American Journal of Botany

# *Araucaria lefipanensis* (Araucariaceae), a new species with dimorphic leaves from the Late Cretaceous of Patagonia, Argentina

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**PREMISE OF THE STUDY**: We describe a new araucarian species, *Araucaria lefipanensis*, from the Late Cretaceous flora of the Lefipán Formation, in Patagonia (Argentina) based on reproductive and vegetative remains, with a combination of characters that suggest mosaic evolution in the *Araucaria* lineage.

**METHODS**: The studied fossils were found at the Cañadón del Loro locality. Specimens were separated into two leaf morphotypes, and their morphological differences were tested with MANOVA.

**KEY RESULTS**: The new species *Araucaria lefipanensis* is erected based on the association of dimorphic leaves with cuticle remains and isolated cone scale complexes. The reproductive morphology is characteristic of the extant section *Eutacta*, whereas the vegetative organs resemble those of the sections *Intermedia*, *Bunya*, and *Araucaria* (the broad-leaved clade).

**CONCLUSIONS**: The leaf dimorphism of *A. lefipanensis* is similar to that of extant *A. bidwillii*, where dimorphism is considered to be related to seasonal growth. The leaf dimorphism in *A. lefipanensis* is consistent with the paleoclimatic and paleoenvironmental reconstructions previously suggested for the Lefipán Formation, which is thought to have been a seasonal subtropical forest. The new species shows evidence of mosaic evolution, with cone scale complexes morphologically similar to section *Eutacta* and leaves similar to the sections of the broad-leaved clade, constituting a possible transitional form between these two well-defined lineages. More complete plant concepts, especially those including both reproductive and vegetative remains are necessary to understand the evolution of ancient plant lineages. This work contributes to this aim by documenting a new species that may add to the understanding of the early evolution of the sections of *Araucaria*.

**KEY WORDS**   *Araucaria*; Araucariaceae; Argentina; Cañadón del Loro; Cretaceous; leaf dimorphism; Lefipán Formation; Maastrichtian; mosaic evolution; Patagonia.

The conifer family Araucariaceae has been identified in the fossil record at least since the Jurassic (Stockey and Taylor, 1978b; Stockey, 1982, 1994; Kershaw and Wagstaff, 2001; Panti et al., 2012). However, remains referred to the family have been reported since as early as the Late Triassic (Lele, 1956; Axsmith and Ash, 2006), although these may represent an araucariaceous stem group (Kunzmann, 2007). During the Mesozoic, the family had a worldwide distribution, but its dominance in paleoecosystems started to decline during the Cretaceous. By the beginning of the Paleocene, Araucariaceae became restricted to South America, Australia, Antarctica, and New Zealand (Berry, 1908; Whitmore and Page, 1980; Dettman and Clifford, 2005). Today, the family comprises three genera, *Araucaria*, *Agathis*, and *Wollemia*, restricted to the southwest Asia-Western Pacific regions, and South America (Seward and Ford, 1906; Berry, 1908; Florin, 1963; Farjon, 2010). This disjunct distribution of extant Araucariaceae and its present low species diversity, in contrast with its higher species diversity in the past, lead to the hypothesis that these extant taxa are relictual (Stockey, 1982; Kershaw and Wagstaff, 2001).

Araucariaceae comprise trees reaching from 10 to 90 m in height, although the most common mature height is around 50 m (Farjon, 2010). *Agathis* and *Wollemia* have been recovered as a

monophyletic group (i.e., 'Agathioid' clade, Escapa and Catalano, 2013) in most recent morphological, molecular, and combined phylogenetic analyses (Gilmore and Hill, 1997; Kunzmann, 2007; Rai et al., 2008; Codrington et al., 2009; Liu et al., 2009; Escapa and Catalano, 2013; contra Setoguchi et al., 1998). The agathioid clade is morphologically distinctive, with seed cones bearing numerous spirally arranged scales, which are interpreted as the ovuliferous scale completely fused to the bract (Florin, 1951; Hyland, 1978; Stewart and Rothwell, 1993; Chambers et al., 1998). Each cone scale bears one free inverted seed. In *Wollemia* the seed is circumferentially winged, whereas in *Agathis* it has two asymmetrical lateral wings (Dickson, 1863; Hyland, 1978; Whitmore, 1980; Chambers et al., 1998; Farjon, 2010). These two genera are also easily distinguished from *Araucaria* by differences in leaf morphology and anatomy (Chambers et al., 1998). *Wollemia* has opposite/decussate, sessile, linear leaves with slightly revolute margins, whereas *Agathis* has subopposite to opposite phyllotaxy and short-petiolate leaves with broad, flat blades (de Laubenfels, 1978, 1979; Page, 1990; Farjon, 2010).

