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Ginkgoites villardeseoanii sp. nov., a ginkgophyte with insect damage from the Upper Cretaceous (Maastrichtian) Lefipán Formation (Chubut, Patagonia, Argentina)

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ABSTRACT

Today, the ginkgophytes are represented by the single species *Ginkgo biloba*, naturally distributed in China and cultivated worldwide. However, the ginkgophyte lineage shows an extensive fossil record going back to the Paleozoic of both hemispheres. In South America, its record began in the upper Paleozoic and reached the middle Eocene, and it includes both vegetative and reproductive remains. The Cretaceous macrofossil record of this group in South America is restricted to Lower Cretaceous deposits, where it is relatively abundant, whereas there is a gap in its Upper Cretaceous to lower Paleogene record. We present the new species *Ginkgoites villardeseoanii* collected from Maastrichtian (uppermost Cretaceous) deposits of the Lefipán Formation (Patagonia, Argentina). The studied material consists of three specimens preserved as adpressions of isolated, flabellate, and petiolate (*Ginkgo*-like) leaves, with few epidermal characters preserved. One of the studied specimens shows evidence of insect damage consistent with hole feeding, constituting the first Cretaceous record of interaction between ginkgophytes and insects in the Southern Hemisphere. We infer that this damage was produced when the leaf was still attached to the plant, as the specimen shows evidence of a physiological reaction of the plant in the form of a border of necrotic tissue around the wound. *Ginkgoites* leaves are common among different lineages within the Ginkgoales, having been associated to three families (Ginkgoaceae, Karkeniaceae, and Yimaiaceae). Therefore, *G. villardeseoanii* was assigned to an *incertae sedis* family.

1. Introduction

The rich fossil record of the ginkgophytes goes back to the upper Paleozoic, is worldwide distributed, and includes *Ginkgo* and numerous extinct genera (Seward, 1919; Archangelsky, 1965; Samylina, 1967; Cúneo, 1987; Zhou and Zang, 1989; Stewart and Rothwell, 1993; Zhou, 1997; Troncoso and Herbst, 1999; Naugolnykh, 2007; Crane, 2013; Del Fueyo et al., 2013; Villar de Seoane et al., 2015). Today, the group is represented by the single species *Ginkgo biloba* L., natively distributed in China (Seward, 1919; He et al., 1997; Tang et al., 2012; Crane, 2013) and cultivated worldwide.

Several taxonomic schemes have been proposed for classifying the large diversity of fossil forms in the Ginkgophytes (e.g., Zhou, 1997; Anderson and Anderson, 2003; Naugolnykh, 2007). According to Zhou (1997) at least six families constitute the ginkgophyte lineage (i.e., Trichopityaceae, Karkeniaceae, Umaltolepidiaceae, Schmeissneriaceae, Yimaiaceae, and Ginkgoaceae). These families were circumscribed mostly on the basis of characters of their reproductive structures, since similar types of leaves are shared by different families (see table 2 in Zhou, 1997). However, the number of species described from reproductive structures is relatively low (e.g., Archangelsky, 1965; Krassilov, 1972; Zhou et al., 2002; Zheng and Zhou, 2004; Xu et al., 2017) compared to those described from leaf remains, which comprehend the most common macrofossil remain of the group (e.g., Seward, 1919; Samylina, 1967; Cuneo, 1987; Villar de Seoane et al., 2015; Van Konijnenburg-van Cittert et al., 2021).

Worldwide, the Cretaceous ginkgophyte macrofossil record is mostly restricted to Lower Cretaceous deposits (e.g., Archangelsky, 1965; Lundblad, 1971; Villar de Seoane, 1997; Watson et al., 1999; Yang, 2004; Del Fueyo et al., 2006, 2013; Pott et al., 2014). In contrast, its Upper Cretaceous record is scarcer and comprises several species from Russia (Samylina, 1967; Krassilov, 1972), as

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well as a few records from Albian–Cenomanian–?Turonian strata of Australia (Pole and Douglas, 1999).

In Argentina, the ginkgophytes have a relatively continuous record starting at least in the lower Permian (Feruglio, 1933, 1942; Cúneo, 1987) and reaching the middle Eocene (Villar de Seoane et al., 2015). The Argentinean fossil record of the ginkgophytes has been extensively revised in two recent publications by Del Fueyo et al. (2013) and Villar de Seoane et al. (2015). Since then, a single record referred to ?*Ginkgoites* has been published from the upper Paleocene-middle Eocene Ligorio Márquez Formation (Santa Cruz, Patagonia, Argentina) and it is based on isolated cuticle remains (Carpenter et al., 2018).

In this contribution, we describe the first Upper Cretaceous ginkgophyte macrofossils from South America. Fossils were collected at the lower portion of the Lefipán Formation (Maastrichtian) and are preserved as impressions and compressions of leaves with fragmentary cuticular remains. The Lefipán specimens are assigned to a new species based on macro- and micro-morphological features, and their affinities to other ginkgoaleans of similar age and/or distribution are discussed in detail. Moreover, this new species shows evidence of insect damage, constituting the first Cretaceous record of plant-insect interaction for the ginkgophytes in the Southern Hemisphere. We review previously reported evidence of ginkgophyte-insect interaction in the fossil record and discuss it the light of the herbivore-response physiology of the extant *Ginkgo biloba*.

1.1. Institutional abbreviations

MPEF-Pb, Museo Paleontológico Egidio Feruglio, Paleobotanical Collection, Trelew, Chubut, Argentina; **BH,** L. H. Bailey Hortorium Herbarium, Cornell University, Ithaca, NY, USA.

2. Materials and methods

2.1. Geological setting

The Lefipán Formation corresponds to the final stage in the infilling of the Jurassic–lower Paleocene Cañadón Asfalto Basin (Cúneo et al., 2013; Figari et al., 2015), and it is best exposed along the Middle Chubut River Valley (Fig. 1A), where it overlays outcrops of the Campanian-lower Maastrichtian Paso del Sapo Formation (Scasso et al., 2012; Fazio et al., 2013; Figari et al., 2015; Vellekoop et al., 2017; Butler et al., 2020). This formation was deposited during the Maastrichtian to early Paleocene at the Paso del Sapo embayment, in a tide-dominated delta that accumulated at the foothills of the NNW-SSE paleo-Cordillera (Scasso et al., 2012). It consists of marine to marginal marine fossiliferous sandstones, and mudstones with intercalated coquinas and conglomerates (Scasso et al., 2012).

The latest Cretaceous (Maastrichtian) to earliest Paleocene (Danian) age of the Lefipán Formation was determined in base of molluscs (Medina et al., 1990; Medina and Olivero, 1994; Scasso et al., 2012; Aberhan and Kiessling, 2014), as well as terrestrial (Baldoni, 1992; Baldoni and Askin, 1993; Barreda et al., 2012) and marine palynomorphs (Vellekoop et al., 2017). Within the formation, the K/Pg boundary was constrained to 4 m of sequence using biostratigraphic markers (Barreda et al., 2012). However, the boundary layer itself is apparently not preserved due to a minimum stratigraphic hiatus adjudicated to a sea level regression across the K/Pg boundary (Barreda et al., 2012; Vellekoop et al., 2017).

