

## FIRST REPORT OF FEEDING TRACES IN PERMIAN *BOTRYCHIOPSIS* LEAVES FROM WESTERN GONDWANA

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**ABSTRACT:** The genus *Botrychiopsis* consists of leaves with substantial heteromorphism, present in late Paleozoic Gondwanan floras. The genus is recorded in paleofloras from Australia, India, South Africa, Brazil, and Argentina, and occurs from the latest Mississippian to the early Permian. Here, we report and analyze the first record of plant-insect interactions found in the *Botrychiopsis*-type leaves from the basinal deposits of Permian Argentina and Brazil. The samples are from three different Permian deposits: Arroyo Totoral, Bajo de Véliz (Argentina), and Morro do Papaléo (Brazil). Evidence of insect-plant interactions was present in only eight of 154 specimens analyzed. We found evidence of margin and hole feeding damage made by insects. This represents the first evidence of plant-insect interactions in *Botrychiopsis* leaves from Permian Gondwanan deposits. The occurrence of herbivory only on the Permian species *B. plantiana* may indicate that consumption of these leaves began during this interval, not in the Carboniferous, as occurred with *Cordaites* leaves.

### INTRODUCTION

The genus *Botrychiopsis* consists of leaves with substantial heteromorphism, occurring in late Paleozoic Gondwanan floras. Archangelsky and Arrondo (1971) distinguished three species: *Botrychiopsis weissiana* (Kurtz) Archangelsky and Arrondo (1971), *Botrychiopsis valida* (Feistmantel) Archangelsky and Arrondo (1971), and *Botrychiopsis plantiana* (Carruthers) Archangelsky and Arrondo (1971). Later, Rigby (1985) erected an additional species from Australia, *Botrychiopsis ovata* (McCoy) Rigby (1983). Studies indicate that chronostratigraphy is important for the definition of distinct species of *Botrychiopsis* (Archangelsky and Arrondo 1971; Jasper et al. 2003). The genus is recorded in paleofloras from Australia (Rigby 1973; Retallack 1980), India (Srivastava 1997), South Africa (Rayner 1985, 1986; Rayner and Coventry 1985; Anderson and Anderson 1985; Kovács-Endrödy 1991), Brazil (Guerra-Sommer and Cazzulo-Klepzig 1993; Jasper et al. 2003), and Argentina (Archangelsky and Cúneo 1987; Andreis and Archangelsky 1996), and occurs from the latest Mississippian to the early Permian (Jasper et al. 2003; Césari et al. 2011). Some authors have suggested an association between the occurrence of the different species of *Botrychiopsis* and the presence at glacial-interglacial phases (Archangelsky and Arrondo 1971; Jasper et al. 2003).

*Botrychiopsis weissiana* is restricted to the late Carboniferous of Australia and South America. The morphological characters of *B. weissiana* include an alate basal portion of the frond, a twisted insertion of the pinnae with pronounced imbrications, and ovoidal-spatulate morphology of the frond apical pinnule (Table 1) (Archangelsky and Arrondo 1971). The species seems to have become extinct at the Carboniferous–Permian boundary (Jasper et al. 2003). In Argentina, *B. weissiana* is a valuable stratigraphic marker for the upper Paleozoic, and together with *Nothorhacopteris argentinica* and *Ginkgophyllum diazii*, its presence defines the *Nothorhacopteris-Botrychiopsis-Ginkgophyllum* (NBG) Zone (Late Mississippian to Early Pennsylvanian, according to

Césari et al. 2011), recognized in several Argentinean deposits, such as the Paganzo and Calingasta-Uspallata basins (Archangelsky et al. 1987).

In contrast, *B. plantiana* is temporally confined to the early Permian of Australia and South America (Jasper et al. 2003). The species has foliage with long bipinnate leaves and a robust main rachis. The lamina of the pinnules is entire, with the outline varying from sublobate-rhomboidal to elliptical. The pinnules have an open venation derived from the rachis veins, which are denser at the base and becomes more dispersed along the lamina (Table 1). In the southern Paraná Basin, Guerra-Sommer and Cazzulo-Klepzig (1993) proposed a phytozonation with *B. plantiana* occurring in association with abundant *Gangamopteris*-like leaves. This association represents the transition between the Sakmarian and Artinskian (Iannuzzi 2013). According to Guerra-Sommer et al. (1991, 2001), *B. plantiana* should be considered as the remaining representative of a plant group adapted to rigorous periglacial cold climates of global icehouse conditions (Montañez et al. 2007).

