

New evidence of plant-insect interactions in the Lower Permian from Western Gondwana

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ABSTRACT

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A new record of insect damages-containing glossopterid leaves is recovered from the Rio da Estiva outcrop, Itaiópolis country, northernmost Santa Catarina State, southern Brazil. The plant fossil-bearing strata are situated, stratigraphically, from the basal to middle part of the Rio Bonito Formation, a unit of the Lower Permian sequence of the Paraná Basin. This plant assemblage is characterized as “pure *Glossopteris* Flora”, and contains remains of glossopterid leaves (*Glossopteris* spp. and *Gangamopteris* sp.), seeds (*Samaropsis* sp. and *Cordaicarpus* sp.) and fructification (*Ottokaria* sp.). We analyzed 102 samples, of which only ten showed evidence of insect damages. Three types of leaf feeding traces are observed: leaf margin feeding traces, hole feeding traces and trench feeding traces. The damages occurred in leaves of *Glossopteris* sp., *Glossopteris communis*, *Glossopteris occidentalis* and *Gangamopteris obovata*. The evidence of consumption of foliar tissues indicated that glossopterids hosted a functional feeding group of predominantly chewing and sucking type of insects. The differences found in the patterns and frequencies of consumption in different localities of equivalent ages suggested that herbivory was more intensive in some plant communities than in others. Besides this, the present study expanded geographically the distribution of records of plant-insect interactions in “*Glossopteris* flora” through the central portion of the eastern rim of Paraná Basin.

Key-words—*Glossopteris* flora, Herbivory, Rio Bonito Formation, Paraná Basin, Early Permian.

पश्चिमी गोंडवाना से प्राप्त निम्न पर्मियन में पादप-कीट अन्योन्य-क्रियाओं का नवीन प्रमाण

ई आर एस पाइन्हीरो, जी.पी. टायबुश एवं राबर्टो इआन्नुज़ी

सारांश

रियो डा एस्टिवा शैल दृश्यांश, ईटइओपोलिस देश, सुदूरउत्तरी सैंटा कैटरिना राज्य, दक्षिणी ब्राज़ील से कीट क्षति-ग्लोसोप्टेरिड पत्तियां सन्निहित नवीन अभिलेख प्राप्त हुआ है। पादप जीवाश्म-धारी पट्टीदार पराना द्रोणी निम्न पर्मियन अनुक्रम की यूनिट रियोबॉनिटो शैलसमूह के आधार से मध्य भाग तक स्तरिक रूप में स्थित हैं। पादप समुच्चय “शुद्ध ग्लोसोप्टेरिस वनस्पति-जात” के रूप में विशिष्ट गुणयुक्त है तथा ग्लोसोप्टेरिड पत्तियों (*ग्लोसोप्टेरिस* जातियां व *गंगामोप्टेरिस* जाति), बीज (*सैमरॉप्सिस* जाति व *कॉर्डैकार्पस* जाति) एवं फलनों (*ओट्टोकेरिया* जाति) के अवशेष सन्निहित हैं। हमने 102 नमूने विश्लेषित किए जिनमें से दस ने कीट क्षति के प्रमाण दर्शाए। तीन तरह के पत्ती आहार अनुपथ प्रेक्षित किए गए हैं: पत्ती उभ्रत आहार अनुपथ, छिद्र आहार अनुपथ एवं खांचा आहार अनुपथ। *ग्लोसोप्टेरिस* जाति, *ग्लोसोप्टेरिस कम्युनिस*, *ग्लोसोप्टेरिस ओसिडेंटैलिस* एवं *गंगामोप्टेरिस ओबोवेटा* की पत्तियों में क्षति हुई। पर्णिल उतकों के उपभोग के प्रमाण ने इंगित किया कि ग्लोसोप्टेरिडों ने प्रबल पूर्व चबाने के एक क्रियात्मक आहार समूह तथा चूषक प्रकार के कीटों की परपोषी की। सम आयु की विविध उपवस्तियों में खपत के प्रमाणों एवं आवृत्तियों में पाए गए भेदों ने सुझाया कि कुछ पादप समुच्चयों की अपेक्षा अन्य में शाकाहारी वर्ग ज़्यादा गहन था। इसके अलावा, मौजूदा अध्ययन ने पराना द्रोणी में पूर्वी परिधि के मध्य भाग से “*ग्लोसोप्टेरिस*पेड़-पौधे” में पादप-कीट परस्पर क्रियाओं के अभिलेखों को भौगोलिक रूप से विस्तृत किया।

