



PALEONTOLOGY

First record of insect-plant interaction in Late Cretaceous fossils from Nelson Island (South Shetland Islands Archipelago), Antarctica

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Abstract: Despite the enormous paleobotanical record on different islands of the Antarctic Peninsula, the evidence of insect activity associated with fossilized plants is scarce. Here we report the first evidence of insect-plant interaction from Cretaceous deposits, more precisely from a new locality at the Rip Point area, Nelson Island (Antarctic Peninsula). The macrofossil assemblage includes isolated *Nothofagus* sp. leaf impressions, a common component of the Antarctic paleoflora. Two hundred leaves were examined, of which 15 showed evidence of insect activity, displaying variations in size, shape, and preservation. Two types of interaction damage, galls and mines, were identified. A single specimen retained a circular scar recognized as galling scar, while meandering tracks were considered mines. These traces of herbivore insect activity, correspond to the oldest known record of this type of interaction of West Antarctica and the oldest record of insect-plant interaction in *Nothofagus* sp. reported so far.

Key words: Paleoecology, Nelson Island, insect-plant interaction, Cretaceous, Antarctica.

INTRODUCTION

Nowadays, Antarctica is the most inhospitable and isolated continent, protected by the Antarctic Treaty (Santos 2021, Sampaio 2022), but not immune to anthropogenic influence (e.g., Schwanck et al. 2022). Having about 98% of its surface covered by ice, scientific activity in this region sparks the imagination of the public (Kellner 2022) and is increasingly more diverse and complex (e.g., Simões et al. 2022). However, during the Cretaceous, this continent experienced a much warmer environment, supporting temperate forests with floristic assemblages, thriving similar to the present-day ecosystems found in Chile, Australia, and New Zealand (Cantrill & Poole 2012). Once plants

comprise the base of most terrestrial trophic webs and insects are the main herbivores on land, it is expected that these distinct groups of organisms developed some ecological association through their evolutionary histories. The fossil record indicates that such plant-insect associations existed throughout the last 420 million years (Mya), originating in the Devonian or perhaps earlier (Anderson & Trewin 2003, Labandeira 2013, Möller et al. 2017). Thus, insect-plant interactions in the fossil record are identified since plants advanced on land, enabling us to understand the earliest diversification of phytophagous insects, community dynamics, paleoclimate, and the establishment of coevolution between

plants and insects throughout time (Gandolfo & Zamaloa 2021).

Given the importance of insect herbivory in extant ecosystems, there is a need to understand how this ecological relationship operated in the past. Fossil evidence of insect herbivory include incomplete leaf margins damaged by external foliage feeders, leaves perforations made by piercing-and-sucking feeding apparatuses, oviposition and galling processes, seed predation, coprolites into vegetal tissue, among others. The interaction on plant tissue is evidenced by reaction/damage tissues (Van Amerom 1966, Van Ameron & Josten 1973, Van Amerom & Boersma 1971, Scott & Taylor 1983, Labandeira & Phillips 1996, Labandeira & Allen 2007).

Leaf mines are the most easily recognizable structures among all types of damage (Slater et al. 2012). These are produced by larvae of holometabolous insect orders, which consume living parenchyma through its growing instars, inside the leaf of the host plant (Labandeira 2002, 2006, Imada et al. 2022), a habit developed in the Late Triassic (Labandeira 2006, Labandeira & Currano 2013). The subsequent diversification of angiosperms during the Cretaceous resulted in the diversification of phytophagous insect clades and, consequently, an array of extraordinary novel ways to interact and produce mines in plant organs (Stephenson & Scott 1992, Labandeira et al. 1994, Ding et al. 2015, Filho et al. 2017). Leaf mines dug by insects have been extensively described in an array of Cenozoic angiosperms (Crane & Jarzembowski 1980, Wilf et al. 2005, McDonald et al. 2007). Although comprehensive descriptions of leaf miners in Cretaceous angiosperms are documented (Labandeira et al. 1994, Krassilov et al. 2007, Donovan et al. 2014), records of such interactions in plants that inhabited the Gondwanan landmasses are scarce.

Among the Gondwana endemic angiosperm lineages, *Nothofagus* is a basal lineage of Fagales, represented by 43 extant species of trees and shrubs that occur in South America, Australia, Tasmania, New Zealand, New Caledonia, and New Guinea (Swenson et al. 2001). *Nothofagus* first appeared in the Late Cretaceous (McGlone et al. 1996) and is particularly relevant, once its origin and dispersion center seem to be Antarctica, where they are currently extinct (Leppe et al. 2012, Vento et al. 2022). A phylogenetic analysis supports the early diversification of this taxon, as it reveals Paleogene fossil leaves from Patagonia closely related to modern species (Vento et al. 2022). Antarctic *Nothofagus* fossils are represented for all by leaf impressions, but wood fragments, branches, and pollens have been also reported (Hill & Jordan 1993, Hill 2001, Cantrill & Poole 2012).