*Botrychiopsis valida* has been found in lower Permian deposits of India (Archangelsky and Arrondo 1971) and Brazil (Jasper et al. 2003). The species is identified by the presence of a robust and well-defined main rachis with solid longitudinal nervures, from which subopposite sessile pinnules emanate and with slightly acute insertion angles. These pinnules are variably decurrent to confluent, separate to slightly imbricate, and have entire laminae that may or may not have insertions on their borders (Table 1). The pinnules have an open venation, derived from the rachis nervures, denser in their basal and central portions and becoming diffuse through the distal portions of the pinnules, which branch two to four times (Archangelsky and Arrondo 1971; Jasper et al. 2003). Based on the range of this taxon, Jasper and others (2003) suggested a new phytozone for Paraná Basin deposits, the *B. valida* subzone, encompassing *B. valida* occurring in the late Artinskian–Kungurian interval. However, this subzone was considered invalid because its proposal contravened some of the rules established by the International Stratigraphic Guide (ISD),

TABLE 1.—Comparative chart of the morphological features useful for diagnosis of *Botrychiopsis* species from Gondwana based on descriptions by Archangelsky and Arrondo (1971), and Rigby (1973, 1989).

Morphological features	<i>B. weissiana</i>	<i>B. plantiana</i>	<i>B. valida</i>	<i>B. ovata</i>
Basal axis	Alate	Pinnate	Pinnate	Pinnate
Pinna insertion*	Twisted	Planate	Planate	Approx. planate
Pinna imbrications*	Pronounced	Slight	Slight	Slight
No. of pinnules per pinna*	7	9	5	13
Max. length of pinna*	6.5 cm	6 cm	5 cm	± 8.5 cm
Insertion angle of pinnae*	45° to 50°	45° to 70°	70° to 80°	20° to 35°
Pinnule shape*	base somewhat confluent; ovalate to subcircular	Sublobate-rhomboidal to elliptical	Undifferentiated confluent (pinnatifid)	Subcircular to orbiculate
Max. size of pinnules on pinnae*	3.1 × 2.0 cm	1.3 × 1.7 cm	± 1.5–2.0 cm	2.0 × 1.6 cm
Concrescence of pinnules	Basal and middle ones: separate; distal ones: somewhat confluent	Basal ones: separate; distal ones: slightly confluent	All confluent	Basal and middle ones: separate; distal ones: somewhat confluent
Apical pinnule	Ovoidal-spatulate	Spatulate with distal rounded margins	Rhombic with sinuous margins	Spatulate with distal rounded margins

\* Middle part of frond-like foliage (chart adapted from Archangelsky and Arrondo 1971)

according to Iannuzzi et al. (2007). In any case, *B. valida* is the last species of the genus *Botrychiopsis* to disappear in western Gondwana.

Finally, *B. ovata* is restricted to Australia, occurring in deposits of the upper Carboniferous to lower Permian. The most diagnostic morphological feature of the species is the occurrence of a large number (more than 10) of subcircular to orbiculate pinnules inserted on very long pinnae positioned in the middle portion of the frond (Table 1) (Rigby 1973). The stratigraphic range of *B. ovata* that was proposed by Rigby (1989) could be considered as the most long-lived species of the genus *Botrychiopsis* that existed in Gondwana.

Records of plant-insect associations begin in the Devonian (Labandeira et al. 2014) but become more common during the late Carboniferous, especially those from coal balls associated with Euramerican swamp forests (Scott and Taylor 1983; Chauhan et al. 1985; Scott et al. 1985, 1992; Labandeira and Beal 1990; Chaloner et al. 1991; Labandeira and Phillips 1996; Labandeira et al. 1997; Labandeira 1998, 2002, 2006). Records of phytophagy during the early Carboniferous are extremely rare in Gondwana (Iannuzzi and Labandeira 2008).