संकेत-शब्द—*ग्लोसोप्टेरिस* पेड़-पौधे, शाकाहारी वर्ग, रियो बॉनिटो शैलसमूह, पराना द्रोणी, पर्मियन पूर्व।

Novas evidências de interações inseto-plantas no Permiano Inferior do Gondwana

RESUMO

Um novo registro de folhas de glossopterídeas contendo danos por insetos foi obtido no afloramento de Rio da Estiva, município de Itaiópolis, região norte do Estado de Santa Catarina, no Brasil meridional. Os estratos portadores dos fitofósseis estão situados, estratigraficamente, na porção basal a mediana da Formação Rio Bonito, uma unidade do Permiano Inferior da Bacia do Paraná. Esta assembléia fitofossilífera é considerada como uma "Flora de *Glossopteris* pura", contendo restos de folhas de glossopterídeas (*Glossopteris* spp. e *Gangamopteris* sp.), sementes (*Samaropsis* sp. e *Cordaicarpus* sp.) e frutificações (*Ottokaria* sp.). Foram analisadas 102 amostras, das quais somente dez mostram evidências de danos por insetos. Três padrões de consumo foliar foram observados: traços de alimentação marginal, traços de alimentação circular e de alimentação linear sobre lâmina. Os danos foram observados em folhas de *Glossopteris* sp., *Glossopteris communis*, *Glossopteris occidentalis* e *Gangamopteris obovata*. A evidência de consumo de tecidos foliares indica que as glossopterídeas eram herbivorizadas por insetos predominantemente com aparelho bucal mastigador. As diferenças encontradas nos padrões de frequência de herbivoria entre as diferentes localidades de idades equivalentes sugeriram que a atividade foi mais intensa em algumas comunidades do que em outras. Além disso, o presente estudo expandiu geograficamente a distribuição de registros de interação inseto-planta na flora de *Glossopteris* através da porção central da margem oriental da Bacia do Paraná.

Palavras-chave—Flora de *Glossopteris*; Herbivoria, Formação Rio Bonito, Bacia do Paraná, Eopermiano.

INTRODUCTION

The analysis of interactions between plants and insects in the fossil record is an expanding field in Palaeontology. Herbivory is normally studied through the evidences preserved in leaf compressions and impressions, since leaves are the most common plant organ in the fossil record. The evidence of plant-insect interactions for the Palaeozoic includes herbivory, galls, possible mines, oviposition and leaf skeletonization (Beck & Labandeira, 1998; Adami-Rodrigues *et al.*, 2004a). To recognize herbivory in the fossil record, it is normally necessary to detect the presence of plant reaction tissues such as calluses or anomalous tissues induced by trauma while the plant organ was still alive (Meyer & Maresquelle, 1983; Labandeira, 1998).

The record of vascular plants, arthropods, and their probable interactions is well described for the Palaeozoic. The Palaeozoic insects are comparable to modern forms in terms of mouthparts (Labandeira, 1997) and functional feeding groups (Labandeira, 1998). Some authors have suggested that groups of insects have been herbivorous since the Palaeozoic (Popov & Wootton, 1977; Labandeira, 1998), and some were already endophytic (Labandeira & Phillips, 1996). Records of plant-insect associations start in the Devonian but become more common during the Carboniferous, highlighting especially those from coal balls associated with Euroamerican swamp forests (Scott & Taylor, 1983; Scott *et al.*, 1985; Labandeira & Beal, 1990; Chaloner *et al.*, 1991; Scott *et al.*, 1992; Labandeira & Phillips, 1996; Labandeira *et al.*, 1997; Labandeira, 1998, 2002, 2006). In comparison, studies on phytophagy for that period are extremely rare in Gondwana (Iannuzzi & Labandeira, 2008).

