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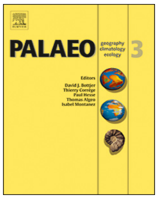

Patterns of insect-mediated damage in a Permian *Glossopteris* flora from Patagonia (Argentina)

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ABSTRACT

A total of 2523 fossil plant specimens from the La Golondrina Formation (Permian, Santa Cruz Province, Argentina) were examined in order to assess the diversity, frequency and representation of insect damage. Although no evidence of arthropod bodies have been found in the unit, their past presence is recorded through various types of plant-insect interactions, involving oviposition, external feeding, piercing and sucking, galling, and potential mine structures. Results show that at least 186 specimens (all of them plant leaves) suffered from some type of insect herbivory. Among the many damage types identified, some of them recognized for the first time in Gondwanan floras, oviposition and external feeding occurred most frequently, followed by piercing and sucking and galling. Glossopterid foliage was the preferred target over the rest of plant groups, and it was common to find more than one type of damage on the same leaf, suggesting these were exploited for multiple purposes by the insects. Compared to the Northern Hemisphere Permian floras, the La Golondrina Formation herbivory levels were low, and similar to those of other *Glossopteris* floras from Gondwana.

1. Introduction

Even though by the Permian the major landmasses were brought together into the supercontinent Pangaea (Scotese, 2014), four main phytogeographic provinces remained distinctive based on their vegetational composition (Archangelsky, 1990; Ziegler, 1990; Wnuk, 1996; McLoughlin, 2001; Rees et al., 2002). Forests in Euramerica, Angara and Cathaysia were typified by various seed plants, such as peltasperms, gigantopterids, cycads, conifers and cordaitaleans, whereas *Glossopteris*-dominated forests prevailed in Gondwana (Wnuk, 1996; McLoughlin, 2001).

On account of the abundant record of compression/impression fossil floras reflecting the structure of Permian plant assemblages, in these last years, a myriad of studies examining both qualitative and quantitative aspects of arthropod damage have come to light. These studies resulted in the recognition of interesting patterns regarding the plant hosts and their herbivores. For example, compared to Northern Hemisphere floras (Beck and Labandeira, 1998; Labandeira and Allen, 2007; Glasspool et al., 2003; Vasilenko, 2007; Krassilov and Karasev, 2008; Schachat et al., 2014, 2015), the intensity and diversity of insect-mediated damage in glossopterid floras is considered to have been low (Adami-Rodrigues and Ianuzzi, 2001; Adami-Rodrigues et al., 2004a, 2004b; Prevec et al., 2009; McLoughlin, 2011; Cariglino and Gutiérrez, 2011; Srivastava and Agnihotri, 2011; Souza Pinheiro et al., 2012; Slater et al., 2015; Gallego et al., 2014).

The present contribution describes plant-insect interactions evident on the Permian compression/impression flora of the La Golondrina Formation, including damage traces on *Glossopteris* leaves, ferns, sphenophylls, and other elements. This paper aims to assess the richness, composition and frequencies of occurrence of damage on the different plant hosts from this flora, and to discuss and compare this record with other coeval floras worldwide. Accordingly, besides providing the first thorough description of the types of damage in the unit, a semi-quantitative analysis of the plant-insect associations was conducted, allowing the characterization of herbivory patterns for further comparisons with other Permian assemblages. Because *Glossopteris*-dominated forests ruled the southern landmasses for 50 million years, surveying the interactions in the La Golondrina Formation paleoflora adds valuable knowledge of Permian terrestrial ecosystems and the ways they evolved.

2. Geological setting

The La Golondrina Formation is restricted to the northeast of Santa Cruz Province, in Patagonia, Argentina (Fig. 1). The lithostratigraphic succession comprises the Laguna Lillo, Laguna Polina and Dos Hermanos members (Archangelsky, 1996) (Fig. 2). Detailed stratigraphic and sedimentological descriptions of the area have been undertaken

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Fig. 1. Geographical location of the La Golondrina Formation.

(Jalfin, 1987; Jalfin et al., 1990; Panza et al., 1994; Gutiérrez et al., 2006). Paleoenvironmental interpretations of the unit suggest that infilling of the La Golondrina Basin occurred in two fluvial allocycles, from a relatively low-energy braided river system with variable sinuosity and sedimentation rates (Laguna Lillo and Laguna Polina members) replaced by a higher energy, less sinuous fluvial system (Dos Hermanos Member) (Jalfin, 1987; Jalfin et al., 1990; Andreis and Archangelsky, 1996).

All three members yield an abundant, diverse *Glossopteris*-dominated flora, including vegetative and reproductive structures of glossopterids, ferns, sphenophytes, cordaitaleans, lycophytes, and other less common elements, such as conifers (Archangelsky, 1959; Cariglino, 2011; Cariglino et al., 2009, 2012). It is, however, the Laguna Polina Member from where most of the interactions are registered (Supplementary Information 1). This may be a result of both, the extensive spread and finer lithology of the middle member fossil outcrops, which allows better and more detailed preservation of plants, in contrast to the coarser lithology and reduced number of fossil outcrops from the Laguna Lillo and Dos Hermanos members (see Cariglino, 2011, 2015; Fig. 2).

Based on the paleofloristic assemblage, the La Golondrina Formation is considered to range in age from the late Cisuralian to the Lopingian (Archangelsky and Cúneo, 1984; Archangelsky, 2006; Archangelsky et al., 1996). In an attempt to circumscribe the age of the formation, Cariglino (2013, 2015) used glossopterid fructifications as fossil indices for Permian biostratigraphic correlations. Given every glossopterid fructification was recovered from the Laguna Polina Member, a potential Kungurian–Wuchiapingian age is inferred for the middle member, suggesting at least an Artinskian age for the Laguna Lillo Member, and a Changhsingian age for the Dos Hermanos Member (Archangelsky, 1992; Cariglino, 2013, 2015). Unfortunately, the finding of other evidences (i.e., paleopalynology, ash or tuff levels) applicable to more reliable dating methodologies in the La Golondrina Formation has turned so far, unsuccessful.

3. Materials and methods

For this study, > 2500 compression/impression fossils were collected from the three members of the La Golondrina Formation during fieldtrips to the area in 2008, 2010, 2013 and 2014 by the author.

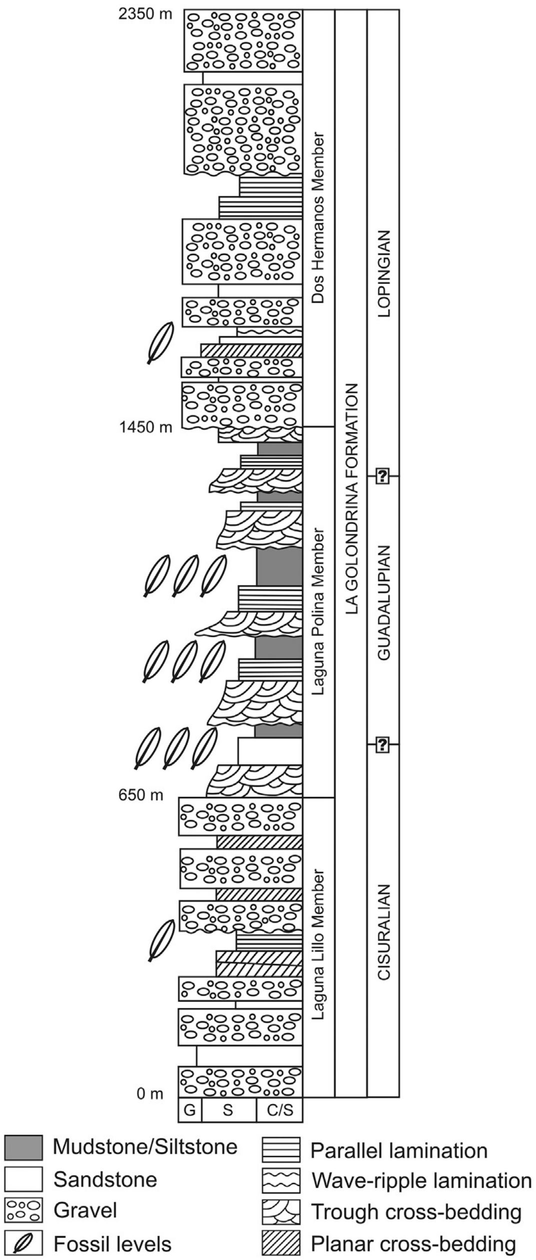

Fig. 2. Lithostratigraphic succession of the La Golondrina Formation. (Modified from Jalfin, 1987.)