The number of records of herbivory found in Permian strata from Gondwana has increased considerably during the last decade. For the Indian Permian, Chauhan et al. (1985), Srivastava (1987), Maheshwari and Bajpai (1990), Pant and Srivastava (1995), and Banerji and Bera (1998) reported evidence of plant consumption by arthropods. Prevec et al. (2009) and McLoughlin (2011) analyzed types of plant-insect associations on glossopterids and other morphotypes from upper Permian beds of South Africa. Guerra-Sommer (1995), Adami-Rodrigues et al. (2004a, 2004b), and Pinheiro et al. (2012a, 2012b) described evidence of phytophagy in glossopterids from the early Permian in Brazil. In Argentina, Cariglini and Gutiérrez (2011) and Gallego et al. (2014) described plant-insect interactions from Argentinean Paleozoic basins. For Antarctica, Kellog and Taylor (2004) and Slater et al. (2012) analyzed examples of plant-animal interactions in coprolites. Finally, for Australia, Holmes (1995) described examples of margin feeding from the late Permian of New South Wales. McLoughlin (1994a, 1994b, 2011) analyzed new records of herbivore damage in samples from the upper Permian of the Sydney and Bowen Basins. Here, we report and analyze the first record of plant-insect interactions found in the *Botrychiopsis*-type leaves from Permian deposits of Argentina and Brazil.

## MATERIALS AND METHODS

### Geological Settings

The material was identified during a review of several paleontological collections from Brazil and Argentina. The samples with insect herbivore damage are housed in: (1) Museu de Paleontologia (MP) of the Departamento de Paleontologia e Estratigrafia of the Instituto de Geociências, at the Universidade Federal do Rio Grande do Sul (DPE-IGeo-UFRGS), Brazil, under prefix the MP-Pb; (2) Museu de Paleontologia of the Universidade Federal de Pelotas (MP-UFPe), Brazil, under the prefix NEP-B; and (3) Museo Paleontológico Egidio Ferruglio (MPEF), Argentina, under the prefix MPEF-Pb.

The samples are from the following three different Permian deposits:

1. Arroyo Totoral—This locality is in La Rioja Province, northwestern Argentina. The deposit containing the fossils belongs to the Paganzo Basin, Arroyo Totoral Formation, from the early Permian. The Arroyo Totoral Formation crops out in the Malanzán-Solca-Anzulón paleovalley, and is considered to represent fluvial and lacustrine depositional environments (Andreis et al. 1984; Cúneo and Archangelsky 1996).
2. Bajo de Véliz—Bajo de Véliz Formation crops out in the San Luis Province, western Argentina. This formation is found in the Paganzo Basin, is early Permian in age, and presents alluvial and lacustrine facies (Limarino et al. 1996).
3. Morro do Papaléo—The Morro do Papaléo outcrop is located in Mariana Pimentel municipality, Rio Grande do Sul state of southern Brazil. The locality belongs stratigraphically to the uppermost Itararé Group (Taciba Formation) that occurs in the Paraná Basin (Souza and Iannuzzi 2009; Pinheiro et al. 2012a), and represents lacustrine deposits from a major transgressive-regressive cycle named by Milani et al. (1998) as the Gondwana I Supersequence. The Morro do Papaléo locality is lower Permian (Souza and Iannuzzi 2009).

### Foliar Damage

We inspected each slab containing impressions/compressions of *Botrychiopsis* leaves from the above-mentioned collections. The samples were classified for the presence of damage types (DTs) and functional

TABLE 2.—*Fronde samples with evidence of plant-insect interaction from Permian basins in Argentina and Brazil.*

Prefix	Species	Locality	Damage type	Feeding group
MP-Pb 4706	<i>Botrychiopsis plantiana</i>	Morro do Papaléo	DT12	Margin
MP-Pb 4708 (a, b)	<i>Botrychiopsis plantiana</i>	Morro do Papaléo	DT12	Margin
MP-Pb 4710	<i>Botrychiopsis plantiana</i>	Morro do Papaléo	DT12	Margin
MP-Pb 4733(a, b)	<i>Botrychiopsis plantiana</i>	Morro do Papaléo	DT12	Margin
MP-Pb 2677	<i>Botrychiopsis plantiana</i>	Morro do Papaléo	DT02	Hole
MPEF-Pb 2822	<i>Botrychiopsis plantiana</i>	Arroyo Totoral	DT12	Margin
MPEF-Pb 2823	<i>Botrychiopsis cf. plantiana</i>	Arroyo Totoral	DT02	Hole
NEP-B 90	<i>Botrychiopsis plantiana</i>	Bajo de Véliz	DT12	Margin

feeding groups (FFGs) based on the Damage Type Guide of Labandeira et al. (2007). The evidence of herbivory is recognized in the fossil record by detecting the presence of plant reaction tissues such as calluses or other anomalous tissues induced by trauma while the plant organ was alive (Meyer and Maresquelle 1983 *apud* Labandeira 1998).