For the Permian, the direct evidence of plant-insect associations decreased in general globally. In Gondwana, these records are even more scarce (Labandeira, 2002, 2006). For the Indian Permian deposits, Chauhan *et al.* (1985), Srivastava (1987, 1996), Srivastava and Srivastava (2010), Srivastava and Agnihotri (2011) reported evidence of plant consumption by arthropods. Guerra-Sommer (1995) and Adami-Rodrigues *et al.* (2004a, b) described evidence of phytophagy in glossopterids for the Lower Permian in Brazil. Prevec *et al.* (2009) identified new evidence of plant-insect associations in the South African Upper Permian strata. Recently, McLoughlin (2011) described galls and oviposition scars from Permian glossopterid foliage from Australia and South Africa.

During the Permian, the Gondwana continent was almost entirely covered by a well-known vegetation known as "*Glossopteris* flora" (Wnuk, 1996). Particularly, in the Paraná Basin, the record of "*Glossopteris* flora" is mostly characterized by remains of sphenopsid stems (*Paracalamites* sp.) and leaf shoots (*Phyllothea* spp., *Sphenophyllum* spp., *Schizoneura* sp.), lycopsid stems (*Brasilodendron* sp., *Lycopodiopsis* sp.), fronds of ferns (*Pecopteris* spp., *Sphenopteris* spp.), leaves of glossopterids (*Glossopteris* spp., *Gangamopteris* spp.) cordaitaleans (*Cordaites* sp.) and seeds (*Cordaicarpus* spp., *Samaropsis* spp.), among other types of plant remains (Rösler, 1978; Bernardes-de-Oliveira, 1980; Rohn & Rösler, 2000; Iannuzzi & Souza, 2005; Tybusch & Iannuzzi, 2008; Iannuzzi, 2010).

Records of foliar feeding traces are rare for Gondwana as a whole. In this context, our main goal was to report and analyze new evidences of plant-insect interactions found in the *Glossopteris* flora plant assemblage from the Lower Permian of the Paraná Basin, southern Brazil. This contribution is part of the Master Thesis of the senior author (E.R.S. Pinheiro).