In the laboratory, every plant organ/fragment was recorded and inspected carefully for signs of damage. Each specimen was identified to the finest taxonomic scale possible, or was logged as indeterminate. For assessment of general patterns of herbivory, the different plant specimens were grouped as glossopterids (*Glossopteris* Brongniart + *Gangamopteris* McCoy + fertile elements), sphenophytes (*Sphenophyllum* (Brongniart) Koenig + *Annularia* Sternberg + *Neocalamites* (Halle) Bomfleur et al. + *Schizoneura* Schimper and Mougeot emend. Bomfleur et al.), ferns and fern-like foliage (*Asterotheca* Presl [= *Pecopteris* Brongniart] + *Dizeugotheca* Archangelsky and de La Sota + *Sphenopteris* (Brongniart) Sternberg + *Damudopteris* Pant and Khare ex Chandra and Rigby + *Dichotomopteris* Maithy), and “others” (cordaitaleans + lycophytes + coniferophytes + *incertae sedis* + indeterminates). The insect damage classification follows the Damage Type Guide criteria proposed by Labandeira et al. (2007), whereby various types of damage (DTs) were identified based on distinctive sets of features. On few occasions, the DTs characterization provided in the guide did not strictly apply to the interactions herein observed. However, since the variations were considered trivial to suggest a new damage type or leave it as indeterminate, they were still attributed a DT, in every case stating which the slight discrepancies were.

The material was photographed using a Canon EOS 40D with an EF 50 mm macro lens and external flash unit. For detailed analysis and DT identification, specimens were photographed under strong unilateral light at different angles to enhance the surface relief using a Nikon DS-Fi1-U2 digital camera attached to a Nikon SMZ800 stereomicroscope. Digital images were later corrected for contrast in Adobe Photoshop CS5.

All fossil material is housed at the Museo Regional Provincial "Padre Manuel Jesús Molina" paleobotany collection in Rio Gallegos, Santa Cruz province, under the prefix MPM-PB 2497–2902 (2008); MPM-PB 4394–4999, 15103–15160 (2010); MPM-PB 16155–16365 (2013); and MPM-PB 16793–17393, 17539–17565 (2014).

4. Results

4.1. Insect damage traces

4.1.1. Margin feeding (Fig. 3A–H)

4.1.1.1. Number of specimens damaged. 58 specimens.

4.1.1.2. DTs represented. 12, 14, 15, 26, 142.

4.1.1.3. Plant hosts. Glossopteris, Sphenophyllum, Dizeugotheca, Pecopteris (=Asterotheca), Sphenopteris, Megistophyllum Archangelsky, Cordaites Unger.

4.1.1.4. Remarks. The consumption of leaf marginal tissue occurs on several plant groups in the La Golondrina Formation, including glossopterid foliage, sphenophylls, ferns, and plants of indeterminate affiliation. Although it is not strongly stereotyped, this generalized feeding can be recognized by the development of reaction tissue and the presence of veinal stringers or flaps.

Typical excisions ranging in extent from shallow to deep and attributable to DT12 (Fig. 3A–D) are commonly represented, in some cases with smaller indentations along the damaged border that indicate the trajectory of consumption by a mandibulate arthropod (Fig. 3D). This type of damage had been previously identified on glossopterid leaves from material collected during the 1950s and 1980s (Cariglino and Gutiérrez, 2011); newly recovered material provides evidence of this damage also on fern-like foliage (Fig. 3A) and sphenophylls (Fig. 3B).

When the excision reaches the midrib (Fig. 3E) the damage can be assigned to DT14. Other deeply incised damage observed on *Glossopteris* leaves is DT15, in which the consumption of the tissue occurs inwardly from the leaf margin, adopting an elongate shape that thins towards mid-lamina (Fig. 3F).

Less common, but also present on a few *Glossopteris* leaves, was DT26, where the interveinal tissue was preferentially consumed leaving veinal stringers untouched (Fig. 3G).

Lastly, a *Glossopteris* specimen shows cuspate margin feeding with a thick reaction rim with transverse lineations, assignable to DT142 (Fig. 3H).

4.1.1.5. Comparisons. Margin feeding has been extensively documented in Permian compression/impression floras from Gondwana (see Slater et al., 2015). The most common damage type is DT12; however, apical feeding (DT13), a damage type not observed in any of the fossils from the La Golondrina Formation, has been recorded on several *Glossopteris* leaves and other broadleaf taxa (i.e., *Noeggerathiopsis* Feistmantel, *Rubidgea* Tate, *Belemnopteris* Feistmantel) from Australia, India, Brazil, South Africa, and other Argentinian assemblages (Bernardes de Oliveira and Pons, 1977; Srivastava, 1979; Millan and Dolianiti, 1982; Rohn, 1984; Anderson and Anderson, 1985; Scott et al., 1992; McLoughlin, 1994a, 1994b; Chandra and Singh, 1996; Srivastava and Agnihotri, 2011; Gallego et al., 2014). Similarly to the La Golondrina paleoflora, marginal damage was found on sphenophylls from India (Feistmantel, 1880) and Madagascar (Appert, 1977). Deep marginal incisions in some *Glossopteris* leaves herein attributed to DT15 are also present in *Glossopteris* from South Africa (Prevec et al., 2009) and Sri Lanka (Edirisooriya et al., 2018). Finally, the thick reaction rim with transverse lineations seen on one specimen from the La Golondrina and assigned to DT142, is similar to the damage on a *Glossopteris* leaf from the Bowen Basin in Australia (McLoughlin, 1994b, Pl. 7, Fig. 7).

4.1.2. Hole feeding (Fig. 3I–R)

4.1.2.1. Number of specimens damaged. 26 specimens.

4.1.2.2. DTs represented. 01, 02, 08, 50, 64, 78, 113.

4.1.2.3. Plant hosts. Glossopteris.

4.1.2.4. Remarks. Hole feeding is another type of external feeding, recognizable as perforations of the lamina with reaction tissue surrounding the damage that never reach the margin of the leaf. Damage may reflect targeted consumption of interveinal tissues, may be circular, polygonal or polylobate, and may be arranged in distinctive patterns on the plant organ.

Hole feeding has been recorded in *Glossopteris* foliage in the La Golondrina Formation. Examples of circular perforations < 1 mm in diameter assignable to DT01 were observed in several leaves (Fig. 3I), whereas perforations larger in size (DT02) scattered randomly on the leaf were less frequent (Fig. 3L).

Very small, rectilinear, parallel-sided, elongate perforations ranging from 2 to 5 mm in length and 0.1 mm in width following the secondary venation on the mid-lamina are assigned to DT08 (Fig. 3J–K). Also observed on *Glossopteris* were elongate-elliptical excisions that were constrained by the secondary venation of the leaf and extending from the mid-lamina to the margin (Fig. 3M–N), here ascribed to DT78, with the exception these excisions are not adjacent to each other.

DT50 is defined by linear series of holes either on one or both sides adjacent to the primary vein, a feature that can be seen in a *Glossopteris* leaf, where transversely paired slits are aligned along both sides of its midrib (Fig. 3R).

Also previously noted from older collections (Cariglino and Gutiérrez, 2011), a frequently observed damage type is DT64 (Fig. 3P–Q), characterized by a linear pattern of perforations usually along the leaf margin. In one specimen (Fig. 3Q), it is possible to observe preferential consumption of the interveinal tissue.

Finally, one specimen shows a single circular perforation 2 mm in diameter surrounded by a distinct rim about 1 mm in width. This type of hole damage is referable to DT113 (Fig. 3O).

