et al.* (2007). Most specifically, BA-Pb-13832 (Fig. 2.1–3) and 13833 (Fig. 3.1–4) are assigned to DT 12 ("circular, shallow to deep excision of leaf margin"), and specimen BA-Pb-13874 (Fig. 4.1–3) to DT 64 ("a linear pattern of perforations adjacent to leaf margin"). In the case described herein, however, vertical alignment of perforations occurs not only along the margins, but on the blade too. Specimen BA-Pb-13876 (Fig. 5.1–4) presents oviposition marks, similar to those in DT 101 ("lenticular-ovoidal foliar scars occurring singly or unpatterned and scattered"). Evidence of herbivory and oviposition is undeniable, considering the presence of a reaction tissue bordering the scars, the typical and defined damage pattern (*i.e.*, BA-Pb-13874; Fig. 4.2), and the marked ovoidal outline and scattered pattern of egg scars of the insect (*i.e.*, BA Pb-13876, Fig. 5. 2).

CONCLUSIONS

This is the first detailed description of insect-plant interactions in a Paleozoic flora from Argentina. The material studied herein adds further evidence to the already well analyzed interactions of insects and plants during the late Paleozoic in other parts of Gondwana.

Nevertheless, further studies are needed to increase the amount of megafloral elements that may show evidence of insect damage. Collections research and the addition of new material obtained during recent fieldtrips to the area of La Golondrina, will definitely help towards this, and also contribute to our understanding of the past environment there preserved. Better understanding of the relation between different Permian basins in Gondwana should be a consequence of this too.

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