Palynological studies show a considerable change in the composition of the Lefipán flora across the K/Pg boundary (Barreda et al., 2012). Its Maastrichtian (Cretaceous) palynoflora was

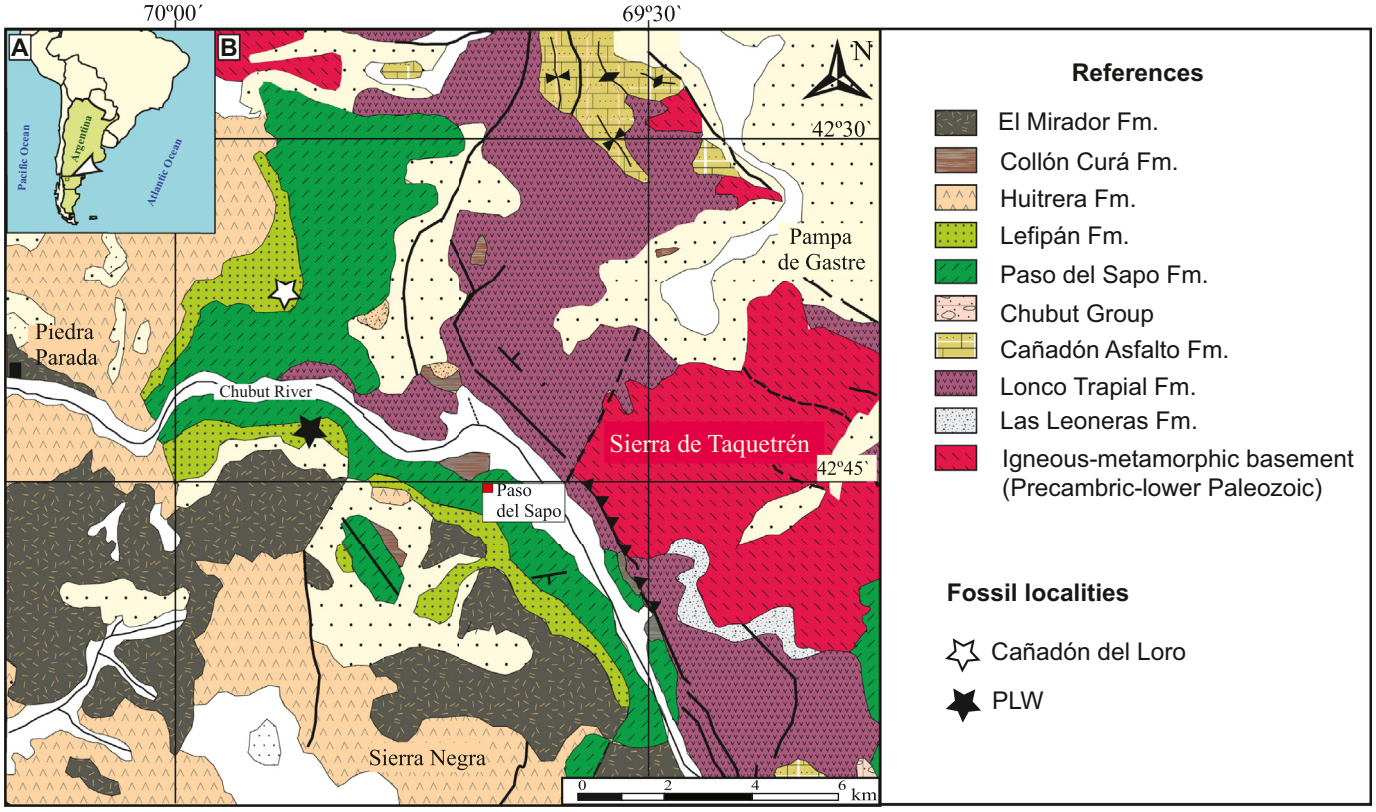


Fig. 1. Geologic map of the studied area (modified from Fazio et al., 2013). **A,** localization of the studied area. **B,** detail of the area including the Cañadón del Loro (white star) and PLW (black star) localities, Chubut Province, Argentina.

dominated by angiosperms and ferns, with Podocarpaceae as common trees, consistent with a warm and humid adapted vegetation (Baldoni, 1992; Baldoni and Askin, 1993; Barreda et al., 2012), and in concordance with the diverse macrofloral remains (e.g., Cúneo et al., 2008; Wilf et al., 2017; Andruchow-Colombo et al., 2018; Martinez et al., 2018). The Danian (Paleocene) vegetation is only known from palynological records, which have been described in detail by Barreda et al. (2012). According to these authors, the early Danian flora was highly disturbed with many palynomorphs of the assemblage associated with plants that had high adaptability to changing environments (e.g., *Classopollis*), whereas towards the late Danian, there was a recovery of several Cretaceous taxa that suggests a temperate to warm climate (Barreda et al., 2012).

Fossils studied herein come from two Lefipán localities, Cañadón del Loro and PLW (after *Perfil Lefipán West*), which outcrop at the northwest of Chubut Province, Patagonia, Argentina (Fig. 1) and belong to the Maastrichtian portion of the formation. The PLW locality, sometimes referred as LefW (e.g., Donovan et al., 2016; Escapa et al., 2018; Stiles et al., 2020), is located at the southern margin of the Chubut River (Fig. 1B, black star) and belongs to the San Ramón section (Scasso et al., 2012), together with two additional localities (PLE -after *Perfil Lefipán East*- or LefE, and PLL -after *Perfil Lefipán Loro*- or LefL). These three localities yield a diverse paleoflora, including a highly diverse assemblage of angiosperm leaves (Cúneo et al., 2008, in press; Stiles et al., 2020) with a wide variety of insect damage types (Donovan et al., 2016, 2018), two conifer families (Podocarpaceae and Araucariaceae; Wilf et al., 2017; Escapa et al., 2018; Cúneo et al., 2021), and cycads (Cúneo et al., 2021). The Cañadón del Loro locality is placed at the northern margin of the Chubut River (Fig. 1B, white star) and, stratigraphically, it is below the localities from the south of the Chubut River (Andruchow-Colombo et al., 2018). The flora of Cañadón del Loro is characterized by a less diverse angiosperm component than that of the southern localities (Martínez et al., 2018; Cúneo et al., 2021), conifers of the families Araucariaceae and Cupressaceae (Andruchow-Colombo et al., 2018; Cúneo et al., 2021), and ferns (Cúneo et al., 2021).

The material object of this study was previously mentioned in Cúneo et al. (2007, 2021) and includes three partially preserved, isolated leaves. One of the specimens from PLW was recovered from the PL1 fossiliferous level (Fig. 2A, black star), and the second one from an unknown fossil horizon within this locality. The specimen from Cañadón del Loro comes from the fourth fossiliferous level (Fig. 2B, white star).

2.2. Fossil preparation and illustration

The fossil specimens are preserved as impressions and compressions. Sediment covering the fossil remains were mechanically removed with 3.0 mm angled slit knives. Fragments of cuticle were isolated from specimen MPEF-Pb 10897b by performing a peel with adhesive tape; the tape was then mounted on stubs with double