4.1.2.5. Comparisons. Despite hole feeding at the La Golondrina Formation was observed only on *Glossopteris* foliage, this interaction has been recorded in other Permian Gondwanan floras on *Ginkgoites* Seward, *Cordaites*, *Lidgettonia* Thomas sporophylls, scale leaves and even sphenophytes roots (Prevec et al., 2009; Souza Pinheiro et al., 2012; Gallego et al., 2014; Slater et al., 2015). The La Golondrina Formation paleoflora is, however, unique in the variety of hole feeding damage it presents, with 7 DTs identified. Among these, DTs 50, 78 and 113 are recognized in Permian paleofloras for the first time.

Fig. 3. (A–H) *Margin feeding*. A. DT12 on fern-like foliage (MPM-PB 4449). B. DT12 on *Sphenophyllum* (MPM-PB 17327). C. DT12 on *Glossopteris* (MPM-PB 16859). D. DT12 in detail, observe small indentations on excision (MPM-PB 17089). E. DT14, excision reaching midrib of a *Glossopteris* (MPM-PB 17549). F. DT15, deeply incised marginal excision (black arrow) and DT02, hole feeding larger than 1 mm in diameter (white arrow) (MPM-PB 17079). G. DT26, observe veinal stringers (black arrow) (MPM-PB 17084). H. DT142, cuspate margin feeding with a thick rim perpendicularly striate (MPM-PB 17092). (I–R) *Hole feeding.* I. DT01, examples of circular hole damage < 1 mm in diameter (white arrows) (MPM-PB 17391). J–K. DT08, rectilinear slot feeding with length to width ratio > 2.5 (MPM-PB 16168, 17,082). L. DT02, large hole feeding on *Glossopteris* (MPM-PB 4520). M–N. DT78, irregular removal of tissue between secondary veins (MPM-PB 2510, 17,090). O. DT113, rounded hole feeding with well-developed, thick rim (MPM-PB 17179). P–Q. DT64, small circular holes aligned on the margin, note veins left untouched (white arrows in Q) (MPM-PB 4538, 17,094). R. DT50, hole damage arranged as linear series at each side of the midrib on a *Glossopteris* (MPM-PB 16284). S. DT17(?), only specimen with poorly developed skeletonization (MPM-PB 17071).

4.1.3. Surface feeding (Fig. 4A–F)

4.1.3.1. Number of specimens damaged. 24 specimens.

4.1.3.2. DTs represented. 28, 29, 31, 82, 97, 103.

4.1.3.3. Plant hosts. *Glossopteris*, *Sphenophyllum.*

4.1.3.4. Remarks. Unlike hole feeding, where consumption of the foliar tissue leads to perforation of the lamina, surface feeding does not remove the entire thickness of the leaf, leaving abrasion surfaces where tissue layers are still present.

A commonly observed surface abrasion in the present study was DT97, characterized by a u-shaped area sub-parallel to secondary venation, bordered by a distinct reaction rim (Fig. 4D–E).

Circular or elliptical abrasion surfaces variable in diameter and with a noticeable reaction rim assignable to DT31 were found in both

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Fig. 4. (A–F) *Surface feeding*. A. DT28, abrasion between parallel veins (black arrows) (MPM-PB 17551). B. DT31, circular abrasion of surface tissue on *Sphenophyllum* (MPM-PB 17325). C. DT82, polylobate window feeding at both sides of primary venation (MPM-PB 16188). D–E. DT97, u-shaped abrasion surface (black arrows); also DT29 (white arrow on D) showing the removal of surface tissues with a weak reaction rim (MPM-PB 17072, 17,393). F. DT103, elongate surface feeding (black arrows) following principal venation (MPM-PB 17083). (G–L) *Piercing-and-sucking*. G. DT46, randomly distributed circular punctures infilled with carbonized matter (black arrows), note presence of hole feeding DT01 (white arrows) (MPM-PB 17542). H, L. DT47, scattered circular punctures with a central dome, also potentially evidenced on lycophytes microphylls (black arrows in L) (MPM-PB 16800, 17,076). I. DT48, elliptical punctures with carbonized material distributed in a random pattern (MPM-PB 17370). J. DT133, circular punctures on parallel veins (black arrows), note the presence of small punctures on midrib (white arrows) potentially attributable to DT138 (MPM-PB 17066). K. DT138, circular to ellipsoidal punctures on the midrib of *Glossopteris* (MPM-PB 4834). (M–U) *Galling*. M–N. DT120, circular to slightly polylobate galls with a thick reaction rim on or close to the primary venation of *Glossopteris* leaves (MPM-PB 17102, 17,358). O. DT52, single circular gall surrounded by radiating partitions (MPM-PB 17087). P–R. DT107, *Glossopteris* leaves showing circular to lacriform galls with a roughened surface surrounded by a thin reaction tissue and a central mark (exit hole) (MPM-PB 4764, 4975, 16,323). S. DT260, numerous circular galls scattered on part and counterpart of a *Glossopteris*, with distinct pustulose surfaces (MPM-PB 4875). T. DT85, elongated gall, l:w ratio > 4, located on a midrib of a *Glossopteris* (MPM-PB 17095). U. First and only specimen of *Sphenophyllum* with a gall in one of its leaflets (MPM-PB 17105).

Glossopteris and *Sphenophyllum* leaves (Fig. 4B).

Strip feeding between secondary veins bordered by an uneven reaction rim potentially attributable to DT28 is observed in one specimen (Fig. 4A), although caution is necessary when defining this type of damage since it could be easily confused with abiotic tissue degradation.

The removal of a large area of surface laminar tissue surrounded by a poorly developed reaction rim is seen in the basal portion of a *Glossopteris* leaf, here assigned to DT29 (Fig. 4D, white arrow), although the delicately convoluted margin may require assignation to a new DT. Another large, polylobate abrasion surface on a *Glossopteris* leaf with a distinct reaction rim (Fig. 4C) can be attributed to DT82, based on its almost symmetrical distribution to either side of the midrib.

One last example of surface damage is DT103, observed on another *Glossopteris* specimen, in which elongate window feeding occurs parallel or almost parallel to the midrib, constrained by the secondary venation (Fig. 4F).

4.1.3.5. Comparisons. According to Schachat et al. (2014), in northern paleofloras, surface feeding prominently appeared in the Early Permian, whereas its record in Gondwana remained relatively infrequent, with few observations from Australia, South Africa, Brazil and Argentina (McLoughlin, 1994a, 1994b; Prevec et al., 2009; Souza Pinheiro et al., 2012; Gallego et al., 2014). Surface damage DTs 28, 29, 31, 97 and 103 have been previously recorded in other paleofloras. However, the large, polylobate abrasion surface observed in a *Glossopteris* and herein attributed to DT82, represents the first evidence in Permian Gondwanan floras.

4.1.4. Skeletonization (Fig. 3S)

4.1.4.1. Number of specimens damaged. 1 specimen.

4.1.4.2. DTs represented. 17(?).

4.1.4.3. Plant hosts. *Glossopteris.*

4.1.4.4. Remarks. This is the least common of the external foliage feeding types found at the La Golondrina Formation, with only two examples identified, one from old collection material (only mentioned here to acknowledge the presence of this type of damage). After intense collection during four fieldwork seasons, only one poorly preserved example of a *Glossopteris* leaf yielded what could potentially be DT17, where the interveinal tissue has been consumed, leaving thickened veins caused by the necrotic reaction (Fig. 3S). The poor preservation of this specimen could also lead to interpretation that the tissue has not been completely removed, but thinned, in similar manner to a dense DT103 (surface feeding).

4.1.4.5. Comparisons. Skeletonization is a rare damage in the La Golondrina and other Permian Gondwanan paleofloras, with few mentions from Brazil (Adami-Rodrigues et al., 2004a; Souza Pinheiro et al., 2012), South Africa (Prevec et al., 2009), and Sri Lanka (Edirisooriya et al., 2018). The damage herein considered as skeletonization is similar to that described in *Glossopteris* leaves from Brazil, where the mesophyll tissue is degraded, and the perforations occur among the cells of the interveinal tissue (Adami-Rodrigues et al., 2004a). However, since their material does not show a distinct reaction tissue, they suggest that skeletonization occurred through detritivory instead of herbivory (Adami-Rodrigues et al., 2004a).