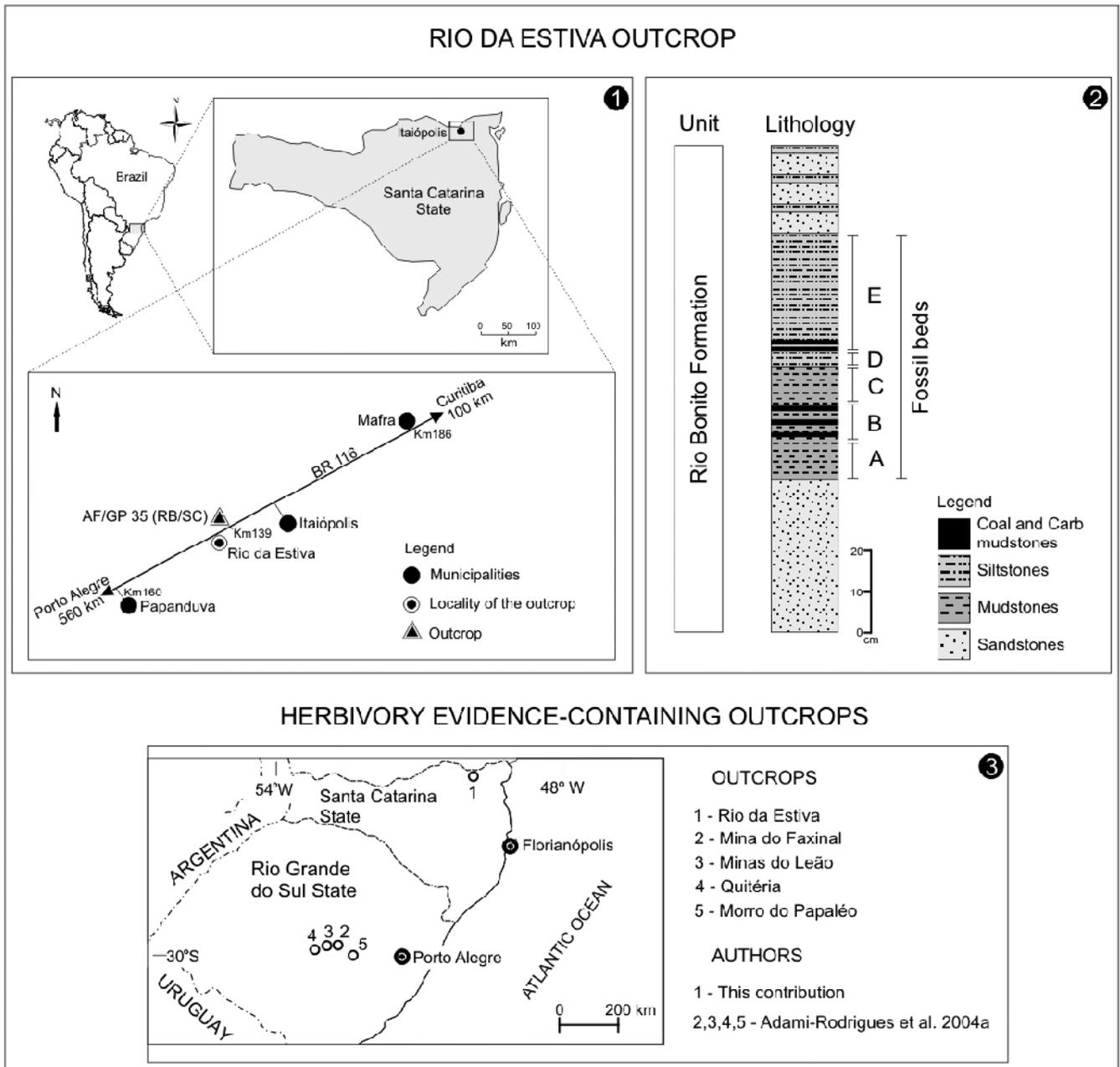


Fig. 1—Location map (1) and stratigraphic section (2) of the Rio da Estiva outcrop, Santa Catarina State, southern Brazil. (3) Distribution of all known herbivory evidence-containing outcrops found in the Lower Permian of the Paraná Basin, including the Rio da Estiva outcrop.

MATERIAL AND METHODS

The material studied was recovered from the Rio da Estiva outcrop (26°16'S - 49°53'W), which is revealed by a narrow road cut on highway BR-116 (Km 139), between Mafra and Papanduva counties, and in the Itaiópolis county, northernmost Santa Catarina State (Fig. 1). The plant fossil-bearing strata are situated, stratigraphically, in the basal to middle part of the Rio Bonito Formation (Fig. 1), a unit of the Lower Permian sequence in the Paraná Basin (Rösler, 1975).

These strata consist mainly of thin mudstones containing several coal-bearing lenses interbedded with sandstone and siltstone beds; the total exposure is only 60 cm thick (Rösler, 1975).

The plant assemblage was defined by Rösler (1978) as “pure *Glossopteris* flora”, and contains impressions/compressions of glossopterid leaves (*Glossopteris* spp. and *Gangamopteris* sp.), seeds (*Samaropsis* sp. and *Cordaicarpus* sp.) and glossopterid fructifications (*Ottokaria* sp.) (Rösler, 1975, 1978). This assemblage was originally considered as

belonging to the Artinskian-Kungurian interval by Rösler (1978). However, an age between Late Sakmarian and Early Artinskian can be accepted for the assemblage because of recent advances in radiometric dating for correlative deposits of the Rio Bonito Formation from the Rio Grande do Sul State (Iannuzzi, 2010).

Medeiros and Thomaz-Filho (1973) characterized, sedimentologically, the area as a periodically flooded tidal flat within a deltaic system, which should explain by Rösler (1975) the succession of very thin coal lenses found along the fossiliferous beds. Despite this, Rösler (1975) did not resolve several questions about the interpretation of the depositional environment present in this outcrop section.

The samples are housed in the paleontological collection of the Department of Sedimentary Geology and Ambiental of the Instituto of Geociências, Universidade de São Paulo (GSA-IG-USP), in São Paulo, Brazil.