Despite *Nothofagus* becoming extensively documented in Upper Cretaceous and Lower Paleogene sedimentary sequences of Antarctic (Birkenmajer & Zastawniak 1989, Hunt & Poole 2003, Hayes et al. 2006, Kellner et al. 2007, Cantrill & Poole 2012, Tosolini et al. 2021), their ecological interactions were not examined in detail and comprehensive descriptions of interaction traces associated with these fossils are still sparse (McDonald et al. 2007).

Recent field efforts have yielded dozens of *Nothofagus* leaf specimens from siliciclastic and volcanoclastic Upper Cretaceous Fildes Formation of Nelson Island, at the Antarctic South Shetland Islands. Some exhibit numerous, serpentiform, high-relief, channel-like lineation identifiable as mine trace fossils. In this paper we examine and describe these structures, comparing them with trace fossils found in other Cretaceous and Cenozoic plants. This new evidence represents the oldest record of leaf mines of West Antarctica and the oldest record of insect-plant interaction in *Nothofagus*. Therefore, it provides

new data on the Antarctic ecosystem during its separation from Gondwana and reports the interactions between herbivorous insects and the angiosperm *Nothofagus* in higher latitudes.

Geologic background

The fossil plants were collected from a new fossil site that crops out in the Northeastern region of Rip Point on Nelson Island at the South Shetland Islands Archipelago (62°14'18.2"S/ 58°58'58.2"W) (Figure 1). The layers belong to the Fossil Hill Formation and are composed of basalt-andesitic suit of lava, interbedded with siliciclastic (sandstones and silty shales) and volcanoclastic (tuffite) horizons, intruded by coarse breccias. These layers are exposed at sea level and form the rocky coastline being accessible only during low tides periods. The sandstones and silty shales vary from light gray to dark gray and reddish color. All the leaf impressions studied here came from this level and predominantly represent *Nothofagus* sp. Above this horizon lies a decimeter tuffite horizon with abundant compressed fragments of carbonized wood varying from 2 cm to 0.6 m. The tuffite layer is extensively intruded by well-rounded boulder-dominated breccias, generally 0.2 to 0.4 m in diameter. The laterally impersistent nature of these beds, which is recurrent in clastic rocks of Nelson and Fildes Peninsula (Southern King George Island), prevent their assignment to a specific lithostratigraphic unit. However, the lithology is similar to those of the lower and middle members of the Fildes Formation. The floristic association suggests that these levels are of Upper Cretaceous-Lower Paleogene age. Previous studies based on the paleoflora composition have indicated a Campanian age (e.g., Shen 1994, Dutra 1997, Dutra & Batten 2000, Trevisan et al. 2022, Bastos et al. 2012, Manfroi et al. 2015, Lima et al. 2021).

MATERIALS AND METHODS

The materials were collected during the 38th Brazilian Antarctic Expedition by the research team of the PALEOANTAR Project (Lima et al. 2021, Piovesan et al. 2021, Santos et al. 2022, Brum et al. 2022, 2023) on Nelson Island (Figure 2). The field work was carried out between December 2019 and January 2020, totaling 48 days (Figueiredo et al. 2020, Kellner 2020). The survey resulted in 1.5 tons of fossil and geological materials. All fossil plants are housed in the paleobotany collection of Museu Nacional/Universidade Federal do Rio de Janeiro (UFRJ).

The paleoflora from this site consist of horsetails (Lycophyta), ferns (Pteridophyta), podocarps, araucarias (Gymnosperms), and *Nothofagus* (Angiosperms). For the present study, only material referable to *Nothofagus*, which is the most predominant fossil plant (Bastos et al. 2012), was considered. About 200 specimens were analyzed under a Stereoscopic Microscope in the Laboratório de Paleontologia of the Universidade Regional do Cariri (URCA). The specimens were measured using a digital caliper and photographs were taken using a Canon EOS 60d digital camera.

Leaf mines were classified following the standard Damage Type System (DT) proposed by Labandeira et al. (2007), which consists of a classification of different types of damage caused by arthropods based on their morphology. The discrimination between insect-inflicted damage and other physical damages, such as those caused by detritivores agents or taphonomic processes, were identified using the following criteria: (1) presence of reaction tissue (an anomalous tissue growth formed by hyperplasia in areas attacked by insects); (2) specificity of a plant taxon or organ to which specific damage can be attributed; and (3) the repetition pattern and shape of damage in specific plant organs