4.1.5. Piercing and sucking (Fig. 4G–L)

4.1.5.1. Number of specimens damaged. 22 specimens.

4.1.5.2. DTs represented. 46, 47, 48, 133, 138.

4.1.5.3. Plant hosts. *Glossopteris*, lycophyte microphylls (?).

4.1.5.4. Remarks. Evidence of piercing and sucking in the La Golondrina Formation is identified as puncture marks up to 3 mm in diameter, scattered on the lamina and midrib of *Glossopteris* leaves, and possibly, also on a lycophyte microphyll.

Generalized piercing-and-sucking traces comprising punctures ranging from 1 to 2.5 mm in diameter, infilled by carbonized material and randomly distributed on the lamina of *Glossopteris* leaves are represented by DT46, DT47 and DT48, differing in their shape (circular for DT46, DT47, and ellipsoidal for DT48), and central region (depressed in DT46, domed in DT47) (Fig. 4G–I). Potentially, DT47 is also present on a lycophyte microphyll, although this is not conclusive given the regular preservation of the specimen (Fig. 4L).

A more specialized piercing-and-sucking damage evident in the La Golondrina Formation is DT133, characterized very small circular punctures, 0.5 mm in diameter, found close to the side of the midrib on the lamina of *Glossopteris* (Fig. 4J). At the right side of the midrib of the same specimen, there are slightly bigger (~1 mm in diameter) circular marks, assignable to DT47 (Fig. 4J).

Finally, small circular to ellipsoidal puncture marks, 1 mm in size that are vertically aligned along the midrib of a *Glossopteris* can be attributed to DT138 (Fig. 4J–K).

4.1.5.5. Comparisons. The record of piercing and sucking extends to the Early Devonian, evidenced on three-dimensionally preserved early vascular plants from the Rhynie Chert (Schachat et al., 2014). In compression/impression floras, piercing-and-sucking damage is found on Permian *Glossopteris* from Brazil, South Africa and India (Adami-Rodrigues et al., 2004a; Prevec et al., 2009; Srivastava and Agnihotri, 2011), and possibly on a lycophyte axis in India (Slater et al., 2015). The piercing-and-sucking scars on *Glossopteris* leaves described from Sri Lanka (Edirisooriya et al., 2018, figs. 4g–h) are similar to those here assigned to DT47 (see Fig. 3J). Additionally, numerous small puncture marks closely arranged in similar manner to one of the La Golondrina Formation specimen (Fig. 4H) were identified on a *Glossopteris* leaf of Brazil (Adami-Rodrigues et al., 2004a, fig. 6j).

4.1.6. *Galling* (Fig. 4M–U)

4.1.6.1. Number of specimens damaged. 17 specimens.

4.1.6.2. DTs represented. 52, 85, 107, 120, 260, n/a.

4.1.6.3. Plant hosts. Glossopteris, *Sphenophyllum.*

4.1.6.4. Remarks. Galling was identified by the presence of distinctive three-dimensional structures with an exit mark within, and a similar pattern relative to their location on the plant organ (e.g., same type of galls placed in the apical section of leaves).

Some specimens feature two or three circular to slightly polylobate marks, in some cases aligned on the midrib, or slightly displaced on the leaf lamina, 1.8–2 mm in diameter, with a thick outer rim and a small central exit hole, potentially assignable to DT120 (Fig. 4M–N).

Larger, single, ovoidal to lacriform galls, up to 7 mm long and 4.1 mm wide were found on various leaves (Fig. 4P–R). These galls are characterized by a thin reaction tissue surrounding a roughened surface with smaller rounded marks in the central area that could potentially be the exit holes, somewhat similar to DT107 in overall shape but larger, with the exception that in the La Golondrina's samples, these always occur singly on one side of the middle–upper lamina of *Glossopteris* leaves, whereas this DT has otherwise been found on fern pinnules (Labandeira et al., 2007).

A third type of gall was recognized as a circular structure 0.9 mm in diameter in which lines of tissue radiate from a central mark (Fig. 4O), assignable to DT52.

Another *Glossopteris* specimen presents an elongated, elliptical scar 6 mm long and 1 mm at its widest, with a central slit 1.5 mm long, centered on the midrib. This type of gall can be ascribed to DT85 (Fig. 4T).

Multiple hemispheroidal scars 1 mm in diameter with a pustulose surface scattered on the lamina of *Glossopteris* leaves are similar to DT260, described on an Early Permian peltasperm from Texas (Schachat et al., 2014), with the difference that the specimens from the La Golondrina Formation are densely affected (Fig. 4S).

Lastly, an example of galling was observed on a *Sphenophyllum* leaflet (Fig. 4U). The gall is ovoid and follows the fan-shaped venation pattern of the leaf. It measures 2.2 mm in length and 1.7 mm at its widest point, and shows a roughened, elevated surface. This is so far the first and only record of galling on a sphenophyll, therefore its assignation to a DT is left open until more specimens are found.

4.1.6.5. Comparisons. Galls have been recorded in Early Pennsylvanian (Beck and Labandeira, 1998) paleofloras from the northern hemisphere; however, in Gondwana, the earliest reports are Permian (McLoughlin, 2011; Cenci and Adami-Rodrigues, 2017). Galls can occur in all plant organs, such as the petiole or lamina of the leaf, or on reproductive structures. In Permian Gondwanan paleofloras, galls are evidenced exclusively on glossopterid leaves (McLoughlin, 1990, 2011, 2012; Pant and Srivastava, 1995; Banerjee and Bera, 1998; Prevec et al., 2009; Souza Pinheiro et al., 2012; Labandeira and Prevec, 2014; Slater et al., 2015), being the gall on the *Sphenophyllum* leaflet herein described the first and only evidence of this type of interaction in a non-glossopterid element. Moreover, the abundance and diversity of galls in the La Golondrina Formation paleoflora contrasts with previous observations of the scarcity of this interaction in *Glossopteris*-dominated forests (McLoughlin, 2011).

4.1.7. *Oviposition* (Fig. 5A–N)

4.1.7.1. Number of specimens damaged. 79 specimens.

4.1.7.2. DTs represented. 72, 76, 100, 101, 102, 136, 137, n/a.

4.1.7.3. Plant hosts. Glossopteris, *Kladistamuos* Carrizo and Archangelsky.

4.1.7.4. Remarks. A wide range of endophytic oviposition styles have been identified in the paleoflora from the La Golondrina Formation, all of them on *Glossopteris* foliage with the exception of one example on the pteridosperm *Kladistamuos golondrinensis* (Carrizo and Archangelsky, 2013).

The most common DT is DT101 (Fig. 5D, G, J), where circular to lenticular to ovoidal scars with a marked reaction rim are scattered randomly on the leaves. This type of interaction was described previously from old collection material (see Cariglino and Gutiérrez, 2011).

Another common type of oviposition is characterized by circular to ovoid scars oriented along secondary veins and usually paired one at each side of the midrib, found on several *Glossopteris* leaves (Fig. 5H). These linear series of scars are located along the mid-lamina and could potentially be assigned to DT136, only differing in that the scars are not connected by necrotic tissue. Similar oviposition scars are rarely observed on or adjacent to the leaf margin of these same leaves (DT102) (Fig. 5I).

Clusters of oviposition scars arranged in adjacent linear series on the lamina of *Glossopteris* leaves attributable to DT100 have been also observed (Fig. 5F).

Elongated to broadly obovate scars ranging from to 2.7 to 4.5 mm long and 1.3 to 2.4 mm wide placed along the midrib are present on several *Glossopteris* leaves. In most cases they are in a linear configuration (Fig. 5C), although two linear series were also observed (Fig. 5E). The position of the scars, on the midrib of the leaves, places them within DT76. Ellipsoidal scars assignable to DT72 were found on the stem of *Kladistamuos golondrinensis* (Fig. 5A–B), this being the only oviposition evidence found on a non-glossopterid element.

On a few specimens, transversely oriented, elongated, lenticular scars were arranged in a vertical row in the lower section of the midrib (Fig. 5K–M). These oviposition traces are ascribed to DT137.

Finally, also on the midrib of one *Glossopteris* leaf, there are at least 11 rounded oviposition marks equally-spaced 5 mm apart, with a prominent reaction rim (Fig. 5N). There is currently no oviposition DT that applies to this damage.