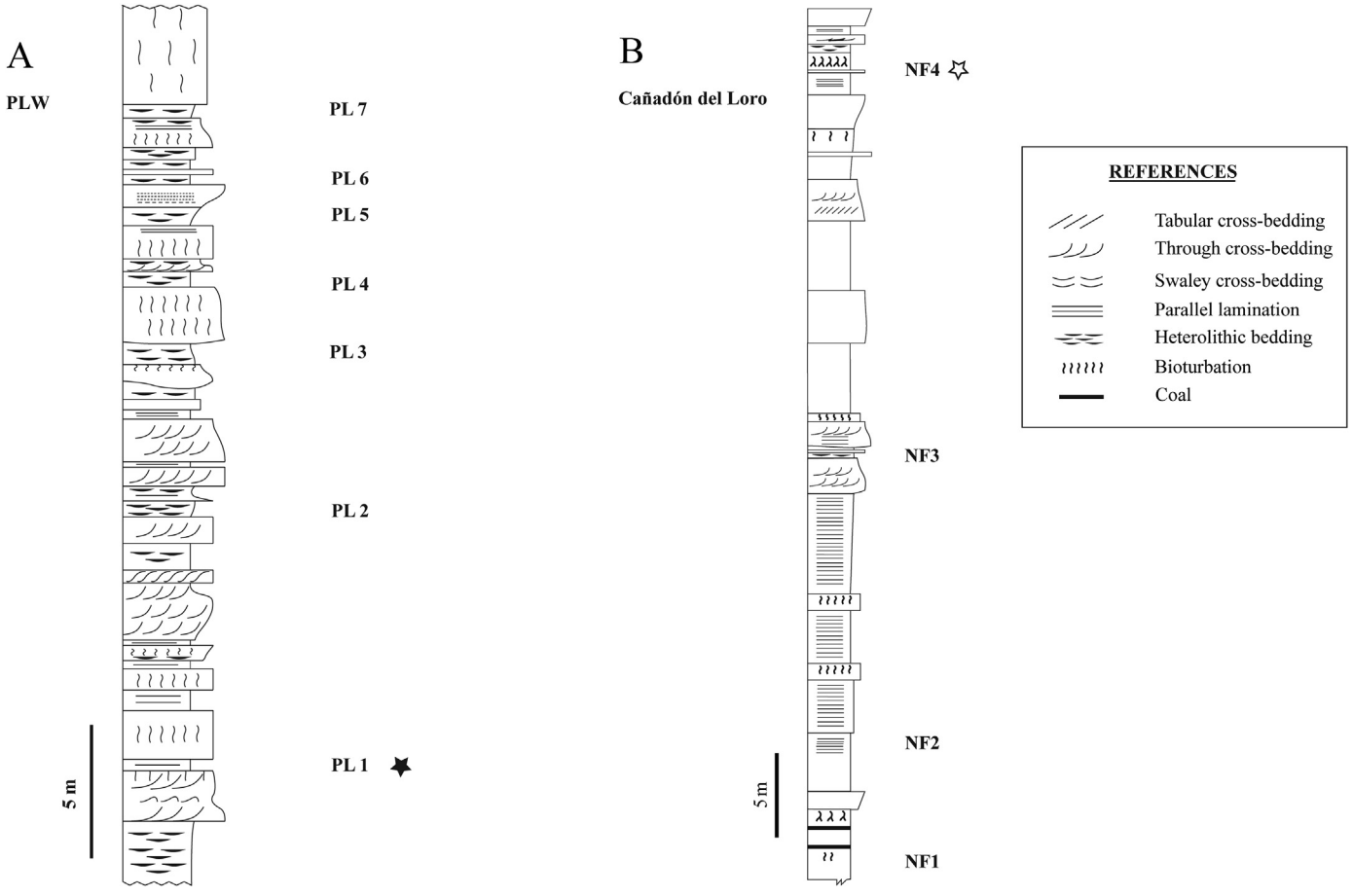
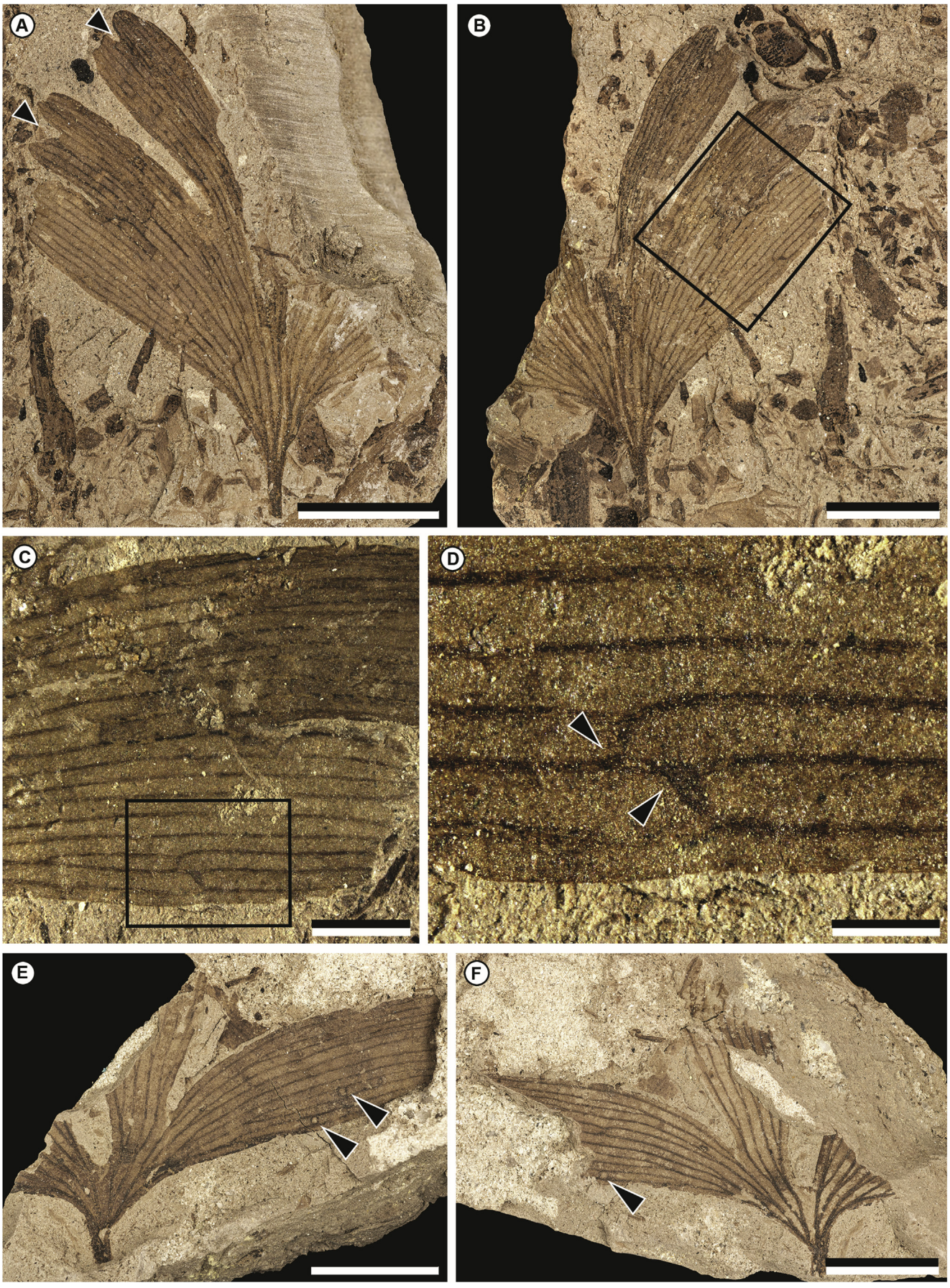


Fig. 2. Stratigraphic sections of the studied localities, where the specimens referred to *Ginkgoites villardeseoanii* sp. nov. were collected. **A,** stratigraphic section of the locality PLW (Perfil Lefipán West) with the position of the fossiliferous levels PL1-PL7 indicated; black star indicates the fossiliferous level where MPEF-Pb 10907a, b was collected. **B,** stratigraphic section of the locality Cañadón del Loro with the position of the fossiliferous levels NF1-NF4 indicated; white star indicates the fossiliferous level where the specimen MPEF-Pb 10897a, b was collected.


A
B
C
D
E
F

sided carbon tape for observation with scanning electron microscope. The stubs were coated with gold using a 108 Manual Sputter Coater with 120 mm vacuum Chamber (Ted Pella Inc., California, USA), and observed and photographed with a Phenom XL desktop Scanning Electron Microscope (Thermo Fisher Scientific, Massachusetts, USA) at the Gandolfo Lab (LH Bailey Hortorium, Cornell University).

Images of macromorphology were obtained with a Nikon D850 (Nikon, Tokyo) camera with an AF Micro Nikkor 60 mm 1:2.8 (Nikon) at BH, and with a Nikon DS-Ri2 camera attached to a Nikon SMZ18 stereoscopic microscope at the Gandolfo Lab. Additional images of epidermal morphology were obtained with a Nikon SMZ18 stereoscopic microscope at the Gandolfo Lab with a Nikon DS-Ri2 camera attached. Images were processed with Adobe Photoshop Lightroom Classic 10.2 (Adobe, Mountain View, California) for white balance and micro-contrast enhancing, and with Adobe Photoshop 22.3.1 for assembling the plates.

The fossil specimens studied are permanently housed in the Paleobotany Collections of the Museo Paleontológico Egidio Feruglio (repository abbreviation MPEF-Pb), Trelew, Chubut Province, Argentina.