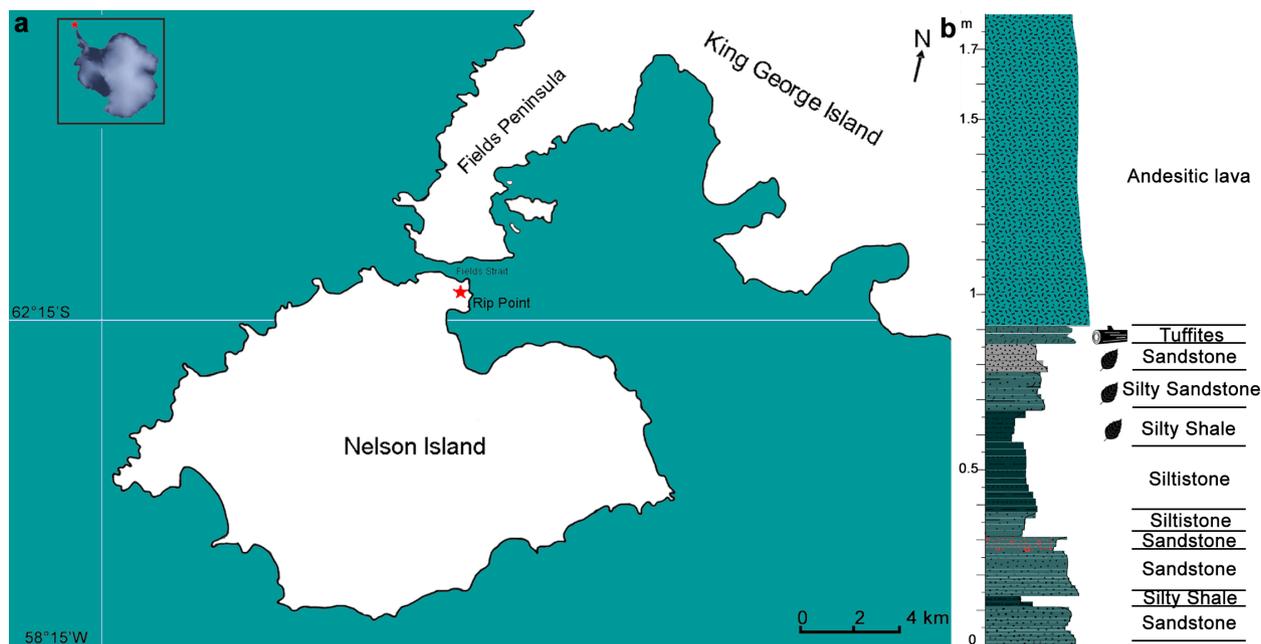


Figure 1. a) Location of the site at Rip Point (Nelson Island) where the specimens were collected. **b)** Stratigraphic profile of the site. The occurrences of tree trunks and leaves are marked in the stratigraphic column. Modified from Trevisan (2011).

(Maccracken et al. 2022). The latter can be evidenced by the presence of mines in leaves, which are usually recognized by their distinctive morphological patterns.

RESULTS

Host plant assemblage

The dense leaf accumulation, devoid of predominant orientations of the *Nothofagus* sp. leaves, indicates that the beds correspond to a leaf aggregation assemblage, presenting a parautochthonous assemblage of deciduous species. The leaf impressions lack organic connections, being mostly represented by incomplete leaf blades. Detailed morphological features are scarce due to poor preservation.

Insect-plant interactions

Out of the 200 leaves examined, 15 show evidence of insect activity, varying in size, shape, and preservation modes. Two types of interaction damage were identified: galls and

mines (Figure 3). Only one specimen preserved a circular scar, identified here as a galling scar. Meandering tracks with unhindered paths were regarded as mines (Table I). These tracks were variable in size, widths, and shapes as described below.

Although mines extend freely through the leaves, crossing secondary and tertiary veins, they rarely cross the main vein. The vascular tissues were not consumed by the phytophagous trackmaker once no reaction tissue or distortions in the crossed leaf venation were observed. The mines maintain a regular width through their trajectory (Table I).

Host plant

The dense accumulation lacking predominant orientations of the *Nothofagus* sp. leaves indicates that the beds correspond to a leaf litter, presenting a parautochthonous assemblage of deciduous species. The leaf impressions lack organic connections, being mostly represented



Figure 2. a) Fossil collection site at Rip Point ($62^{\circ}14'18.2''S / 58^{\circ}58'58.2''W$) with the Fields Peninsula on King George Island at the background. b) The exact place where the fossils studied here were collected. c) Leaf impressions in situ.

by incomplete leaf blades. Therefore, due to their preservation, morphological characters are scarce.

Specific descriptions

Specimen 464Pbe (Figure 4a) is a small fragment of a leaf impression (31 x 23 mm), that presents a small serpentine mine measuring 22 mm. It nests between two secondary veins. The specimen 462Pbe (55 x 27 mm) contains a small, slender, and serpentine mine that intersects secondary veins until reaching the leaf margin, measuring 13 mm in length (Figure 4b). In specimen 460Pbe, there is a longer sigmoid mine, measuring 44 mm, starting close to the base, going towards the right margin, crossing the secondary vein in its path. This specimen

also preserves two circular galls between two secondary veins, measuring 3 mm (Figure 3). The specimen 470Pbe (73 x 47 mm) presents a straight mine measuring 1.5 mm in length, crossing secondary veins on the left part of the leaf (Figure 4c). On the right side of the leaf blade, there is a bifurcated mine towards the leaf base, measurements of 20 mm and 12 mm in each bifurcation, respectively.

The specimen 461Pbe (64 x 48 mm) exhibits small mines, one of which forms a complete circle measuring 30 mm in the upper region of the leaf, close to the leaf apex between the secondary veins (Figure 4d). Also, this specimen presents signs of leaf consumption along the mines, which is rare in the fossils analyzed here.