### RESULTS

In total, 154 samples of *Botrychiopsis* leaves were analyzed. Evidence of insect-plant interactions was present in only eight of these specimens (5.2%). With respect to localities, the number of specimens with interaction traces was: five from the Morro do Papaléo outcrop (Faxinal Section), two from the Arroyo Totoral outcrop, and one from the Bajo de Véliz outcrop (Table 2). Only two damage types belonging to two functional feeding groups described by Labandeira et al. (2007) were present:

#### DT12: Margin Feeding Traces

**Specimens Studied.**—*Botrychiopsis plantiana* (Carruthers) Archangelsky and Arondo (1971): MP-Pb 4706, MP-Pb 4708 (a, b), MP-Pb 4710, MP-Pb 4733(a, b), NEP-B 90, and MPEF-Pb 2822 (Figs. 1A–D, F, G, I, J, 2A–C).

**Locality.**—Morro do Papaléo, Bajo de Véliz, and Arroyo Totoral.

**Description.**—Marginal traces of pinnule excision. A response mechanism with clear reaction-tissue rims is evidenced by thickening and color difference of the contour surrounding the pinnule edge where phytophagy has taken place.

**Dimensions.**—Excisions from 1 to 9 mm long on the pinnule edge.

#### DT02: Hole Feeding Traces

**Specimens Studied.**—*Botrychiopsis cf. plantiana* (Carruthers) Archangelsky and Arondo (1971): MP-Pb 2677, and MPEF-Pb 2823 (Figs. 1E, H, 2D, E).

**Locality.**—Arroyo Totoral and Morro do Papaléo.

**Description.**—Complete consumption of all tissues within a circumscribed region of a pinnule, resulting in a circular surface pattern surrounded by pronounced reaction rims similar to those described above for margin feeding.

**Dimensions.**—Ellipses with the major axis ranging from 1 to 2 mm in length.

### DISCUSSION

This is the first evidence of plant-insect interaction in *Botrychiopsis* leaves from Permian Gondwanan deposits. The genus *Botrychiopsis* is represented by four species in Brazil, Argentina, South Africa, India, and Australia during the Late Mississippian–early Permian interval. However, damage was found only in *B. plantiana*, a species typical of the early Permian. Another species analyzed, *B. weissiana*, typical of the late Carboniferous of Argentina, did not exhibit any evidence of insect herbivory. Of the 154 samples studied, none was classified as *B. valida*.

Based on the kinds of damage types recorded, the specimens from Argentina differed from those from Brazil. The Brazilian outcrop had four examples of margin feeding, and only one of hole feeding, whereas the Argentinean sites showed one leaf with hole feeding and two leaves with margin feeding. The differences in damage recorded among the localities could be a consequence of variation in the depositional environments. Several authors have found that ecosystems in different successional stages may show different patterns of herbivory (Poorter et al. 2004; Vehviläinen et al. 2007; Leuschner et al. 2009), and this may be reflected in the fossil record. Another explanation is that each depositional environment is associated with a different insect fauna, which consequently had different patterns of plant consumption. Finally, the difference among sites may be merely a reflection of differences in various biostratigraphic and fossilization processes (Pinheiro et al. 2012a).