3. Systematic paleontology

Subclass Ginkgoidae Engler, 1897
Order Ginkgoales Gorozhankin, 1904
Family *Incertae Sedis*

Fossil Genus *Ginkgoites* Seward, 1919
Type Species: *Ginkgoites sibirica* (Heer) Seward, 1919

Ginkgoites villardeseoanii Andruchow-Colombo sp. nov.
Figs. 3–7

Derivation of name. The species is dedicated Dr. Liliana Villar de Seoane, former researcher at the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina) for her extensive research on ginkgophyte and other gymnosperm fossil taxa from Argentina.
Holotype. MPEF-Pb 10908a, b; PLW locality, unknown fossiliferous level (Fig. 3A–D).
Paratypes. MPEF-Pb 10897a, b; Cañadón del Loro locality, fossiliferous level 4 (Fig. 4A, B). MPEF-Pb 10907a, b; PLW locality, fossiliferous level PL1 (Fig. 3E, F).
Diagnosis. Flabellate, petiolate leaves, 2–4 lobated, each lobe with a distal notch. Lamina at least 35.2–38.2 mm long and 35.2–60.2 mm wide. Veins dichotomize (3–) 4–5 times; vein density: 12–19 veins/cm. Vein anastomoses are scarce. Epidermal cells with undulated anticlinal walls.
Geographic occurrence. Cañadón del Loro and PLW localities at the north and south margins of the Chubut River respectively, Chubut province, Argentina.
Stratigraphic occurrence. Fossiliferous level 4 at Cañadón del Loro locality; and PL1 at PLW locality, Lefipán Formation.
Description. Isolated flabellate and petiolate leaves, narrowing towards the leaf base, lamina at least 35.2–38.2 mm long and 24.3–36.5 mm wide (35.2–60.2 mm wide estimated, Figs. 3–5). The lamina is dichotomously divided, with the central incision most pronounced producing two main lobes, each lobe divided in two secondary lobes that can show minor incisions (or apical notch, Figs. 3A, B, E, F, 4A, B, 5). Petiole (incomplete) at least 5 mm long and 1.1–1.5 mm wide (Fig. 3E). Two veins enter the lamina and start dichotomizing immediately (Figs. 3F, 5A, C), in one specimen the first dichotomy is so basal that it looks as if three veins were entering the lamina (Fig. 3A). The two veins entering the lamina dichotomize (3–) 4–5 times (Fig. 5A, C). There are 9–11 veins per lobe; lobes are 5.2–8.3 mm wide (vein density: 12–19 veins/cm). Some vein anastomoses were found in the leaf lobes, near the leaf margin (Fig. 3C, D, black arrowhead).
Epidermal cells are mostly rectangular and elongated in the petiole area (Fig. 4C), along the leaf margins (Fig. 4D), and over the veins (Fig. 4E, arrowhead). In other portions of the leaf, epidermal cells tend to be less elongated and more irregular in shape, varying between isodiametric, hexagonal, rectangular, and triangular (Figs. 4D, E, 6A–C). Epidermal cell walls are undulated (Fig. 6C). Stomatal apparatuses are poorly preserved (Fig. 6B–F), the only one completely preserved shows five subsidiary cells (Fig. 6E).
Notes. No resin bodies were observed in the fossil leaves studied. One of the specimens showed a few circular perforations 0.5–0.7 mm in diameter with a border of a darker color (Figs. 3E, F, black arrowheads, 7).

4. Discussion

4.1. Assignment to Ginkgoites

The fossil genus *Ginkgoites* was created by Seward (1919) to encompass fossil leaves that are practically identical to those of the extant *Ginkgo biloba*. Seward did this with the objective of adopting "a designation that does not necessarily imply even generic identity" (Seward, 1919, p. 11) since numerous leaf fossils had been reported as differing from *Ginkgo* in features that implied, at least, specific differences (Seward, 1919). After that, numerous authors used *Ginkgoites* in this sense, this is to refer to fossil *Ginkgo*-like leaves that can be distinguished from *Ginkgo* by morpho-anatomical characteristics (Harris, 1935; Florin, 1936; Stewart and Rothwell, 1993). Instead, Zhou and Zhang (1989) and Zhou (1997) proposed that the name *Ginkgoites* should be used for fossil ginkgoalean leaves that would either belong to plants generically identical to *Ginkgo* or allied types that lack sufficient information to be assigned to the extant genus. This use of the genus *Ginkgoites* proposed by Zhou and Zhang (1989) is supported in the finding of fossil associations of certain *Ginkgo*-like leaves with reproductive structures that markedly differ from those of the extant species (e.g., Archangelsky, 1965; Zhou et al., 2002). If such leaves were to be found isolated, they might be referred to the genus *Ginkgo*, but when taking their reproductive structures into account, it becomes evident that they belong, at least, to a different genus. In this sense, the *Ginkgoites* foliage type has been associated with three different ginkgoalean families: Ginkgoaceae, Karkeniaceae, and Yimaiaceae (Zhou, 1997). Therefore, a *Ginkgo*-like leaf does not necessarily imply a co-generic (nor co-familiar) affinity with *Ginkgo*. Of these three ginkgophyte families that have been associated with *Ginkgoites* leaves, Karkeniaceae and Ginkgoaceae have a proven record in South America, and particularly in the Lower Cretaceous of Argentinean Patagonia

Fig. 3. Leaf morphology of the specimens of *Ginkgoites villardeseoanii* sp. nov. collected in the PLW locality of the Lefipán Formation. **A,** General view of the holotype MPEF-Pb 10908a, black arrowheads show notch at the apex of the lobes. **B,** General view of the holotype MPEF-Pb 10908b. **C,** Detail of MPEF-Pb 10908b, detail of B showing one of the leaf secondary lobes showing the venation pattern. **D,** MPEF-Pb 10908b, detail of C showing a portion of the lobe where there is an apparent anastomosis of two adjacent veins (arrowhead). **E,** General view of the specimen MPEF-Pb 10907a, arrow showing insect damage. **F,** General view of the specimen MPEF-Pb 10907b. Scale-bars A, B, E, F: 10 mm. Scale bar C: 3 mm. Scale-bar D: 1 mm.