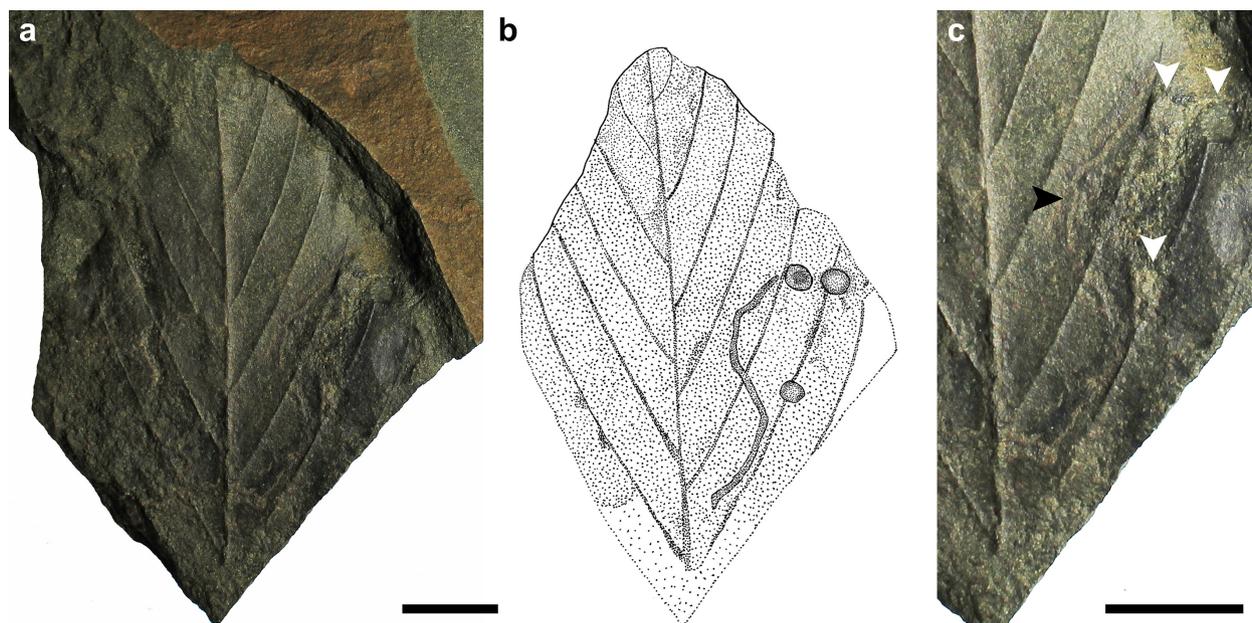


Figure 3. Specimen 460Pbe containing mine and galls. a) Complete view of the specimen. b) Schematic drawing with emphasis on the observed structures. c) Details of the mine and galls. White arrows: galls. Black arrow: mine. Scale: 5 mm.

Table I. Summary of hallmarks on Nelson Island fossils.

Specimen	Type of interaction	DT	Comments
460Pbe	Mine and galls	94	Small, serpentine, between secondary veins. Circular galls between secondary veins and mines
461Pbe	Mine	93	Circular, bifurcated, between secondary veins
462Pbe	Mine	141	Thin, serpentine, between secondary veins
463Pbe	Mine	41	Serpentine, one end curved
464Pbe	Mine	105	Small, serpentine, between secondary veins
465Pbe	Mine	90	Straight, transverse to the secondary veins
466Pbe	Mine	41	Small, crossing secondary veins
467Pbe	Mine	105	Small, curved, between secondary veins
468Pbe	Mine	105	Sinuuous shape, close to the main vein
469Pbe	Mine	41	“V” shaped between secondary veins
470Pbe	Mine	90	Small, transverse to secondary veins
472Pbe	Mine	96	Small, rectilinear, between secondary veins
473Pbe	Mine	41	Small, between secondary veins
474Pbe	Mine	94	Small, serpentine, between secondary veins
475Pbe	Mine	90	Small, serpentine, between secondary veins