RESULTS

Initially, we inspected each leaf impression searching for the presence of all kinds of damage as described in the literature for the Permian (Beck & Labandeira, 1998; Adami-Rodrigues *et al.*, 2004a), such as: (a) feeding activity at the foliar apex, (b) leaf margin feeding, (c) hole feeding of foliar lamina, (d) trench feeding of the foliar lamina, (e) skeletonization, (f) oviposition scars, (g) punctures, (h) mines, and (i) galls.

However, in total, 102 samples of fossil leaves were analyzed, the insect-plant interactions were present in only ten of these samples and three types of damages were assigned for them: leaf margin feeding, hole feeding of foliar lamina, and trench feeding of the foliar lamina.

Feeding traces

a. Leaf margin feeding traces

Specimens studied (Pl. 1.1, 2)

Glossopteris sp.: GP/3T2441(A) and GP/3T2443;

Glossopteris communis Feistmantel 1876: GP/3T2447, GP/3T2448, and GP/3T2449;

Gangamopteris obovata (Carruthers) White 1908: GP/3T2450.

Description—Marginal traces of foliar excision. There is the presence of a plant defense mechanism with clear reaction tissue rims, evidenced by a thickening of the coloured contour surrounding the leaf edge where phytophagy has taken place.

Dimensions—Excisions 5 to 17 mm long on the foliar edge.

b. Hole feeding traces

Specimens studied (Pl. 1.2, 3, 5)

Glossopteris sp.: GP/3T2441(A), GP/3T2441(B), GP/3T2441(C), and GP/3T2441(D);

Glossopteris communis: GP/3T2445, GP/3T2447, and GP/3T2448.

Description—Complete consumption of all foliar tissues within a circumscribed region of a leaf, resulting in circular polylobate surface patterns surrounded by apparently a pronounced reaction rims similar to the ones described above to *foliar margin feeding*. The cavity resulting from removal has the major axis aligned with the direction of secondary venation of the foliar lamina.

Dimensions—Ellipses with the major axis ranging from 0.5 to 9 mm in length.

c. Trench feeding traces

Specimens studied (Pl. 1.2, 4, 5, 6, 7)

Glossopteris sp.: GP/3T2441(A), GP/3T2441(B), GP/3T2441(C), GP/3T2441(D), and GP/3T2443;

Glossopteris communis: GP/3T2439(A), GP/3T2439(B), GP/3T2446, and GP/3T2447;

Glossopteris occidentalis White 1908: GP/3T2442.

Description—Elongate structures parallel to the secondary venation of the leaf, surrounded by a reddish

PLATE 1



Evidence of herbivory in glossopterid leaves from the Rio da Estiva outcrop, in the Lower Permian strata from the southern Paraná Basin. In:

1. *Gangamopteris obovata* (GP/3T 2450), with evidence of foliar margin feeding.
2. *Glossopteris* sp. (GP/3T 2441A), showing margin, ovoid and linear consumptions.
3. *Glossopteris communis* (GP/3T 2445), exemplifying ovoid removal of foliar lamina (arrow).
4. *Glossopteris communis* (GP/3E 2439B), with linear removal of foliar lamina.
5. *Glossopteris* sp. (GP/3T 2441B), with ovoid and linear removals.
6. *Glossopteris occidentalis* (GP/3T 2442), general view of leaf showing linear removal of foliar lamina (arrow).
7. *Glossopteris occidentalis* (GP/3T 2442), detail of linear removal of foliar lamina, showing a reaction tissue rim and the parallel position in relation to the secondary venation.

Scales: white bars = 1 cm, black bar = 0.5 cm.