4.1.7.5. Comparisons. The earliest fossil record of oviposition known is on calamitalean stems from the Late Pennsylvanian of France (Béthoux et al., 2004), but it is by the Permian when this interaction becomes common (Schachat et al., 2015). In Gondwanan paleofloras, oviposition scars are frequently observed on *Glossopteris* foliage, although evidence of ovipositional damage has been identified on other taxa, such as *Noeggerathiopsis*, *Ginkgoites*, scale leaves and even sphenophyte axes (Cúneo, 1987; Prevec et al., 2009; Gallego et al., 2014). In addition, oviposition on the pteridosperm *Kladistamuos golondrinensis* is presented herein for the first time.

Oviposition scars on the midribs of *Glossopteris* leaves (DT76) have been observed in material from South Africa (Prevec et al., 2009) and Brazil (Adami-Rodrigues et al., 2004a). Their arrangement in two linear series has been also described in *Glossopteris* from South Africa (Prevec et al., 2009) and Australia (McLoughlin, 2011), although it is more common to find them randomly scattered either singly or in clusters (DTs 100, 101). The *Glossopteris* leaves from South Africa also presented evidence of lenticular to ellipsoidal oviposition scars with a surrounding callus, sited near or adjacent to the leaf margin (DT102) (Prevec et al., 2009).

Recently, Gallego et al. (2014) described multiple bulbous transverse U-shaped oviposition scars vertically arranged on the basal section of the midrib of a *Glossopteris wilsonii* (Seward) Archangelsky et al. The same type of oviposition was observed on a *Glossopteris* from the La Golondrina Formation (Fig. 4M). Based on their similar placement, it seems probable that the bulbous U-shaped scars are and the scars observed in other leaves (Fig. 4K–L) represent different preservational states of the same damage (DT137).

The equally-spaced oviposition marks observed on the midrib of a

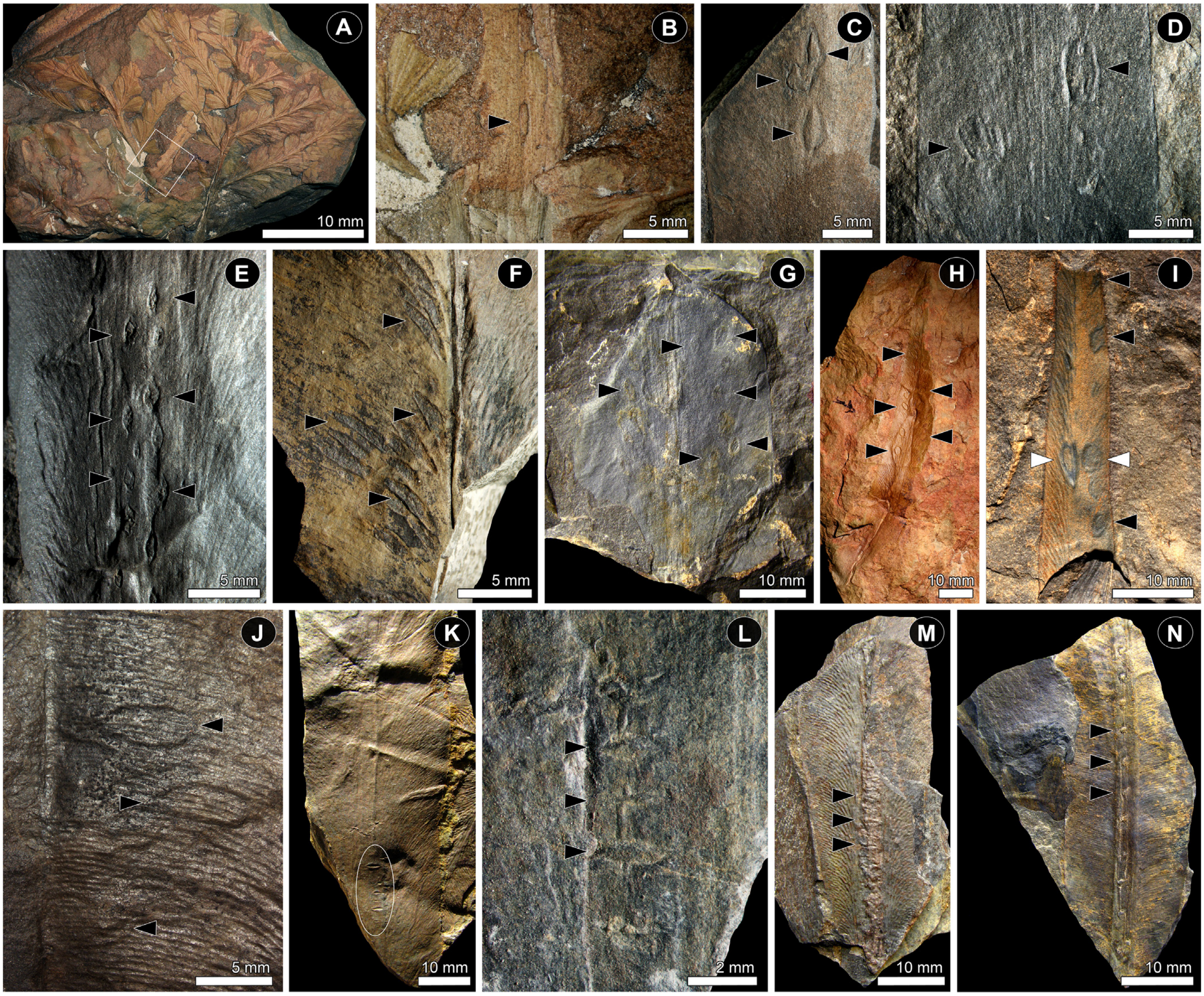

Fig. 5. (A–N) *Oviposition*. A–B. DT72, oviposition on stem of *Kladistamuos* (detail of A in B, black arrow points to oviposition scar) (MPM-PB 16933). C, E. DT76, oviposition on the midrib of *Glossopteris*; observe the two linear series along the midrib in E (black arrows) (MPM-PB 17075, 17233). D, G, J. DT101, various lenticular oviposition scars randomly scattered on *Glossopteris* leaves (MPM-PB 16180, 16,191, 17,013). F. DT100, lenticular-ovoidal scars arranged in a compact cluster (MPM-PB 17093). H. DT136, paired oviposition scars displayed in mid-lamina (MPM-PB 16862). I. DT102, oviposition scar on the margin (black arrow), note also DT136 (white arrow) (MPM-PB 16946). K–M. DT137, different preservational states of the same lenticular oviposition scars transverse oriented on the midrib of *Glossopteris*. Observe the basal placement of the scars on the midrib (encircled in white in K) (MPM-PB 16163, 16169, 17182). N. Potential new DT, oviposition scars equidistantly located along the midrib of a *Glossopteris* (MPM-PB 16364).

Glossopteris (Fig. 4N) are comparable to those in material described on a *Glossopteris* leaf from KwaZulu-Natal in South Africa (Prevec et al., 2009), although these were elliptical in shape and spaced more closely to each other. The concurrent pattern observed in these two distant floras provides enough evidence to propose a new DT.

4.1.8. *Indeterminate damage (Fig. 6A–I)*

4.1.8.1. Number of specimens damaged. 1 specimen.

4.1.8.2. Plant hosts. Glossopteris.

4.1.8.3. Remarks. Numerous rounded to slightly elongated bulges, ranging from 1 to 1.7 mm in diameter, occur along the distal portion of the midrib of a *Glossopteris* leaf (Fig. 6A–B).

4.1.8.4. Comparisons. This damage, suggestive of some type of galling, has not been observed in any other specimens from La Golondrina nor other fossil floras, precluding further comparisons.