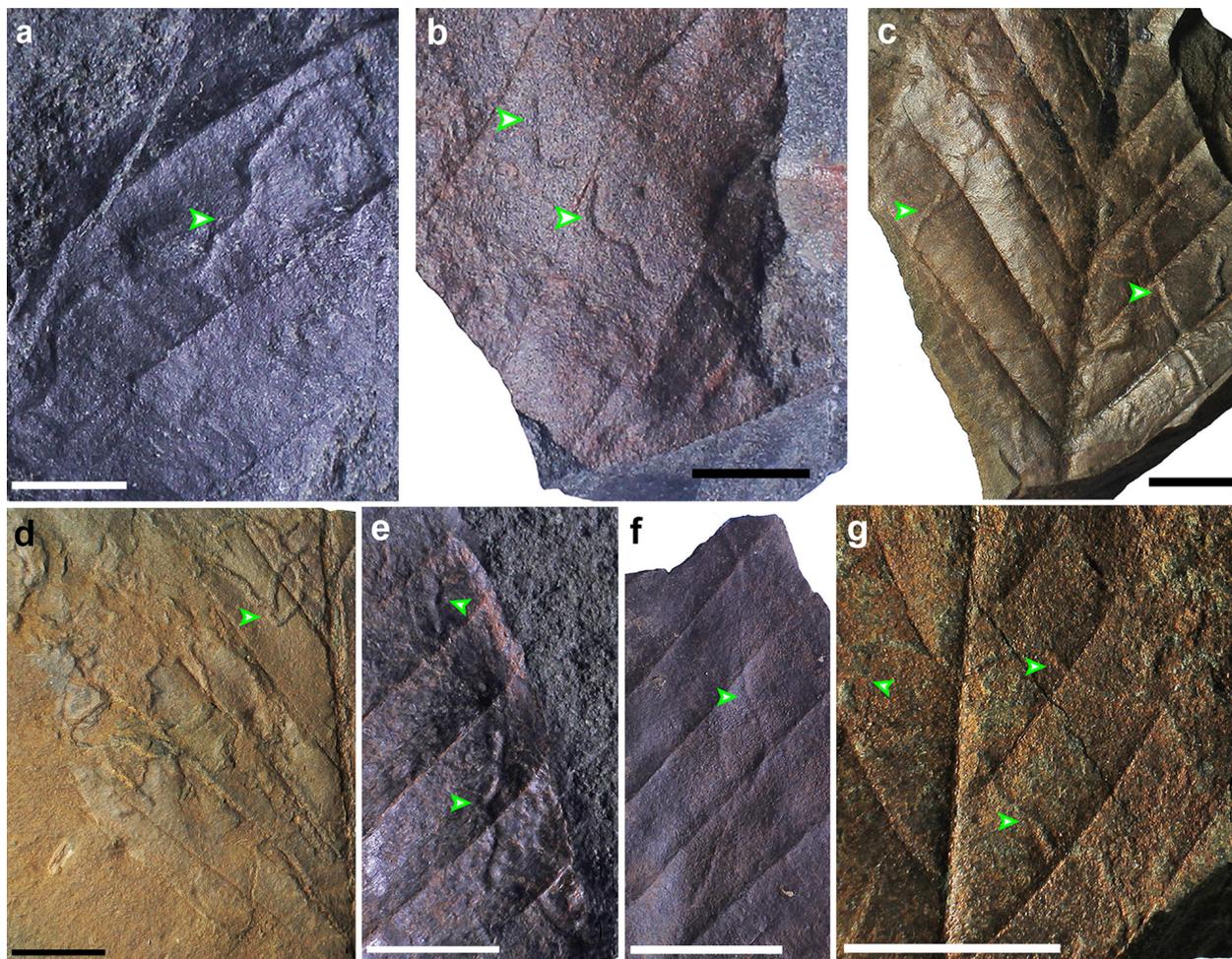


Figure 4. Leaf mines present in *Nothofagus* sp. from Nelson Island (Rip Point): a) Small serpentine mine between secondary veins in specimen 464Pbe (similar to DT 105) (scale: 5 mm); b) Slender serpentine shape crossing secondary veins in specimen 462Pbe (similar to DT 141) (scale: 10 mm); c) Specimen 470Pbe with mines distributed transversally to secondary veins on both sides of the leaf blade (similar to DT 90) (scale: 10 mm); d) Circular bifurcated mine between secondary veins in specimen 461Pbe (similar to DT 93) (scale: 10 mm); e) Serpentine mine, close to the leaf margin, crossing secondary veins and with one of the extremities curves in specimen 463Pbe (similar to DT 41) (scale: 10 mm); f) Straight mine, transversal to the secondary veins in specimen 465Pbe (similar to DT 90) (scale: 10 mm); g) Mine on the center of the leaf, crossing secondary and main vein in specimen 466Pbe (similar to DT 41) (scale: 5 mm).

In the specimen 463Pbe (59 x 36 mm), there is one small serpentine mine, crossing the secondary veins of the leaf and close to the leaf margin, measuring 30 mm of length (Figure 4e). In the specimen 465Pbe (38mm x 3 mm), there is an almost straight mine, crossing transversally three secondary veins from the leaf base towards its apex (not preserved), measuring 25 mm (Figure 4f). In the specimen 466Pbe (39 x 30

mm), two small mines transversal to the main vein are observable, crossing the leaf blade. The upper mine measures 19 mm and the lower one measures 17 mm, both cross the main and secondary veins (Figure 4g), which is uncommon in the remaining material studied here. The specimen 473Pbe (74 x 65 mm) is a fragment of a central leaf impression, with no preserved apex, margin, or base border, in which a serpentine

mine with 21 mm is observed distally, towards the leaf margin, between secondary veins (Figure 5a). In specimen 472Pbe (27 x 38 mm), there is a small straight mine, slightly curved (Figure 5b), measuring 17 mm, crossing two secondary veins. The specimen 475Pbe (70 x 60 mm) presents a serpentiform mine measuring 17 mm between two secondary veins, without crossing the main vein (Figure 5c).