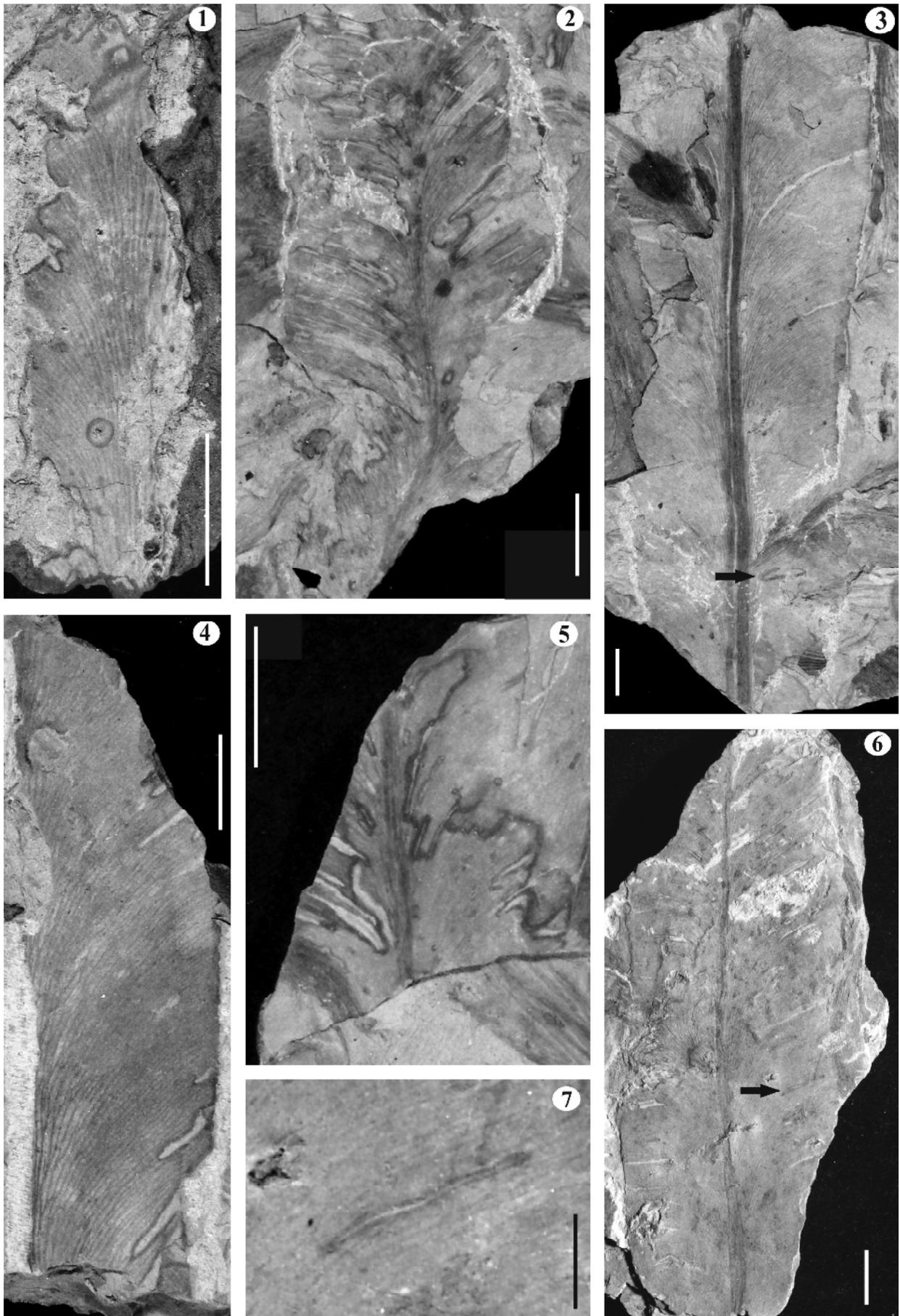


PLATE 1

	Leaf margin feeding	Hole feeding	Trench feeding
Santa Catarina State, Brazil (this paper)	<i>Glossopteris</i> sp. <i>Glossopteris communis</i> <i>Gangamopteris obovata</i>	<i>Glossopteris</i> sp. <i>Glossopteris communis</i>	<i>Glossopteris</i> sp. <i>Glossopteris communis</i> <i>Glossopteris occidentalis</i>
Rio Grande do Sul, Brazil (Adami-Rodrigues <i>et al.</i> , 2004a)	<i>Glossopteris</i> sp. <i>Glossopteris angustifolia</i> <i>Glossopteris brasiliensis</i> <i>Glossopteris</i> cf. <i>communis</i> <i>Cordaites hislopii</i>	<i>Glossopteris</i> sp. <i>Cordaites hislopii</i>	<i>Glossopteris communis</i> <i>Gangamopteris obovata</i> <i>Cordaites hislopii</i>
South Africa (Prevec <i>et al.</i> , 2009)	C2 C2a	C2a	-----
India (Srivastava and Agnihotri, 2011)	<i>Glossopteris communis</i>	<i>Glossopteris communis</i> <i>Glossopteris indica</i>	<i>Glossopteris stenoneura</i>