4.1.8.5. Number of specimens damaged. 3 specimens.

4.1.8.6. Plant hosts. Glossopteris.

4.1.8.7. Remarks. Curvilinear, contiguous to slightly separated traces of constant width but varying length are evident in at least two *Glossopteris* leaves from the La Golondrina Formation (Fig. 6C, I). In the more complete example (Fig. 6C–E, H), the traces extend for 24.6 mm along the right margin of the leaf, laterally expanding to 1/3 of the right side of the lamina, never crossing the midrib. The upper marginal traces are more developed, and bear simple circular marks in the center (exit holes/oviposition mark?), 1 mm in diameter. Leaf veins remain intact across the trace, indicating that the cuticle was not affected, but defining a necrotic zone where the veins are less defined compared to the veins outside the limits of the trace. The interaction

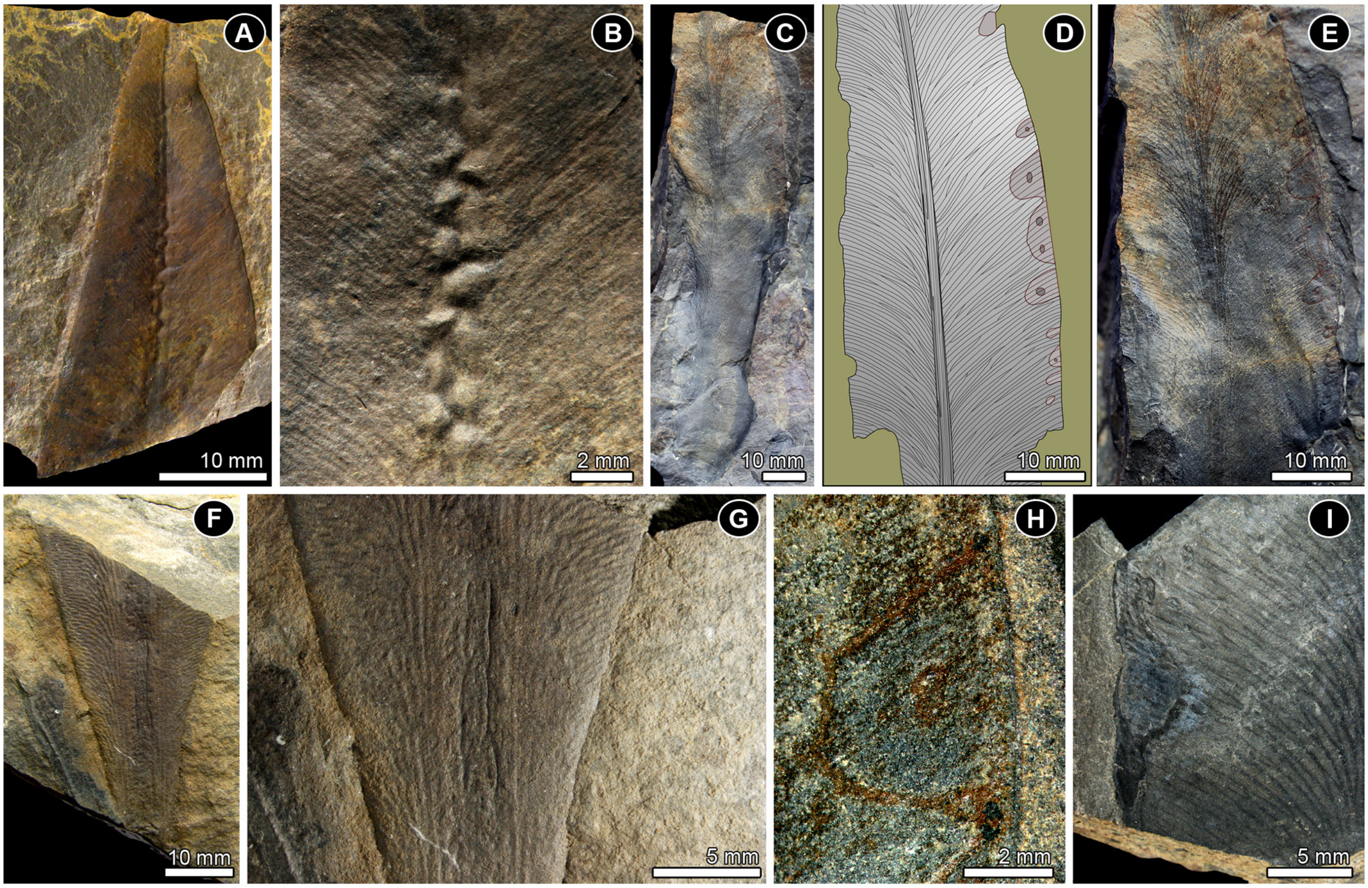

Fig. 6. (A–I) *Indeterminate damage*. A–B. Numerous bulges vertically aligned on the midrib of a *Glossopteris* (MPM-PB 16323). C–E, H—I. Contiguous semicircular traces on the margins of *Glossopteris* leaves, with central circular marks (exit holes?), suggestive of mining (MPM-PB 16170, 17,074). F–G. Paired oviposition scars along each side of the midrib of a *Glossopteris* (MPM-PB 16171).

here described is considered as a potential leaf mine based on the following features: (1) curved linear trace forming an almost continuous loop-pattern, (2) trace delimits a necrotic zone where leaf veins are still visible, although less defined than the robust veins on the rest of the leaf blade, implying that the cuticle is left intact, (3) presence of circular marks (exit holes or oviposition mark?) in the loops. However, other diagnostic characteristics are missing: no frass is preserved and the trace does not show an obvious increase in size as a result of the larva's growth.

Fossil leaf mines are generally identified on the presence of frass, oviposition marks or exit holes, and a gradual increase of width or terminal expansion (pupal chamber). Nevertheless, not all of these features are consistently observed, since the absence of preserved frass could result from a more fluid consistency, or simply that it was expelled out of the mine by the larva itself; exit holes and oviposition marks are not always visible even on extant examples; and lastly, some insects prefer to pupate outside of the leaf tissue, precluding the formation of a pupation chamber or widening of the trace at the end (Hering, 1951).

These specimens are left as indeterminate damage until more material is found to confirm these as the oldest evidence of mining.

4.1.8.8. Comparisons. U-shaped structures on peltaspermalean leaves from Europe were attributed to mines based on the presence of frass and slightly broadened ends (Krassilov and Karasev, 2008). Similarly to the material from the La Golondrina Formation, these sinuous tracks are arranged closely to each other along the margin of the leaf (Krassilov and Karasev, 2008, Fig. 3g); however, they differ in the lack of a central circular mark, such as the ones observed in the material herein described.

A curious case is that of surface damage DT97 (sensu Labandeira et al., 2007), described as U-shaped lesions with a distinct reaction rim. This widespread interaction is considered a precursor of the galls on the Permian medullosan seed fern *Odontopteris readi* (Mamay) Stull et al., assigned to *Ovofoligallites padgetti* Labandeira (Stull et al., 2013). These are ovoid to pyriform, occasionally U-shaped structures that are irregularly spaced on the pinnule, in a similar manner to the *Glossopteris* leaf herein described, but differing in that they do not always arrange along the margin, or evidence circular marks inside the structure (e.g., Stull et al., 2013). In addition, these structures are different in that sometimes they have constricted apices. Therefore, despite a few superficial similarities with *Ovofoligallites*, such as the U-shape and the arrangement along the margin, traces in the *Glossopteris* from the La Golondrina Formation are most likely evidence of some sort of mining. However, it is important to note that this could be another example in which a preceding DT gives origin to a more specific damage, since the lowermost lesions in the *Glossopteris* leaf (Fig. 5D–E) do not show any circular mark (aborted mines?) and could have been referred — analogously to the precursor of *Ovofoliigalites* — to DT97.

4.1.8.9. Number of specimens damaged. 1 specimen.

4.1.8.10. Plant hosts. *Glossopteris*.

4.1.8.11. Remarks. Specimen MPM-PB 16171 (Fig. 6F–G) bears at least five pairs of elongated marks, about 1.8 mm long and 0.2 mm wide, along the basal part of the midrib of a *Glossopteris* leaf, which could represent a new type of endophytic oviposition.

4.1.8.12. Comparisons. Similar paired, spindle-shaped marks attributed to oviposition damage were described on leaflets of *Pterophyllum* Brongniart from the Jurassic of Romania (Popa and Zaharia, 2011). The elliptic structures were arranged in groups of two or three, aligned with the venation of the leaflets. Also described from the Jurassic, but on several *Otozamites* Braun from Australia (McLoughlin et al., 2015), were paired oviposition scars placed near the pinnule apices, oriented parallel to the venation. Despite the target taxa and placement of the scars are different in all three cases, this type of paired oviposition could indicate they were done by the same insect group (its lineage crossing the Pm/Tr boundary and reaching the Jurassic), or alternatively, by different groups of insects with an analogous behavior.