Permian feeding damage on megaphylls was found mostly in glossopterid (Adami-Rodrigues et al. 2004a, 2004b; Prevec et al. 2009; Srivastava and Agnihotri 2011; Pinheiro et al. 2012a, 2012b) and cordaitalean foliage (Adami-Rodrigues et al. 2004a, 2004b; Labandeira and Allen 2007). Another Permian group that was attacked is gigantopterid leaves (Beck and Labandeira 1998; Glaspool et al. 2003; Schachat et al. 2014). Compared to *Botrychiopsis* leaves, gigantopterid fronds show a broader spectrum of damage, including apical feeding traces and skeletonization. The margin and hole feeding traces described in *Botrychiopsis* leaves are the most frequent traces found in late Paleozoic floras. Interestingly, although the genus *Botrychiopsis* is found in Gondwana starting in the late Mississippian, but traces of herbivory were found only in Permian leaves, suggesting a time lag in herbivorization of ca. 27 myr, according to radiometric ages obtained in Australian (Iannuzzi and Labandeira 2008) and Argentinean (Césari et al. 2011) deposits. It seems that *Botrychiopsis* plants were not consumed during the Carboniferous, and when they began to be consumed during the early Permian, they display the most common form of damage, external foliage feeding. It was at this time that climate evolved from an icehouse phase to a hothouse phase (Montañez et al. 2007) which would have led to an expansion of the flora and an increase in the taxonomic diversity of winged insects, such as mayflies, archaic “dragonflies”, and early orthopteroid lineages, some of which were herbivorous (Labandeira and Currano 2013). It appears that the combination of climatic and faunal changes favored the consumption of plant genera that had been available since Mississippian times, such as *Cordaites* and *Botrychiopsis* (Archangelsky et al. 1987; Iannuzzi 2013), but were not previously consumed. Both genera present hole and margin feeding as the first functional feeding groups. The *Cordaites* leaves with evidence of plant-insect association were found in Brazilian deposits from Paraná Basin. Samples of *Cordaites hislopianii* showed traces of DT01, DT02, DT03, DT05, and DT12 (Pinheiro et al. 2012a). In contrast, *Botrychiopsis* leaves from Brazil and Argentina had only evidence of DT02 and DT12.

Margin feeding was the most frequent functional feeding group in *Botrychiopsis* leaves (six of the eight samples). This was expected, since margin feeding is the evidence of plant-insect interaction that is most extensively documented in terrestrial Paleozoic compression deposits