Fig. 2—Comparison of the feeding traces of the Rio da Estiva outcrop, Santa Catarina State, southern Brazil, with similar records found in the other Permian deposits of Gondwana.

reaction tissue similar to the others previous-mentioned damages.

Dimensions—Elongate structures, 2–12 mm in length on the longest axis.

DISCUSSION AND CONCLUSIONS

The samples studied from Rio da Estiva outcrop represent the first formal description of insect feeding traces on glossopterid leaves in the Permian deposits from Santa Catarina State (southern Brazil). This record extends the geographical distribution of these damage types to the centre of outcrop on the eastern rim of the Paraná Basin, which was previously restricted to the southern portion of this basin, e.g. localities from the Rio Grande do Sul State (see Fig. 1).

The Rio da Estiva outcrop is exceptional for the good preservation of the leaf impressions. The 10% of herbivory rate found, herein, can be considered high if the small number of available leaves for study (102 specimens in total) is taken into account. Adami-Rodrigues *et al.* (2004a), in a study also carried out in the Lower Permian of the Paraná Basin, obtained a herbivory frequency of only 8% in 352 samples analyzed. On the other hand, Beck and Labandeira (1998) found 31% of leaves with evidences of phytophagy on a total of 1041 leaves studied from Lower Permian deposits of north-central Texas. The rate of herbivory seems to be related to temperature, humidity, herbivore specificity, and also to sample size (Coley & Aide, 1991; Coley & Barone, 1996; Wilf *et al.*, 2005; Adams & Zhang, 2010). This finding indicates that the influence of sampling effort on estimations of herbivory rates in geological records is a topic that deserves more attention and cannot be satisfactorily used to explain the rate obtained in our case.

Amongst the nine morphotypes of foliar damage described for the Permian (Beck & Labandeira, 1998; Adami-

Rodrigues *et al.*, 2004a), only three were found in the Rio da Estiva outcrop, e.g. margin feeding, hole and trench feeding traces of the lamina. The feeding traces found in Rio da Estiva outcrop are comparable to damage types (DT) reported by Prevec *et al.* (2009) and to insects traces observed by Srivastava and Agnihotri (2010) (Fig. 2). The leaf margin feeding traces are similar to DT12 (margin feeding: cusped excisions of leaf edge) and DT15 (margin feeding: trenched into lamina) described in morphotypes C2 and C2a of glossopterid leaves by Prevec *et al.* (2009). These features also are comparable to leaf margin feeding traces recorded in *Glossopteris communis* by Srivastava and Agnihotri (2010). Similarly, the hole feeding traces are comparable to DT03 (hole feeding: polylobate 1 to 5 mm diameter) found in glossopterid leaf morphotype C2a. (Prevec *et al.*, 2009), and to hole feeding traces found by Srivastava and Agnihotri (2010) in *Glossopteris communis* and *Glossopteris indica* Schimper 1874. However, the hole feeding traces from Rio da Estiva present larger diameter ranges (0.5 to 9 mm). The trench feeding traces are similar to those observed in *Glossopteris stenoneura* Feistmantel 1881 (Srivastava & Agnihotri, 2010), but are not comparable to any DTs reported by Prevec *et al.* (2009). The evidences of consumption of foliar tissues indicate that glossopterids hosted basically a functional feeding group of predominantly mandibulate insects in this plant assemblage likely as seen in other assemblages through the Gondwana.