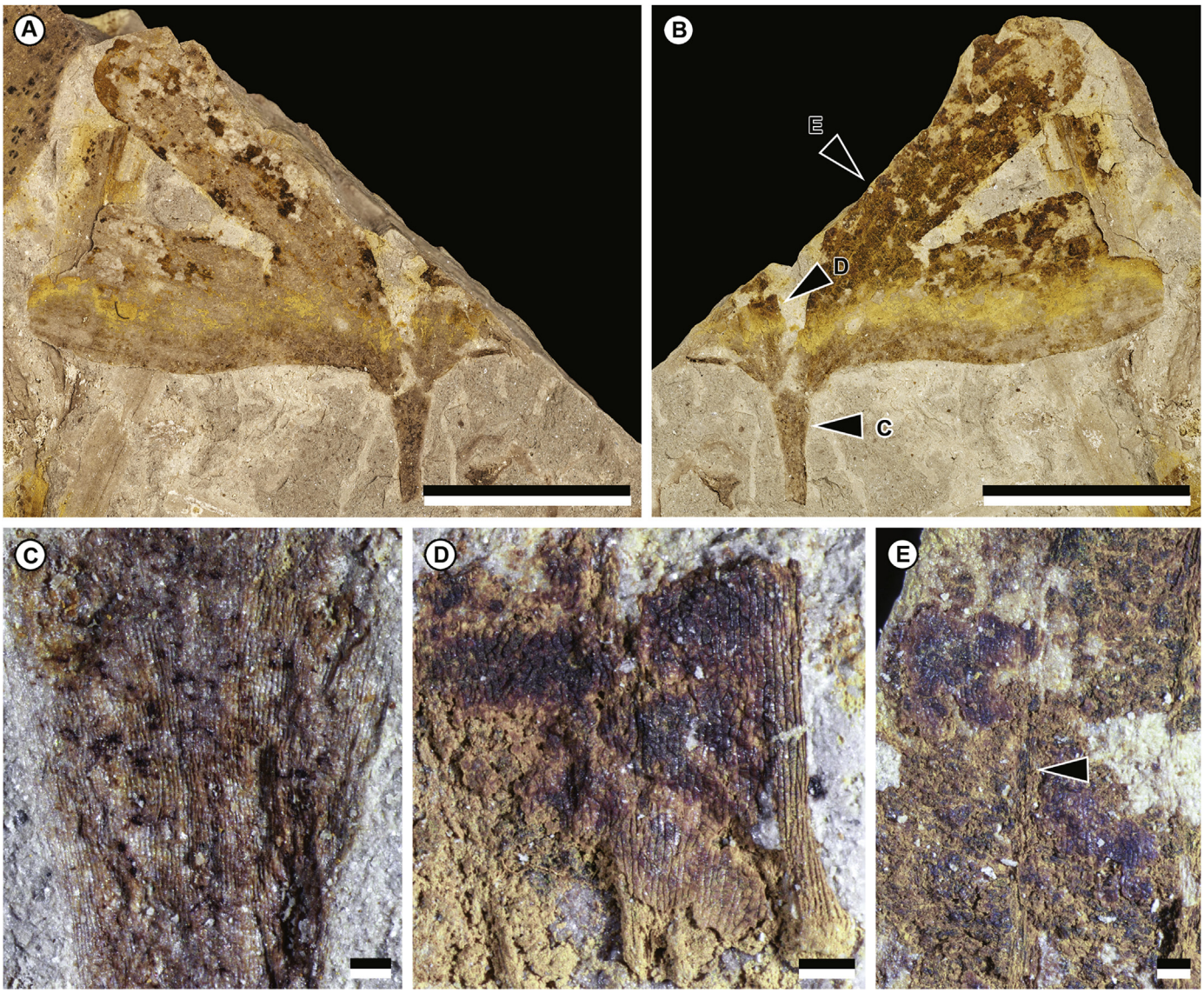


Fig. 4. Leaf morphology of the specimens of *Ginkgoites villardeseoanii* sp. nov. collected in the Cañadón de Loro locality of the Lefipán Formation. **A,** General view of the specimen MPEF-Pb 10897a. **B,** General view of the specimen MPEF-Pb 10897b, arrowheads mark the areas detailed in C–E. **C,** Detail of the area where the petiole and laminae encounter, showing rectangular and elongated epidermal. **D,** Detail of the leaf margin showing rectangular and elongated epidermal cells, and more irregularly shaped cells towards the inner lamina. **E,** Detail of the leaf showing a vein (arrowhead). Scale-bars A, B: 10 mm; C–E: 200 μm.

(Archangelsky, 1965; Del Fueyo and Archangelsky, 2001; Del Fueyo et al., 2013; Guignard et al., 2016). The record of Karkeniaceae is determined by the presence of the reproductive structures referred to *Karkenia incurva* Archangelsky found in association with the leaves of *Ginkgoites tigrensis* Archangelsky (Archangelsky, 1965; Del Fueyo and Archangelsky, 2001). Whereas the record of Ginkgoaceae was determined based on ultrastructural characters of the cuticle of *Ginkgoites tigrensis* Archangelsky (Del Fueyo et al., 2013) and *Ginkgoites skottsbergii* Lundblad (Guignard et al., 2016).

Following Zhou and Zhang's (1989) concept, we assigned the Lefipán fossils to *Ginkgoites* and belonging to an *incertae sedis* family because the leaves are macro-morphologically similar to those of *Ginkgo*, but they lack sufficient characters for including it in any known ginkgoalean family.

Barreda et al. (2012) mentions the presence of ginkgophyte pollen as a minor component of the gymnosperm palynoflora of the Lefipán Fm., which concurs with the low abundance of *Ginkgoites* leaves relative to that of other gymnosperm remains found in the formation (e.g., Wilf et al., 2017; Andruchow-Colombo et al., 2018; Escapa et al., 2018).

4.2. Comparisons

Ginkgoites villardeseoanii markedly differs from all other Patagonian fossil species known (Table 1). Three *Ginkgoites* species have been described for the Lower Cretaceous of Patagonia (Table 1), these are *G. ticoensis* (Archangelsky, 1965; Del Fueyo et al., 2006; 2013) from the Aptian Anfiteatro del Ticó Formation (Passalía et al., 2016), *G. tigrensis* (Archangelsky, 1965; Villar de Seoane, 1997) from the Aptian Bajo Tigre Formation (Passalía et al., 2016), and *G. skottsbergii* (Lundblad, 1971; Del Fueyo et al., 2006; Passalía, 2007; Guignard et al., 2016) from the Albian Piedra Clavada Formation (Archangelsky, 2009; Varela et al., 2012, 2019). Leaves of *G. skottsbergii* are longer and more lobated than those of *G. villardeseoanii* (Table 1) and differ in venation density (Table 1).

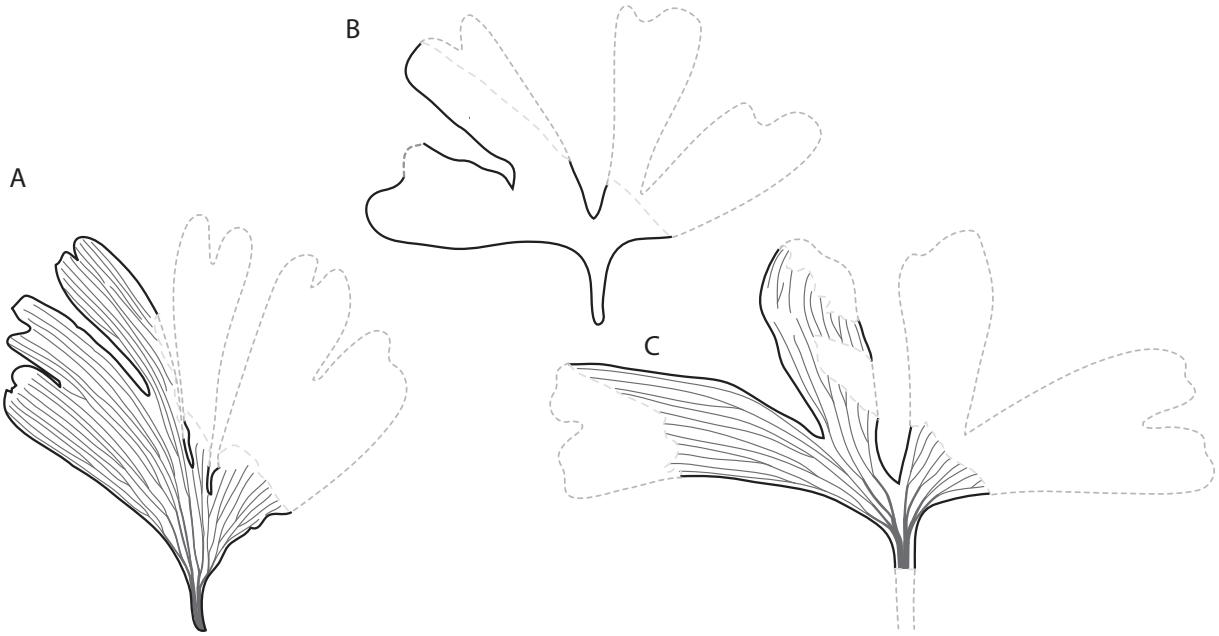


Fig. 5. Drawings showing the leaf morphological variation of *Ginkgoites villardeseoanii* sp. nov. from the Lefipán Formation (not to scale). **A,** MPEF-Pb 10908a. **B,** MPEF-Pb 10897a. **C,** MPEF-Pb 10907b.

Both *G. tigrensis* and *G. ticoensis* leaves partially overlap in size with those of *G. villardeseoanii* (Table 1). However, leaves of *G. tigrensis* present lobes more incised with rounded apices that seem to lack the apical notch characteristic of *G. villardeseoanii* (Archangelsky, 1965; Fig. 3CA), and those of *G. ticoensis* show markedly more incise and slender lobes, as well as a density of venation that lies on the lowermost portion of the variability shown by *G. villardeseoanii*.