The specimen 474Pbe (43 x 37 mm) presents four short serpentiform mines of varied sizes towards the center of the leaf blade, with sizes between 14 and 15 mm (Figure 5d). The specimen 467Pbe (60 x 44 mm) presents a straight mine with 22 mm, curving in its path, and crossing secondary veins (Figure 5e). The specimen 468Pbe (80 x 53 mm) is the best-preserved leaf impression. It shows some mines along the leaf blade, especially a larger and more visible serpentine one that is 35 mm long and crosses four secondary veins (Figure 4f). The specimen 469Pbe (100 x 80 mm) presents a short, slender "V"-shaped mine, measuring 20 mm, that crosses secondary and tertiary veins (Figure 5g).

DISCUSSION

Insect-plant associations are fundamental aspects in land ecosystems, being indispensable components in food chains and are very sensitive to environmental changes throughout time (Wilf et al. 2006, Donovan et al. 2014). Evidence of insect activity associated with fossilized plants in Antarctic continent are scarce. They correspond to perforations, tunnels, and coprolites found in permineralized peats from the Upper Permian period in the Buckley Formation of the transantarctic mountains, as well as coprolite structures from different deposits and perforation in fragments of roots and stems caused by oribatid mites (Kellogg & Taylor 2004). These records indicate that some

arthropod groups developed associations with Antarctic flora since the Paleozoic.

Slater (2014) identified other evidence of insect-plant interactions that include feeding of leaf margin, oviposition scars, and galls in *Glossopteris* sp. leaves from the Permian from the Prince Charles Mountains, East Antarctica. Additionally, there are reports of mines, galls, skeletonization, and leaf margin consumption in leaf impressions and compressions of Nothofagaceae and Cunoniaceae from Eocene deposits from the King George and Seymour islands (McDonald et al. 2007). There were no records of Cretaceous insect-plant interactions, particularly within the *Nothofagus* genus, until the present study.

The interactions identified on Nelson Island are represented primarily by leaf mines, with one specimen showing evidence of galls. Miner insects consist of an extremely specialized feeding behavior, resulting from larvae feeding action. Mines protect the insect from predation and dehydration through the construction of tunnels in the plant tissue (Möller et al. 2017). Eggs are deposited by adult insects in the leaf tissue where the larvae feed and develop inside the parenchyma of the plant, forming varied tracks (Hering 2013). Nowadays, miner insects belong to the Diptera, Coleoptera, and Hymenoptera orders (Liu et al. 2015). The leaf mines described here vary in shape and size and possess little variation in thickness. In comparison to the study by McDonald et al. (2007) developed in King George and Seymour islands, the mines found on Nelson Island are more frequent even with a much smaller sample size. There are also differences in the sizes and shapes and in the designation of DTs, which were not observed in other Antarctic localities. Up to now only one study described damage belonging to functional groups (McDonald et al. 2007), also present in the material analyzed here.