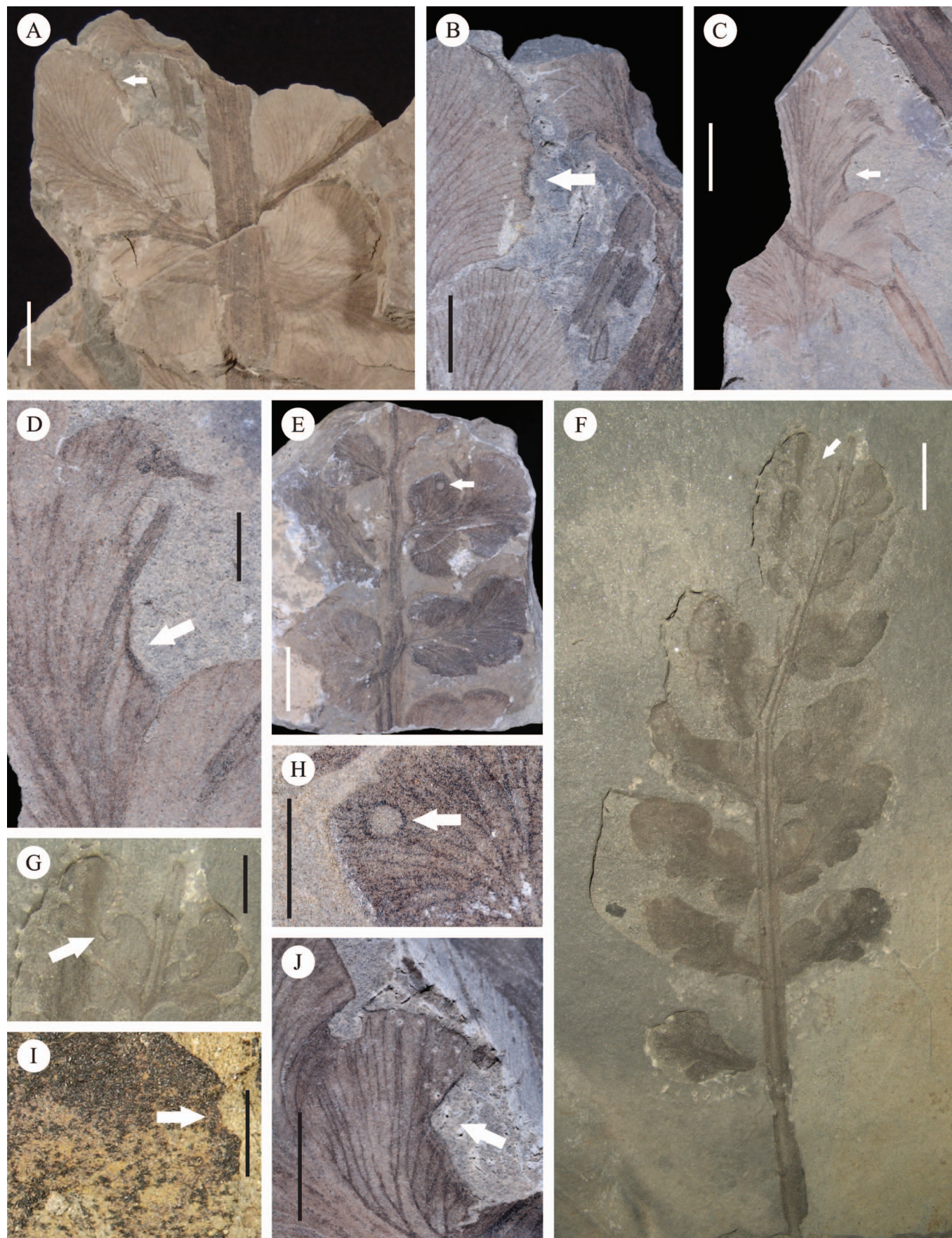


FIG. 1.—Evidence of herbivory in leaves of lower Permian strata from the southern Paraná Basin (Morro do Papaléo outcrop) and Paganzo Basin (Bajo de Véliz and Arroyo Totoral localities). **A)** *Botrychiopsis plantiana* (MP-Pb 4710) with evidence of margin feeding (DT12). **B)** Detail of *Botrychiopsis plantiana* (MP-Pb 4710). **C)** General view of margin feeding trace (DT12) in *Botrychiopsis plantiana* (MP-Pb 4733). **D)** Detail of *Botrychiopsis plantiana* (MP-Pb 4733). **E)** *Botrychiopsis plantiana*