4.2. General patterns of herbivory

4.2.1. Diversity and frequency results

The *Glossopteris* flora preserved in the La Golondrina Formation is dominated — as expected — by glossopterids (foliage, reproductive structures, and root systems in decreasing order), marattiacean and osmundacean ferns, and sphenophytes (predominantly sphenophylls). Also present in the basin, are subordinate lycophytes, cordaitaleans and other elements of pteridospermic or unknown affinity (Archangelsky, 1959; Cariglino, 2011). Accordingly, the bulk of the flora collected in consecutive fieldtrips from 2008 to 2014 and included in this analysis is represented by 1092 glossopterids (43%), 680 ferns (27%), 288 sphenophytes (12%), and a count of 463 specimens for the least represented groups (18%) (Fig. 7).

Results show a high richness of interactions at the La Golondrina Formation, with the addition of several damage types previously unknown for *Glossopteris* floras. Moreover, different insect-mediated damage recognized on groups other than the dominant glossopterids, points to diverse utilization of the flora by the insect fauna in this environment. However, the overall herbivory levels (e.g., proportion of herbivorized specimens and damage occurrences) are low, supporting previous observations about the contrasting diversity of plant-insect interactions in Gondwanan and Laurasian ecosystems.

From a total of 2523 tallied plant specimens, 186 bear evidence of some type of interaction (7.4%). Most of the observed damage was on *Glossopteris* foliage (162 specimens); with lesser consumption of sphenophytes (10 specimens) and ferns (7 specimens) (Fig. 7, S.I. 1). When accounted separately, 15% of the glossopterid specimens show evidence of arthropod herbivory, suggesting that they were preferentially targeted by insects; in contrast, only 3.47% of sphenophytes and 1.03% of fern specimens were herbivorized. The remaining floristic elements grouped together barely suffered any attacks (six specimens, 1.3%) (Fig. 7).

Given that one specimen could host more than one type of interaction, the number of recorded damages was higher than the number of affected plant specimens, adding up to 234 traces within 36 distinct damage types (DTs), in addition to a few undetermined examples (Table 1). If the presence of mining is confirmed, then all foliar, arthropod-mediated functional feeding groups of Labandeira et al. (2007) would be represented in the La Golondrina Formation. The most common feeding modes were oviposition, accounting for 34% of DT occurrences, and external foliage feeding (MF 25% + HF 11% + SF 10% + Sk 1% = 47% of DT occurrences). Less common are piercing and sucking (9% of DT occurrences) and galling (7% of DT occurrences) (Table 1).

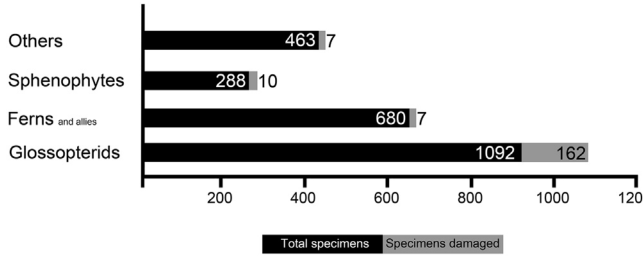

Fig. 7. Preferred plant targets.

Table 1
Number of interactions recorded on main vegetation groups.

	MF	HF	SF	SK	P&S	Gall	Ovip	Indet	Totals
Glossopterids	41	26	22	1	20	16	79	5	210
Ferns and allies	7	0	0	0	0	0	0	0	7
Sphenophytes	7	0	2	0	0	1	0	0	10
Lycophytes	0	0	0	0	1	0	0	0	1
Indets + others	3	0	1	0	1	0	1	0	6
Totals	58	26	25	1	22	17	80	5	234

Among external foliage feeding, the presence of margin feeding was most frequently observed (58 occurrences). Within this functional feeding group, the most commonly recorded (43 occurrences) was DT12, a generalized type of leaf consumption along the margin varying in degree from shallow to deep excisions. This kind of damage was observed in glossopterids, sphenophylls, ferns, cordaitaleans and other elements. The rest of the identified DTs from this functional feeding group are represented by nine or fewer cases, and only on glossopterid foliage. Notably, DT13, a type of damage common in *Glossopteris* leaves from other Gondwanan localities (i.e., Prevec et al., 2009) that is characterized by the removal of the leaf apex, was not recognized in this flora, probably as a result of smaller sample size, and fewer leaves with complete apical regions preserved. Surface and hole feeding both occurred considerably less frequently than margin feeding (25 and 26 occurrences, respectively). Oviposition and hole feeding are the functional feeding groups with the largest number of DTs (7) represented in the collection, whereas the other common FFGs were represented by six or fewer DTs each. Lastly, although skeletonization had been observed by the author in older collections, it remains a very rare damage type, with a questionable DT17 observed in a single specimen.

Feeding on internal plant fluids by piercing-and-sucking insects was observed in glossopterid leaves and potentially on a lycophyte microphyll. Considered to be a host-specific type of feeding (Labandeira et al., 2007), it was recorded in 22 cases, as five identifiable DTs.

Remarkably, 17 galls were documented under five DTs, DT107 occurring the most (eight cases), further suggesting there was a rich invertebrate fauna associated with this *Glossopteris* flora. Moreover, an example of a gall on a sphenophyll is here recorded for the first time.

Finally, although oviposition does not involve consumption of leaf tissue, it is considered a FFG based on the scarring left on plant specimens in response to the egg insertion into the tissues (Labandeira et al., 2007). Seven DTs reflecting oviposition were detected in a total of 80 cases in the La Golondrina Formation flora, all (with the exception of one case on the seed fern *Kladistamuos*) in glossopterid foliage.

5. Discussion

5.1. The La Golondrina Formation flora

The dominance of glossopterids in this paleoflora, followed by ferns and sphenophylls, partly explains the greater number of observations of plant-insect interactions on these hosts. Even so, differences in herbivory between the glossopterids and the other two plant groups may be a function of leaf lamina size (the larger laminae of glossopterids presenting a more extensive area for exploitation in various ways), as opposed to the more highly divided fern pinnules and sphenophyll leaflets (i.e., Brown et al., 1991). Activities, such as margin feeding in particular, would require greater energy input in the case of smaller leaves, as the insect would have to move more regularly between leaves.

The interactions documented in the paleoflora from the La

Table 2

Comparison of selected northern vs. southern hemisphere Permian floras.

	Sample size	Herbivorized specimens	Number of attacks	Total DTs	Age	References
KwaZulu-Natal (South Africa)	9772	137 (1.4%)	n/s	22	Wuchiapingian–Changhsingian	Prevec et al., 2009
La Golondrina (Argentina)	2523	186 (7.4%)	234 (9.3%)	36	?Artinskian–?Changhsingian	This work
Tepuel-Genoa (Argentina)	291	78 (27%)	n/s	12	Cisuralian (unkown)	Gallego et al., 2014
Colwell Creek Pond (USA)	2140	649 (30.3%)	1390 (64.9%)	52	Kungurian	Schachat et al., 2014
Coprolite Bone (USA)	598	93 (15.6%)	137 (22.9%)	11	Artinskian	Labandeira and Allen, 2007
Paraná Basin (Brazil)	850	68 (8%)	96 (11.3%)	14	Sakmarian–Artinskian	Souza Pinheiro et al., 2012
Taint (USA)	1346	428 (31.8%)	n/s	8	Sakmarian	Beck and Labandeira, 1998

Golondrina Formation can be considered a consequence of three main behaviors: feeding, reproduction and sheltering. Feeding is represented by a wide spectrum of evidence, including continuous and non-continuous marginal feeding varying from shallow to deep excisions, recorded predominantly in glossopterids, but also in sphenophyll leaflets, fern-like pinnules, cordaitalean foliage and *Megistophyllum* sp., a plant of ginkgoalean affinity. Hole feeding was found only on glossopterid foliage, whereas surface feeding was also observed in sphenophyllaleans. All three types of consumption are considered to be generalized herbivory modes made by mandibulate insects. Piercing and sucking, on the other hand, requires sophisticated mouthpart structures that allow precise puncturing of the plant tissues, making of this feeding mode usually more host- and organ-specific (Labandeira and Phillips, 1996; Xu et al., 2018).