Two fossil species from the Paleogene of Patagonia have been referred to *Ginkgoites*, these are *G. patagonica* (Berry) Villar de Seoane, Cúneo, Escapa, Wilf et Gandolfo (Villar de Seoane et al., 2015) from the lower and middle Eocene of Laguna del Hunco and Río Pichileufú localities, and *?Ginkgoites* from the upper Paleocene-lower Eocene Ligorio Márquez Formation (Carpenter et al., 2018). The leaves of *G. patagonica* are markedly larger, generally more lobed, and less densely veined than those of *G. villardeseoanii* (Table 1). The fossils described by Carpenter et al. (2018) couldn't be compared to those of the species here described because they are cuticular remains whereas the leaves of *G. villardeseoanii* preserve almost only macromorphological characters, lacking most epidermal characters.

Two Australian species, *Ginkgo australis* (McCoy) Drinnan et Chambers (Douglas, 1965, 1994; Drinnan and Chambers, 1986; Hill and Carpenter, 1999) and *Ginkgo wintonensis* McLoughlin, Drinnan et Rozefelds (McLoughlin et al., 1995), were described for Cretaceous and Paleogene deposits. *Ginkgo australis* is markedly larger size and more lobated (Douglas, 1965, 1994; Hill and Carpenter, 1999; Villar de Seoane et al., 2015) than *G. villardeseoanii*, whereas *G. wintonensis* is very similar in morphology to *G. villardeseoanii* but it is generally smaller and has a distal sinuous margin (McLoughlin et al., 1995).

Several *Ginkgoites* and *Ginkgo* species have been described for the Lower Cretaceous of India, among these are *Ginkgoites lobata* (Feistmantel) Seward, *Ginkgoites crassipes* (Feistmantel) Seward (Seward and Sahni, 1920), *Ginkgo rajmahalensis* (Sah et Jain) Zeba-Bano, Maheshwari et Bose (Sah, 1953; Mehta and Sud, 1953; Sah and Jain, 1965; Zeba-Bano et al., 1977), and *Ginkgoites feistmantelii* Bose and Sukh Dev (Bose and Sukh Dev, 1958; Baksi, 1968). The lamina of the leaves of *G. lobata* is heart-shaped, showing only a central incision and therefore only two lobes (Seward and Sahni, 1920). Leaves of *G. crassipes* have a single lobe and are less wide than those of *G. villardeseoanii* (Seward and Sahni, 1920). *Ginkgo rajmahalensis* overlaps with *G. villardeseoanii* in leaf size, but has a lower venation density, veins that only dichotomize once or twice, and multiple and slender lobes (Sah, 1953; Mehta and Sud, 1953; Sah and Jain, 1965; Zeba-Bano et al., 1977). The leaves of *Ginkgoites feistmantelii* are considerably smaller in size to those of *G. villardeseoanii*, and have an undivided, reniform to heart-shaped lamina (Bose and Sukh Dev, 1958; Baksi, 1968).

Among Chinese Lower Cretaceous Ginkgoalean species, *Ginkgo coriacea* Florin (Sun, 1993), the leaves associated to the reproductive structures described under *Ginkgo apodes* Zheng et Zhou (2004), *Ginkgoites myrioneurus* Yang (2004), *Ginkgo pediculata* Deng, Yang et Zhou (2020), and *Ginkgo huolinhensis* Dong et Sun (2012) are comparable to *G. villardeseoanii*. Leaves of *G. coriacea* differ from *G. villardeseoanii* in its markedly larger size and in the presence of resin bodies (Sun, 1993). The leaves associated with *G. apodes* are more strongly lobated and markedly smaller in size than those of *G. villardeseoanii* (Zheng and Zhou, 2004). The leaves of *G. myrioneurus* are characterized by their multiple lobes and their densely veined lamina (Yang, 2004). Leaves of *G. huolinhensis* and *G. pediculata* are generally larger than those of *G. villardeseoanii*, and differ markedly in shape, being both multilobed (*G. huolinhensis* with 6–13 lobes, and *G. pediculata* with 8–24 lobes; Dong and Sun, 2012; Deng et al., 2020).

Ginkgo tzagajanica Samylina emend. Horiuchi et Kimura (1986) from the Paleogene of Japan differ from *G. villardeseoanii* in general morphology, being markedly more entire than the Patagonian species (Horiuchi and Kimura, 1986; Golovneva, 2010).

4.3. Leaf vein anastomoses

Ginkgoites villardeseoanii shows a few vein anastomoses in the middle portion of its lobes (Fig. 3B–D). These anastomoses seem to be the result of vein dichotomizations in which one of the daughter veins became almost immediately fused with a neighbor vein. However, these apparent dichotomies that result in veins fusions,

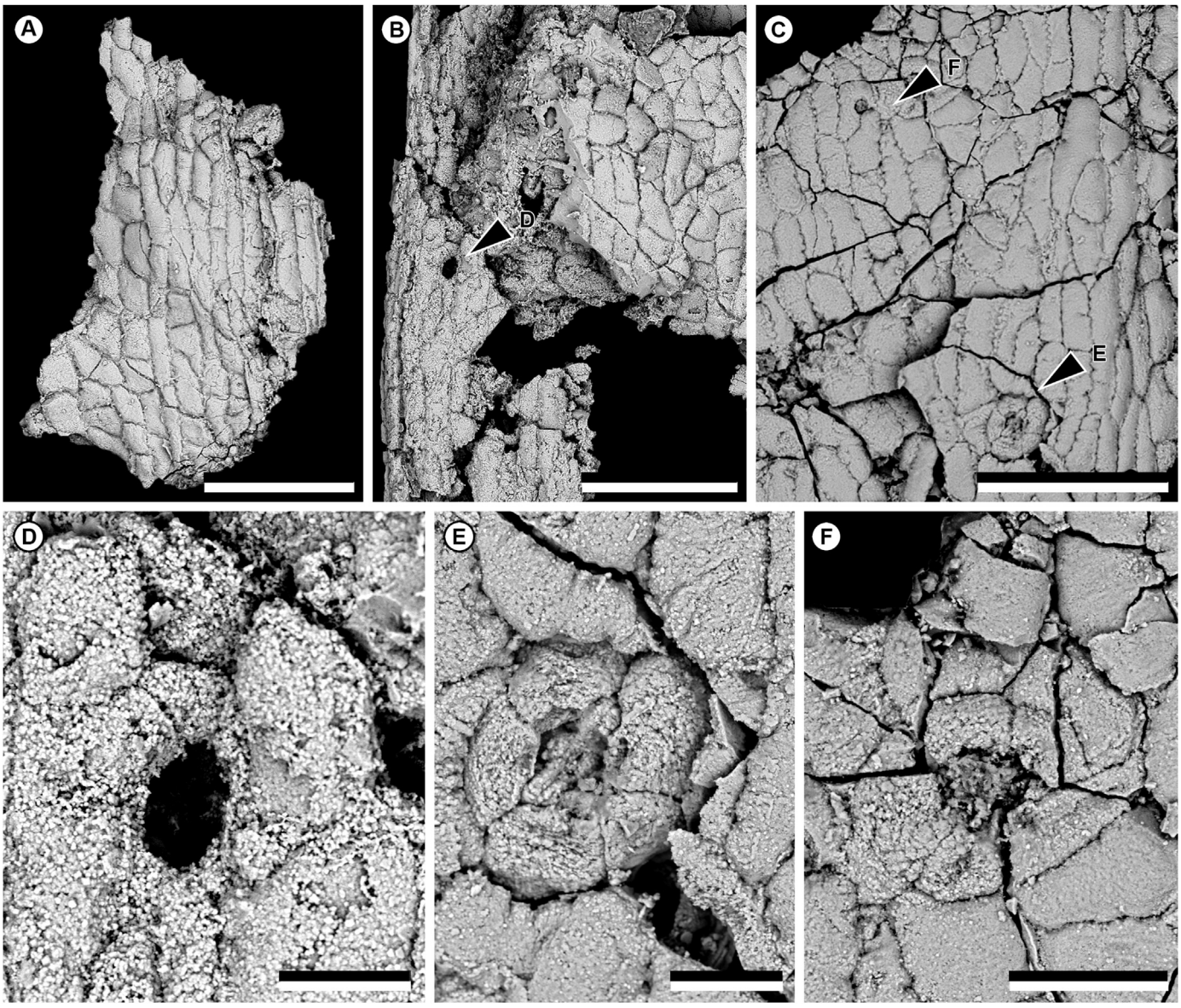


Fig. 6. Leaf epidermal morphology of the specimen MPEF-Pb 10897a of *Ginkgoites villardeseoanii* sp. nov. under Scanning Electron Microscopy. A–C, general view of cuticle fragments showing the arrangement of the epidermal cells, which show undulated walls. B, C, arrowheads indicate the position of stomatal apparatuses. D, detail of stomatal apparatus indicated in B. E, F, details of stomatal apparatuses indicated in C. Scale bars A–C = 200 μm, D, E = 30 μm, F = 50 μm.