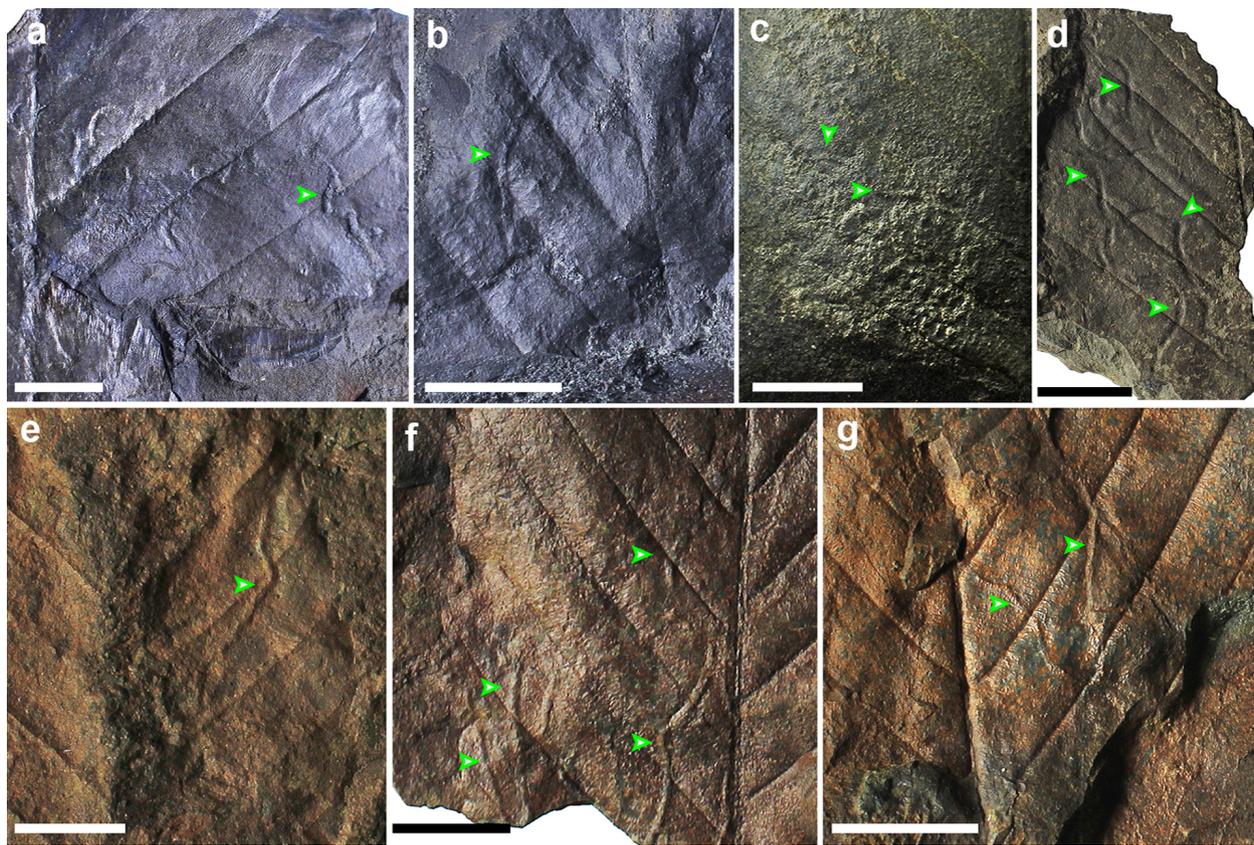


Figure 5. Leaf mines identified in fossil leaves: a) Small mine that crosses a secondary vein in specimen 473Pbe, similar to DT 41; b) Straight, small, crossing secondary veins in specimen 472Pbe, similar to DT 96; c) Small mine between secondary veins in specimen 475Pbe, “S”-shaped, similar to DT 90; d) In specimen 474Pbe, four small deeper mines, with serpentine shape, between secondary veins (similar to DT 94); e) Small, “L”-shaped mine, between secondary veins in specimen 467Pbe, similar to DT 105; f) In specimen 468Pbe, transversal to the secondary veins, one bigger, close to the main vein, and another a little smaller, close to the margin, similar to DT 105; g) Small “V”-shaped mine, crossing secondary veins, slender, similar to DT 41, in specimen 469Pbe. Scale bars: 10 mm.

Galls are formed as a result of a physiological reaction that induces abnormal growth in the host plant tissue, which provides protection and food resources for the developing larvae (Labandeira & Li 2021, Xiao et al. 2022). They represent a type of interaction with high specificity, enabling its identification due to distinct color or shapes (McDonald et al. 2007). The galls described here are small circular structures located in the interveinal spaces of *Nothofagus* sp. leaf, close to a leaf mine. These gall marks are present in specimen 460Pbe, and show the same general morphological features as the galls described

by McDonald (2009: Figure 3.15 a, c, d), Reichgelt (2015: Figure 5b), and Donovan et al. (2018, Figure 3).

The Upper Cretaceous associations on Nelson Island may indicate a relatively lower diversity of herbivore insects in the paleocommunity preserved in Nelson Island, restricted to mines and galls. In plant-insect associations found in the Eocene of King George and Seymour Islands, DTs consist of feeding on leaf margins, galls, mines, and skeletonization (e.g., McDonald et al. 2007). The associations analyzed here suggest a relatively low diversity

of herbivorous insects in the paleocommunity of Nelson Island. It can be demonstrated by the low number of DTs, which is also observed in the Eocene of King George and Seymour Islands (McDonald et al. 2007). This contrasts with other localities worldwide, such as the Miocene of New Zealand, where *Nothofagus* sp. fossils exhibit a remarkable variety of damage types (Möller et al. 2017). Additionally, Miocene *Nothofagus* sp. from New Zealand also shows higher herbivory rates (Möller et al. 2017), in comparison to the Cretaceous (this study) and Eocene paleocommunities of Antarctica (McDonald et al. 2007). A comparison between the two Antarctica sites with records of interaction between arthropods and *Nothofagus* sp. show that fossils from the Eocene of King George Island exhibit a higher number of DTs, including feeding in the leaf margin, galls, mine and skeletonization. The fossil record from the Cretaceous of Nelson Island is restricted to mines and galls, suggesting low herbivory diversity in Antarctica leaves during the Upper Cretaceous, or even between the Cretaceous and Eocene. However, the limited number of studies on insect-plant interactions could have contributed to the low diversity observed. Differences in the number of leaves damaged by insects may be explained by environmental disruptions, ecological changes, or even by fossil preservation (Möller et al. 2017). Taphonomic and depositional factors could also account for the scarcity of leaves with preserved damages on Nelson Island, and perhaps also in King George and Seymour islands.

According to McQuilan (1993), *Nothofagus* sp. can host up to 30 herbivorous species and, throughout evolutive time, corresponding to several species of invertebrate herbivores (Russel et al. 2000). The study of phytophagous (groups of insects that develop interactions with plants) associated with *Nothofagus* sp. are scarce, both in fossils and extant species.