In the case of the La Golondrina Formation flora, insect reproduction is extensively recorded in the form of oviposition scars, and with one exception, this occurred exclusively on *Glossopteris* leaves. The benefit of oviposition on plants as a reproductive strategy is the protected environment it provides for the development of the nymph or larva; therefore, finding the most suitable substrate plays a key role. The abundant and diverse oviposition marks on glossopterid foliage indicate that these leaves were preferentially targeted by insects, further suggesting a relatively high specificity.

Sheltered reproductive environments are also evident in the form of possible mines and several galls found in many *Glossopteris* specimens, as well as the first recorded example on a *Sphenophyllum*. Galls are produced by a range of organisms besides to insects, such as mites, fungi, viruses and bacteria. In insects, the oviposition by the female can generate an abnormal tissue growth that forms a chamber in which the nymph will stay until reaching a more advance stage of development. Consequently, besides shelter, the gall also provides nutrients for the developing insect. Galls are considered to be highly specialized interactions, usually developing in specific plant-specimens or organ-sites, such as twigs or the midvein of a leaf. In the La Golondrina Formation flora, galls were recognized only on foliage. Evidence of mining, on the other hand, is still ambiguous for this as well as most Paleozoic floras (Beck and Labandeira, 1998; Adami-Rodrigues et al., 2004a; Prevec et al., 2009; Slater et al., 2015), although what seems to be the unequivocal first record of this kind of interaction has been described on the seed fern *Vjaznikopteris rigida* Naugolnykh, from the Permian-Triassic boundary in the Volga River Basin, Russia (Krassilov and Karasev, 2008).

More than one type of interaction commonly occurs on glossopterid leaves from the La Golondrina Formation. Their larger size and greater abundance in the flora probably contributed to the higher incidence of interactions compared to the other plant groups. Similarly, preferential feeding on plants with larger leaf blades has been observed in Permian assemblages from Cathaysia (e.g., Glasspool et al., 2003), Gondwana (e.g., Adami-Rodrigues et al., 2004b) and Euramerica (e.g., Labandeira and Allen, 2007) adding to the idea of megaphyllous leaves providing a multipurpose resource for insects. Another remarkable aspect of these leaves is the apparent absence of trichomes or glands for defense. In fact, of the many species of *Glossopteris*, few have been described with epidermal structures (Srivastava, 1969; Guerra-Sommer, 1992; Maheshwari and Tewari, 1992; Degani-Schmidt and Guerras-Sommer, 2016). Although the presence of trichomes does not necessarily imply an anti-herbivory mechanism for the plant, their presence could discourage the consumption of tissues by impeding insect movement or requiring specialized mouthparts to overcome these physical impediments. The ferns from the La Golondrina Formation, however, had stems densely covered in trichomes, potentially acting as deterrents to herbivorous insects. This is certainly a topic that requires further exploration.

5.2. *Comparison with other Permian floras*

The Permian flora from the La Golondrina Formation repeats some of the herbivory patterns observed in other studies, such as the preferential targeting of megaphylls and the predominance of external foliage feeding over other functional feeding groups. However, there are several other patterns that are worth noting. When comparing the proportion of herbivorized specimens between the Northern and Southern Hemisphere impression/compression floras, the values are remarkably higher for those in the north than in the south (Table 2). Although the recorded herbivory levels for three Early Permian paleofloras from the US yielded values ranging from 15 to 31% (Beck and Labandeira, 1998; Labandeira and Allen, 2007; Schachat et al., 2014, 2015), all values from Gondwanan floras fall below 8% (Prevec et al., 2009; Souza Pinheiro et al., 2012; this study). The Early Permian Tepuel-Genoa paleoflora (Chubut, Patagonia Argentina) is the only exception, with an observed herbivory level of 27%, closer to the values from the northern Permian floras. However, Gallego et al. (2014) stated clearly that only glossopterid, *Cordaites* and *Ginkgoites* foliage were considered in their study 'since they host all of the observed arthropod damage types' (p. 102); the exclusion of other plant groups generating a bias towards a highly herbivorized sample. Because the Tepuel-Genoa paleoflora is abundant and anomalously diverse for its age (Cúneo, 1996), a full account of the plant taxa and its insect-mediated damage would probably yield lower herbivory levels, perhaps approximating the values observed in the other *Glossopteris* floras analyzed. The low herbivory levels exhibited by southern floras (located in mid to high paleolatitudes, e.g., 30° and above) in contrast to those from the north (located in equatorial paleolatitudes) seems to be a consistent pattern, evidenced by the fact that even when sample sizes are increased considerably, the proportion of herbivorized specimens still did not show meaningful variations (Table 2).

When compared to other *Glossopteris* floras, the La Golondrina flora shares most similarities with the Late Permian flora from South Africa (Prevec et al., 2009) in the abundance of oviposition and external foliage feeding. Although present, oviposition was not a common interaction in either the Brazilian or the Tepuel-Genoa floras (Adami-Rodrigues et al., 2004a, 2004b; Souza Pinheiro et al., 2012; Gallego et al., 2014). By contrast, the Colwell Creek Pond and Mitchell Creek Flats floras from North America yielded various oviposition types (Beck and Labandeira, 1998; Labandeira and Allen, 2007; Schachat et al., 2014, 2015). A similar pattern is evident regarding galling; this type of interaction was rarely recorded in most Gondwanan Permian floras, whereas in the Colwell Creek Pond, Mitchell Creek Flats and La

Golondrina floras, galls were diverse and abundant (Table 2).

Finally, there seems to be a positive correlation between the total number of identified DTs and sample size, as noted from this and other studies (Prevec et al., 2009; Schachat et al., 2014). Overall, fewer DTs were recognized in studies with smaller sample sizes, whereas those with > 2000 specimens yielded a greater variety of damage, even in those cases where the level of herbivory was low (Table 2). A plausible explanation for this could be that vegetational groups in the Northern Hemisphere had characteristics that made them more palatable to insects than those in the south (predominantly glossopterids) so that herbivory levels would remain low, even if feeding strategies diversified. Alternatively, it could be reflecting latitudinal differences, as seen from the considered northern floras, located at low latitudes, whereas those from the south were located at middle to high latitudes during the Permian (Scotese, 2014; McLoughlin, 2001). As several recent studies have indicated, plant-insect interactions in extant floras show a latitudinal gradient, being more intense towards the equator (i.e., Coley and Barone, 1996; Adams and Zhang, 2009; Moles et al., 2011), tracking general insect diversity patterns. Although more studies are needed to attest such latitudinal gradient in fossil floras, this trend seems to have been consistent in Permian vegetation assemblages.

6. Conclusions

The importance of the present work stems from the qualitative observations and the semi-quantitative analysis that not only allowed the recognition of various new damage types, but also the herbivory patterns occurring in this flora. This adds to our understanding of food web complexity in past terrestrial ecosystems, especially during a time where events of global magnitude that shaped the biota occurred, including the total retraction of the polar ice caps which initiated during the Carboniferous and a series of extinctions from the Middle Permian until the end of the period, culminating in the greatest mass extinction ever recorded.

Although in-depth comparisons with coeval floras are partly hampered by differences in sampling, preservational style and the type of analyses conducted, these preliminary results show that some herbivory patterns (i.e., the preferential targeting of megaphylls, the predominance of external foliage feeding over other functional feeding groups, and the low herbivory levels, similar to those in other Gondwanan assemblages but different with the Northern Hemisphere ones), are consistent with those observed in other Permian plant-insect interaction studies. The La Golondrina Formation flora was abundant and diverse, and the richness of damage types recognized suggests that the associated invertebrate fauna was similarly diverse and prevalent.

Even though in recent years research focusing in fossil plant-insect interactions has greatly increased, it is clear that more studies following a standardized protocol for sampling and identification of damage types are needed to fully understand how the ecosystems functioned and in which ways environmental variables affected them.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2018.06.022.

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