arise in slightly larger angles than "normal" dichotomies in the same leaf. Leaf veins anastomoses have been reported for the extant *Ginkgo biloba* (Arnott, 1959), although occurring generally more distally in the leaves and being of slightly different morphology than those observed in *G. villardeseoanii*. Arnott (1959) characterized the most common anastomoses in four types (types A–D). The ones observed in the material from Lefipán are partially compatible with type C (Fig. 3D, black arrowhead). Arnott (1959) defined type "C" anastomoses as occurring when the adjacent veins produced by 2 separate dichotomies unit, similarly to what occurs in Fig. 3D (black arrowheads). As occurs in *G. biloba*, anastomoses in *G. villardeseoanii* were observed near the leaf margin.

4.4. Ginkgophytes in the Mesozoic of Argentina

The ginkgophytes have an extensive Mesozoic macrofossil record in Argentina. In Triassic deposits, it is represented by leaves of the genera *Baiera*, *Chiropteris*, *Ginkgo*, *Ginkgoidium*, *Ginkgoites*, *Rhipidopsis*, *Saportaea*, and *Sphenobaiera*, and by mega- and microsporangiate structures of *Hamshawvia* and *Stachyopitys*, respectively (Frenguelli, 1937; Artabe et al., 2007; Morel et al., 2011; Villar de Seoane et al., 2015; Gnaedinger and Zavattieri, 2017; Bodnar et al., 2020). The Jurassic macrofossil record of the group is notably scarce in the region, especially when considering the large amount of rich fossiliferous localities from that age, since it comprises only a few wood records referred to *Baieroxylon* and *Ginkgomyeloxylon* (Gnaedinger and Herbst, 2009; Gnaedinger, 2012). The Cretaceous macrofossil record, which is mostly restricted to its lowest portion (Table 1), comprehends leaves of *Ginkgoites* (Archangelsky, 1965; Lundblad, 1971; Villar de Seoane, 1997; Del Fueyo et al., 2006, 2013; Passalía, 2007; Guignard et al., 2016), megasporangiate structures of *Karkenia*, and *Allicospermum* seeds (Archangelsky, 1965).

Only three families have been identified in the macrofossil record of ginkgophytes in the Mesozoic erathem of Argentina. This is due to the high similarity of leaf forms among families, which has

Fig. 7. Detail of the herbivore damage observed on the specimen MPEF-Pb 10907a of *Ginkgoites villardeseoanii* (complete specimen illustrated in Fig. 3E). In the lower portion of the lobe, two circular perforations with a darker border that are consistent with the damage type DT01 (*sensu* Labandira et al., 2007) are present. Scale bar = 3 mm.

been discussed in a previous section (see 4.1 Assignment to *Ginkgoites*), to the scarcity of megasporangiate structures, on which the familiar definitions are mostly based (Zhou, 1997; Anderson and Anderson, 2003), and to the low number of studies on leaf cuticle ultrastructure (e.g., Del Fueyo et al., 2013; Guignard et al., 2016). The mentioned families are Hamshawviaceae (Anderson and Anderson, 2003; Bodnar et al., 2020), Ginkgoaceae (Del Fueyo et al., 2013; Guignard et al., 2016), and Karkeniaceae (Archangelsky, 1965; Krassilov, 1972). The family Hamshawviaceae was defined by Anderson and Anderson (2003) for remains found in the Triassic Molteno Formation, in South Africa, and in other Triassic fossil localities in the Southern Hemisphere (Anderson and Anderson, 2003; Barboni and Dutra, 2015; Bodnar et al., 2020). Its presence in the Upper Triassic of Northwestern Argentina was reported based on the presence of megasporangiate structures of the genus *Hamshawvia* Anderson et Anderson, in association with microsporangiate structures of the genus *Stachyopitys* A.Schenk (Bodnar et al., 2020). These remains are treated as ginkgophytes because *Hamshawvia* has been found in organic connection with *Sphenobaiera* leaves in a South African locality (Anderson and Anderson, 2003). The presence of the family Ginkgoaceae in Patagonia is represented by two *Ginkgoites* species with exceptional cuticle preservation, *G. ticoensis* from the Aptian (Archangelsky, 1965; Del Fueyo et al., 2013) and *G. skottsbergii* from the Albian (Lundblad, 1971; Del Fueyo et al., 2006; Passalía, 2007; Guignard et al., 2016). Based on leaf cuticule analyses, Del Fueyo et al. (2013) and Guignard et al. (2016) respectively registered Ginkgoaceae ultrastructure for these two species. The family Karkeniaceae was defined by Krassilov (1972), based on the genus *Karkenia* Archangelsky, which was originally described for megasporangiate structures found in the Lower Cretaceous (Aptian) of Southern Patagonia that were associated with *Ginkgoites* leaves (Archangelsky, 1965; Table 1). The Karkeniaceae are also represented in the Aptian of Southern Patagonia by the seeds of *Allicospermum*, also associated with leaves of *Ginkgoites tigrensis* (Archangelsky, 1965; Del Fueyo et al., 2013; Table 1). In this respect, isolated seeds of *Allicospermum* have been referred to the families Karkeniaceae, Yimaiaceae, and Ginkgoaceae in different localities of the world (Zhou et al., 2007; Yang et al., 2008; Zhou, 2009). However, Del Fueyo et al. (2013) determined that *A. patagonicum* from the Anfiteatro del Ticó Formation in Southern Patagonia most probably belonged to the Karkeniaceae.

As it was previously stated, the vegetative remains of *Ginkgoites villardeseoanii* closely resemble the two Southern Patagonian fossil species described by Archangelsky (1965) (Table 1), of which *G. tigrensis* belonged to Karkeniaceae (Archangelsky, 1965; Del Fueyo et al., 2013) and *G. ticoensis* to Ginkgoaceae (Del Fueyo et al., 2013). Therefore, until more information on *G. villardeseoanii* is available, its family-level affinity remains unknown.

4.5. Insect damage

One of the specimens referred to *Ginkgoites villardeseoanii* has a few holes on the lamina that are compatible with insect damage (Figs. 3E, F, 7). The size and morphology of the leaf perforations are consistent with the damage type DT01 representing hole feedings (Labandeira et al., 2007). The damage in the leaf of *G. villardeseoanii* shows a darker border, interpreted as necrotic tissue that evidences a reaction of the plant to the insect attack. That evidence of the plant physiological reaction to the wound implies that the damage was probably done when the leaf was still on the plant. The same type of damage has been reported for angiosperm leaves from the southern localities of Lefipán Formation (Donovan et al., 2018), whereas similar damage types but larger in size were described for angiosperm leaves of both the northern and southern localities of Lefipán (Donovan et al., 2018; Martínez et al., 2018).