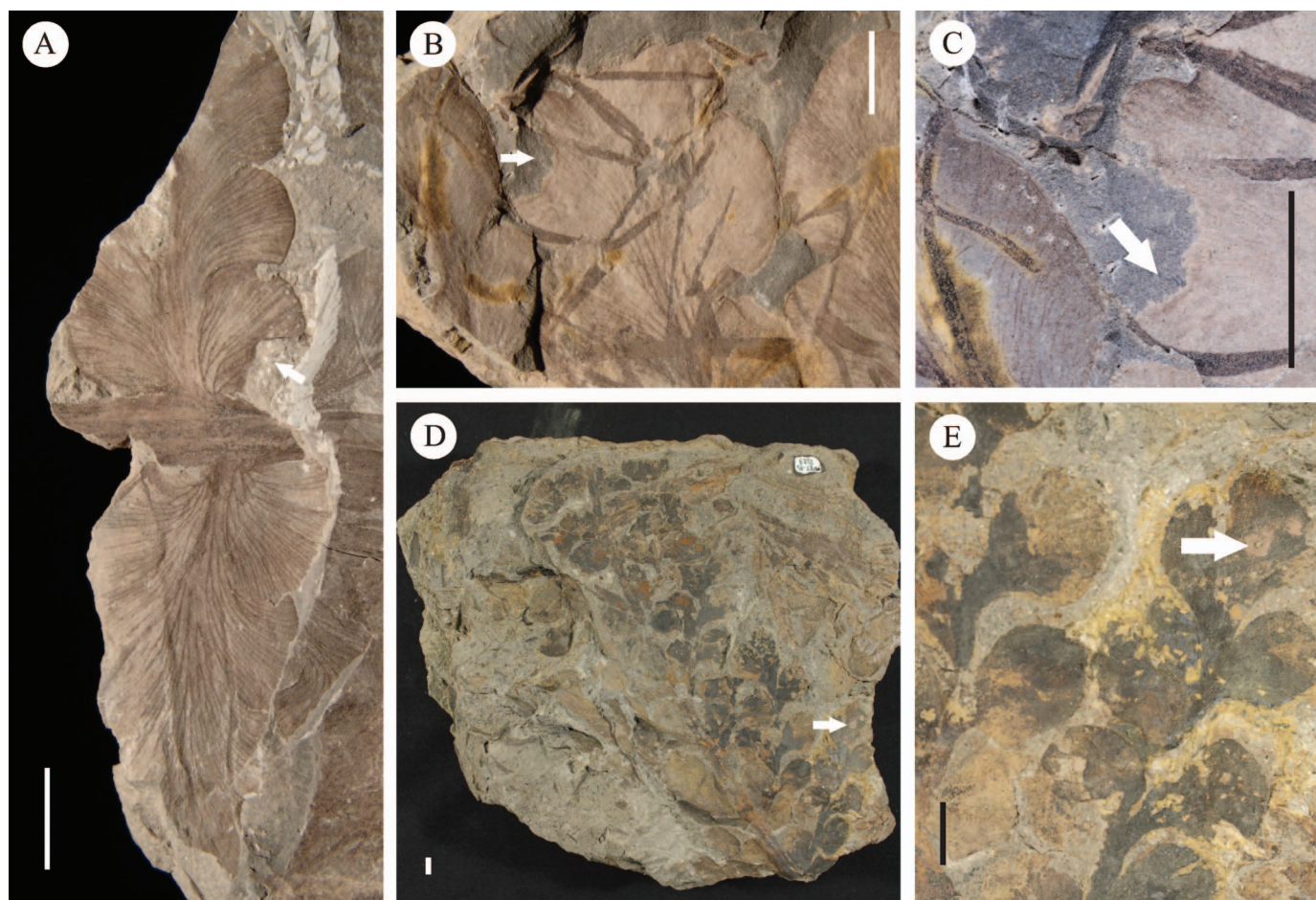


FIG. 2.—Evidence of herbivory in leaves of lower Permian strata from the southern Paraná Basin (Morro do Papaléo outcrop) and Paganzo Basin (Arroyo Totoral locality). **A**) *Botrychiopsis plantiana* (MP-Pb 4706) with evidence of margin feeding (DT12). **B**) General view of margin feeding trace (DT12) in *Botrychiopsis plantiana* (MP-Pb 4708). **C**) Detail of *Botrychiopsis plantiana* (MP-Pb 4733) with evidence of margin feeding (DT12). **D**) *Botrychiopsis* cf. *plantiana* (MPEF-Pb 2823) showing hole feeding trace (DT02). **E**) Detail of *Botrychiopsis* cf. *plantiana* (MPEF-Pb 2823). Scale bars: white = 1 cm, black = 0.5 cm.

(Labandeira 2006). This damage type is normally attributed to early lineages of orthopteroid insects (for classification of the group see Grimaldi and Engel 2005), and primitive members of Coleoptera. Both insect groups are found in South American upper Paleozoic deposits (Pinto and Adami-Rodrigues 1998).

Hole feeding is the second most common functional feeding group in Carboniferous–Permian deposits (Adami-Rodrigues et al. 2004a; Pinheiro et al. 2012a; Gallego et al. 2014) and could be 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 that are very similar to those found in the fossil record (Johnson and Lyon 1991). However, the earliest fossil occurrences of the families Chrysomelidae and Curculionidae are in the Middle Jurassic of Eurasia (Zherikhin and Gratshev 1993; Santiago-Blay 1994). Therefore, it seems to be more likely that the early orthopteroid lineages were responsible for these patterns of consumption (Pinheiro et al. 2012a).

## CONCLUSION

Our contribution is the first report of evidence for plant–insect interactions in *Botrychiopsis* leaves. The occurrence of insect herbivory only in the Permian species *B. plantiana* may indicate that consumption of these leaves began long after this plant appeared during the Carboniferous, as was the case with *Cordaites* leaves. This is an important pattern that should be better understood through future contributions that more broadly address the floristic and faunal evolution in Gondwana during the Carboniferous–Permian interval: why were certain groups of plants with large leaf laminae not attacked by insects during the Carboniferous? The difference between the damage types found in leaves from Brazil and those in Argentina can be explained by positing variable conditions among different depositional environments, which may have had different insect faunas. Our finding of margin and hole feeding traces was expected, since these two functional feeding groups are the most common types of herbivory described from the late Paleozoic. A review of

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(MP-Pb 2677) showing hole feeding trace (DT02). **F**) *Botrychiopsis plantiana* (NEP-B 90), exemplifying margin feeding (DT12). **G**) Detail of margin feeding in *Botrychiopsis plantiana* (NEP-B 90). **H**) Detail of hole feeding in *Botrychiopsis plantiana* (MP-Pb 2677). **I**) Detail of DT12 in *Botrychiopsis plantiana* (MPEF-Pb 2822). **J**) Detail of DT12 in *Botrychiopsis plantiana* (MP-Pb 4706). Scale bars: white = 1 cm, black = 0.5 cm.

paleobotanical collections, and the collection of new material from the field, would be very important to increase the knowledge of herbivory in ancient environments.

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