In terms of the feeding traces, the patterns of margin feeding, which are observed here also, are the most extensively documented in terrestrial Palaeozoic compression deposits globally (Labandeira, 2006). We found this kind of damage in leaves classified as *Glossopteris* sp., *Glossopteris communis*, and *Gangamopteris obovata* (Fig. 2). However, this is the first record of margin feeding for the species *Gangamopteris obovata*. Margin foliar damage is attributed to orthopteroi-

insects, considering that mainly this group had this feeding habit during the Late Palaeozoic (Guerra-Sommer, 1995; Beck & Labandeira, 1998; Labandeira, 1998). However, Adami-Rodrigues *et al.* (2004a) suggested that primitive members of Coleoptera may also be candidates for the consumption of glossopterid external foliage, as that they have also been found in the Early Permian in the Paraná Basin.

Compared to margin feeding, the hole feeding has only intermittent and occasional records throughout the later Pennsylvanian and Permian (Labandeira & Allen, 2007). In the Rio da Estiva outcrop, ovoid and linear consumptions of the foliar lamina were found in specimens of *Glossopteris* sp. and *Glossopteris communis*. The linear removal has been observed in one specimen of *Glossopteris occidentalis* (Fig. 2). This differs a little bit from the results obtained by Adami-Rodrigues *et al.* (2004a) in the southernmost Paraná Basin, who found ovoid consumption in leaves of *Glossopteris* sp. and *Cordaites hislopilii* (Bunb.) Seward and Leslie 1908, and evidences of linear removal in impressions of *Glossopteris communis* and *Cordaites hislopilii*. However, the absence of damages in specimens of the genus *Cordaites* in Rio da Estiva outcrop is probable because it is not present in this locality. It is possible that these consumption patterns are associated with the activity of unknown primitive insects related to coleopterans (Adami-Rodrigues *et al.*, 2004a), since modern beetles of the families Chrysomelidae and Curculionidae produce morphological patterns of herbivory very similar to those found in the fossil record (Johnson & Lyon, 1993).

Curiously, the three kinds of phytophagy in the Rio da Estiva outcrop have larger dimensions compared to the other records of herbivory in glossopterids registered in Paraná Basin (Adami-Rodrigues *et al.*, 2004a). Differences in leaf area loss are related to temperature, and warmer environments show high rates of leaf area loss (Coley & Aide, 1991; Coley & Barone, 1996). Considering that Rio da Estiva outcrop is a site located further north in comparison with the others previously studied by Adami-Rodrigues *et al.* (2004a), located in the Rio Grande do Sul State (Fig. 1), this difference of herbivory pattern of consumption could be explained by a latitudinal gradient. Many studies indicate that low latitudes provide relative environmental stability, higher thermal energy, higher biodiversity and consequently more intense biotic interactions (Coley & Barone, 1996; Pennings & Silliman, 2005; Dyer *et al.*, 2007), which could be applied to plant-insect interactions.

In reality, a north-south floral gradient was actually recorded between Permian plant associations from the Rio Grande do Sul State and the others situated in northern parts of the basin. Iannuzzi (2010) highlighted this floral difference, indicating which plant taxa were restricted to each of these two areas. However, the author did not furnish a specific explanation for this phytogeographic pattern beyond emphasis the palaeogeographic latitudinal gradient existent. According to Iannuzzi (2010), a not yet determinate ecological factor linked

to this latitudinal gradient (for instance, temperature gradient, rainfall regime, etc.) could be probably responsible for this distinct north-south floral distribution.

Finally, comparing patterns and frequencies of consumption in Rio da Estiva outcrop with the study of Adami-Rodrigues *et al.* (2004a), both made with specimens from Lower Permian of Paraná Basin, it is possible to conclude that herbivory was more intensive in some plant communities than in others. These differences in the herbivory patterns can be explained by already above-mentioned latitudinal gradient, but also either by taphonomic processes, palaeoecological factors or simply because each depositional environment may represent a distinct flora and fauna, which may lead to different patterns of plant-insect interactions. All these topics deserve further investigation in future studies.

Therefore, the need is evident of a larger number of studies that approach insect-plant interactions from a palaeoecological perspective, focusing on understanding the patterns, process, and evolution of palaeocommunities.

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