Among Patagonian fossil ginkgophytes (Table 1), some fossils illustrated in Cúneo (1987, figs. 4, 7) might indicate the presence of a similar type of damage in two Permian *Ginkgoites* species from Río Genoa Formation, *G. ferugloi* Cúneo and *G. eximia* Cúneo. Moreover, additional specimens of *Ginkgoites eximia* from the same locality have been reported to show surface, margin and hole feeding damage, as well as oviposition scars (Gallego et al., 2014). A recent study on the fossil record of plant–insect interactions in the Permian and Triassic of Gondwana reports insect damage on ginkgophytes occurring in localities of Argentina, Brasil, and Chile, but conclude that this is not the most affected group during the Permian and Triassic (Cariglino et al., 2021). Studies on the Triassic gymnosperm flora of Molteno Formation, in South Africa, have also shown the presence of insect damage in ginkgoalean foliage, most of which corresponded to terminal leaf feeding (Scott et al., 2004). Additionally, there are reports of insect damage in a Jurassic *Ginkgoites* from China that is associated with the reproductive organs of *Yimaia capituliformis* Zhou, Zheng and Zhang (Zhou et al., 2007; Wang et al., 2011). The insect damages reported for the leaves associated to *Y. capituliformis* differ from the ones here reported, as they comprise galling (isolated and in rows), piercing- and sucking, and marginal feeding types (Wang et al., 2011). Furthermore, insect damage on ginkgoalean foliage was reported from Cretaceous deposits in China (Ding et al., 2015), where it constituted the less affected group of the flora, and from the United States (Labandeira et al., 2002). However, no records of ginkgophyte-insect interaction were previously known for the Cretaceous

Table 1
Origin, morphology, and systematic treatment of fossil *Ginkgo* and *Ginkgoites* leaves from Argentina.

Species and Citations	Origin and Age	Lamina length (mm)	Lamina width (mm)	Lobes	Veins/cm	Petiole width (mm)	Family	Insect damage	Citation
Gt. crassipes	Río Genoa Fm., Ea. Permian	40	26	1	?	?			Feruglio (1933)
Gt. eximia	Río Genoa Fm., Ea. Permian	14–24	30–42	1–2	32–45	2	?	Present*	Feruglio (1942); Cúneo (1987); Gallego et al., (2014)
Gt. feruglioi	Río Genoa Fm., Ea. Permian	≤16	≤33	1	≤30	1.5	?	Present*	Cúneo (1987)
Gt. truncata	Potrerillos Fm., Triassic	25–46	8–25	1	31–32	?			Frenguelli (1946)
G. taeniata	Paso Flores Fm., La. Triassic	22–27	?	4–8	30–40	?	?	NR	Frenguelli, 1937; Villar de Seoane et al., 2015
?G. crassipes	Paso Flores Fm., La. Triassic	40 (estimated)	26 (estimated)	2	?	3	?	NR	Frenguelli, 1937; Zavatt & Mego (2008)
Gt. ticoensis	Anfiteatro del Ticó Fm., Aptian	≤40	30	4	12	1	Ginkgoaceae[1]	NR	Archangelsky 1965; D. Fueyo et al., (2013)
Gt. tigrensis	Bajo Tigre Fm., Aptian	≤45	≤50	4–8	18–20	1–2.5	Karkeniaceae[2]	NR	Archangelsky 1965; Villar de Seoane 1997
Gt. skottsbergii	Piedra Clavada Fm., Albian	≥50	≥40	6–12	13–23	0.8–2.0	Ginkgoaceae[3]	NR	Lundblad (1971); D. Fueyo et al., (2006); Passalía (2007); Archangelsky (2009); Varela et al., (2012), 2019; Guignard et al., (2016)
Gt. villardeseoanii	**Lefipán Fm, Maastrichtian**	**35.2–38.2**	**35.2–60.2 (estimated)**	**2–4**	**12–19**	**1.1–1.5**	**?**	**Present**	**This study**
Gt. patagonica	Laguna del Hunco and Río Pichileufú, ea-mid. Eo.	? –80	? –115	4–8	6–14	? –3	?	NR	Villar de Seoane et al., (2015)
?Ginkgoites	Ligorio Márquez Fm., la.Pc–ea.Eo.	?	?	?	?	?	?	NR	Carpenter et al., (2018)

Notes: **Within Species:** (*G.*) *Ginkgo*, (*Gt.*) *Ginkgoites*. **Within Age:** (Ea) Early, (Eo) Eocene, (J) Jurassic, (L) Late, (Mid) Middle, (Pc) Paleocene. **Within Veins/cm and Petiole width:** (**) data taken from Villar de Seoane et al., (2015); **Within family:** [1]determined by cuticle ultrastructure analysis, associated with seeds of the genus *Allicospermum* (Del Fueyo et al., 2013); [2]associated with megasporangiate organs of the genus *Karkenia*; [3]determined by cuticle ultrastructure analysis (Guignard et al., 2016). **Within Insect damage:** (NR) not reported, and not evident from the published pictures; (Present*) some insect damage types on *G. eximia* were reported by Gallego et al., (2014), others were not reported but their presence is inferred from pictures in the cited publications.

of the Southern Hemisphere. In this context, *G. villardeseoanii* has the first Cretaceous remain of the scarce record of insect-plant interaction for the group in the Southern Hemisphere. If the extant *Ginkgo biloba* is excluded, no Cenozoic records of insect damage in ginkgophytes were reported, nor clearly observable in published images.

Studies in the extant species *Ginkgo biloba* stated that the number of species feeding from these trees is remarkably lower to those attacking other gymnosperm species (Honda, 1997). Moreover, several studies, as well as traditional knowledge from China and Japan, have shown that *G. biloba* has insecticidal and insect-repellent properties (Honda, 1997; Mohanta et al., 2012; Pan et al., 2016). A usual example is the invasive fall webworm, *Hyphantria cunea*, native from North America and introduced to Japan after World War II, which feeds from more than 300 tree species in that country, but avoids *Ginkgo* leaves (Honda, 1997). In this sense, *Ginkgo* has been shown to contain secondary metabolites with anti-feeding activity against certain pests (Mohanta et al., 2012; Pan et al., 2016). The presence of a chemical defense in extant *Ginkgo* has been proposed as one of the reasons for its survival as a "living fossil" (Honda, 1997). In this same line of reasoning, the scarce records of insect damage (Scott et al., 2004; Wang et al., 2011; Table 1) in the large ginkgophyte leaf record might be indicative of anti-feeding properties also in extinct species of the group, and might have helped, not only to its relictual survival, as proposed by Honda (1997), but to the lineage remarkable longevity.

There is a high occurrence of herbivore damage in the flora of the Lefipán Formation (Donovan et al., 2016, 2018; Martínez et al., 2018). This is represented in both the amount of affected leaf specimens and angiosperm leaf morphotypes, as well as in the richness of damage types and associations described, several of which became extinct after the K/Pg event (Donovan et al., 2016, 2018; Martínez et al., 2018). In this context, it is understandable, that even an herbivore-repellent plant, as possibly was *G. villardeseoanii*, had its share of insect damage.

5. Conclusions

We describe *Ginkoites villardeseoanii* sp. nov. based on leaf adpressions found in the Upper Cretaceous (Maastrichtian) deposits of the Lefipán Formation (Chubut Province, Patagonia, Argentina). The leaf macro- and micro-morphological characters preserved in the described specimens of *G. villardeseoanii* do not provide enough evidence to refer it to a known family. That is because of the high similarity that exists among the leaves of the Ginkgoalean families Ginkgoaceae, Karkeniaceae, and Yimaiaceae. Therefore, the new species was referred to an *incertae sedis* family. However, when taking into consideration the Patagonian Cretaceous record for the group, the most probable affinity of *G. villardeseoanii* is either within the Karkeniaceae or the Ginkgoaceae.

The new taxon here described shows evidence of insect damage, constituting the first Cretaceous record of plant-insect interaction for the ginkgophytes in the Southern Hemisphere. The record of plant-insect interaction for the ginkgophytes is scarce, existing so far only a few reported in the Permian, Triassic, Jurassic, and Cretaceous. It was discussed here that this scarcity might be due to the insecticidal and insect-repellent properties of these plants, which have been extensively studied and reported for the only living member of the group, *Ginkgo biloba*. We propose that such anti-feeding properties might have been one of the causes of the remarkable longevity of the lineage.

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