According to Carrillo & Cerda (1987), the number of phytophagous insect species in the current species of *Nothofagus* sp. in Chile could reach 125, corresponding to Coleoptera, Hemiptera and Lepidoptera, including defoliators, wood, seeds, and sap eaters. However, Diptera are also among the main phytophagous insect groups related to *Nothofagus antarctica* (Oerst 1871). In addition, considering the time interval considered by the authors, the abundance of all these taxonomic groups does not change significantly across different collection periods (Vergara & Jeres 2010).

The main invertebrates associated with perennial Nothofagaceas in New Zealand include Coleoptera, Lepidoptera, Diptera, Phasmatodea, and Acari, with the majority found among the Lepidoptera. Most Nothofagaceae species host at least 4 species of defoliator herbivores, as reported by Reichgelt et al. (2015). According to the authors, current perennial Nothofagaceae are efficient producers of food defensive chemicals, turning their leaves hard to consume. However, in deciduous species, the production of defensive chemicals to inhibit the action of herbivores is less efficient. The latter also presents less leaf mass per unit area (Reichgelt et al. 2016).

External leaf feeding marks, skeletonization, and galls were identified, with an absence of other functional groups. According to Reichgelt et al. (2016), the main clade of mining insects is the Coleoptera, which, along with Lepidoptera and Diptera, could be possible agents of leaf damage. Attributing mines to a specific insect taxon is subject to many limitations, especially in the Antarctic fossil record, which rarely preserves animal body fossils. This lack of knowledge about the Cretaceous entomofauna makes a taxonomic attribution of the insects responsible for the structures observed here very difficult. The few numbers of fossilized leaves with miner

may indicate a low diversity of herbivore insects. According to Carvalho et al. (2014), the amount of damage can indicate the presence of herbivore insects even when their fossils are absent. Donovan et al. (2018) verified a decrease in the biodiversity of insect-plant associations from the Cretaceous to the Paleocene. For Antarctica, an increase in the diversity of damage types can be observed from the Cretaceous to the Eocene. Insect fossils in Antarctica are documented from the Permian to the Miocene, but records are rare. Zeuner (1959) reported the presence of an isolated elytra with no further taxonomic identification in Hope Bay (Jurassic). Carpenter (1969) described homopteran wings preserved with plant fragments from the Permian of the Theron Mountains (Plumstead 1962) and an Odonata from the Jurassic of South Victoria Land, as well as a nymph from the Permian in the Mount Glossopteris Formation. An almost complete body fossil of Blattodea, as well as preserved elytra and traits, were reported by Bomfleur et al. (2011).

Despite the low number of insect fossils in Antarctica, these records indicate the presence of phytophagous insects, justifying the occurrence of these types of damage on the leaves.

Climatic factors could have exerted strong limitations to the existence of herbivores, and taphonomic/depositional factors could have been relevant in the expressivity of these records, both of arthropod fossils and evidence of insect-plant interactions. According to Kemp et al. (2014) and Tobin et al. (2012), even with signs of low temperatures, there were periods of warm temperate climate in Antarctica. Through studies with palynomorphs from Seymour Island, Bowman et al. (2013) suggested the increase in temperature before the end of the Cretaceous and the beginning of the Paleogene, what might have been a global event (Wilf et al. 2006). These indicators of higher temperatures could have

contributed to the establishment ecosystems in which plants and associated insects coexisted and left traces of their preserved interactions.

CONCLUSION

Fossil specimens can be altered due to different reasons, that include (but are not limited to) to the processes involved in their preservation. The material from Nelson Island studied here shows the same kind of preservation reported on other leaves from Antarctica (e.g., McDonald et al. 2007), that differ from some exceptional preservation known from a few other deposits (e.g., Xiao et al. 2022). Nonetheless, based on the comparisons with specimens from other regions and based on the identification procedures commonly used to identify insect-plant interactions (e.g., Labandeira et al. 2007), we can confidently rule out that these structures represent taphonomic artifacts.

The present study represents the oldest record of insect-plant interaction of West Antarctica, documented from Cretaceous deposits of Nelson Island. The insect activity in assemblages dominated by *Nothofagus* sp. demonstrates that, besides being a significant component of Cretaceous ecosystems, this angiosperm genus was also an important host for herbivore insects. *Nothofagus* has already been extensively studied from a systematic and paleoenvironmental point of view, but so far did provide limited paleoecological information concerning insect interactions.

Comparisons between the number of analyzed leaves and the quantities of damages suggest a low diversity of herbivores. If other factors such as taphonomy and environmental changes (e.g., temperature change) can be accounted for this low diversity cannot be established at this point. The material analyzed here reveals insights and contribute to the

understanding of the insect-plant interactions happened in Cretaceous paleocommunities present in this important austral continent.

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EBSF, GRO and FJL conceived and designed the study. ASB, GAS, RGF and CDU performed fieldwork in the Antarctic Peninsula collecting several fossil plants used in the study. ASB, GAS, RGF, CDU, JHZR, CT, ML, JMS, FJL, GRO and AWAK contributed to the writing and revision. EBSF and ASB performed image editing. All authors reviewed and contributed to the manuscript.