The genus *Araucaria* includes 20 modern species classified in four sections, originally erected based solely on morphological characters of the extant species (Wilde and Eames, 1952). *Araucaria* section *Araucaria* (=*Columbea* Endlicher emend. Wilde and Eames, 1952) includes the two South American species, *A. araucana* (Molina) K.Koch and *A. angustifolia* (Bertol.) Kuntze. In addition, there are two monotypic sections: *Araucaria* section *Intermedia* White (1947) that includes *Araucaria hunsteinii* K.Schum., confined to Papua New Guinea, and *Araucaria* section *Bunya* Wilde and Eames (1952) that contains *Araucaria bidwillii* Hook., which is restricted to disjunct locations in southeastern and northeastern Queensland, Australia. Finally, *Araucaria* section *Eutacta* Endlicher (1842) includes *A. cunninghamii* Mudie from New Guinea and Queensland, Australia, *A. heterophylla* (Salisb.) Franco native to Norfork Island National Park, Australia, and 14 New Caledonian endemic species (Florin, 1963; Enright, 1995; Enright et al., 1995; Farjon, 2010; Mill et al., 2017). The genus *Araucaria* has two distinct leaf morphologies: (1) sessile, imbricate, usually erect and relatively small leaves persistent on falling branches that are typical of the *Araucaria* section *Eutacta*; and (2) sessile leaves with broad, flat lamina and acute apices that are characteristic of *Araucaria* sections *Araucaria*, *Intermedia*, and *Bunya* (Chambers et al., 1998; Stockey, 1982; Farjon, 2010). All *Araucaria* species (both extant and fossil) have ovuliferous cones with spirally arranged seed complexes, each bearing a single, inverted, central seed embedded in scale tissues (Eames, 1913; Wilde and Eames, 1948; de Laubenfels, 1972; Page, 1990; Stockey, 1994; Farjon, 2010). Also, they all have a ligule at the distal portion of the cone scale complex right over the chalazal end of the seed, which is interpreted to be the free distal end of the ovuliferous scale (Eames, 1913; Wilde and Eames, 1948; Florin, 1951; de Laubenfels, 1988; Stewart and Rothwell, 1993; Stockey, 1994; Farjon, 2010). However, the morphology of the cone scale complex is variable among sections. *Araucaria* section *Araucaria* has nut-like diaspores with non-vascularized, extremely reduced lateral expansions (Carrière, 1855; Seward and Ford, 1906; Wilde and Eames, 1952; Haines, 1983a; Farjon, 2010). *Araucaria* section *Intermedia* produces samara-like complexes that are fan-shaped and have laterally expanded, vascularized, papery-thin wings (Seward and Ford, 1906; Wilde and Eames, 1952; Haines, 1983a; Farjon, 2010). *Araucaria* section *Eutacta* has samara-like ovulated complexes with wings that are well developed, papery thin, and not vascularized

(Carrière, 1855; Seward and Ford, 1906; Wilde and Eames, 1952; Haines, 1983a; de Laubenfels, 1972, 1988; Farjon, 2010). *Araucaria* section *Bunya* produces cone scale complexes with large, heavy, vascularized, woody wings (Carrière, 1855; Seward and Ford, 1906; Wilde and Eames, 1952; Haines, 1983a; Farjon, 2010).

Although there is extensive information on fossil forms within Araucariaceae, only few fossil species are defined based on associated vegetative and reproductive organs (e.g., Kendall, 1949; Harris, 1979; Del Fueyo, 1991; Ohsawa et al., 1995; Wilf et al., 2014). Such organismal concepts are crucial for the development of more stable phylogenetic studies. Herein, we describe a new species based on associated reproductive and vegetative araucarian fossil remains collected at the Cañadón del Loro locality from the Upper Cretaceous Lefipán Formation that crops out at the Chubut Province, Patagonia, Argentina. We also discuss the implications of these new records on the evolution of the genus during the last part of the Mesozoic Era.

## MATERIALS AND METHODS

### Geologic setting

The Lefipán Formation belongs to the Cañadón Asfalto Basin and crops out at the Chubut River middle valley, near Paso del Sapo village, NW Chubut Province, Patagonia, Argentina (Fig. 1A). The entire unit was deposited during the Maastrichtian (Late Cretaceous)–Danian (Paleocene) in a tide-dominated deltaic setting (Scasso et al., 2012).

The age of the Lefipán Formation is constrained by biostratigraphic proxies, i.e., marine faunas, terrestrial palynomorphs and dinoflagellates. In the first case, bivalves, gastropods, amonoids, decapods, and corals initially defined the Maastrichtian-Danian time span of deposition (Medina et al., 1990; Olivero et al., 1990; Medina and Olivero, 1994; Kiessling et al., 2005). This age was confirmed by terrestrial pollen and spore assemblages (Baldoni, 1992), and more recently and in more detail by Barreda et al. (2012), who showed a clear Maastrichtian-Danian transition associated to dinoflagellates (see also Vellekoop et al., 2017).

A highly diverse paleoflora has been recovered from Maastrichtian localities of the Lefipán Formation located south of the Chubut River (Fig. 1A); the local assemblages are dominated by angiosperms with lower proportion of gymnosperms and ferns (Cúneo et al., 2008). From the same Maastrichtian localities, palynological studies have shown a rich fern-angiosperm association, with gymnosperms (mostly podocarps) as a frequent element (Barreda et al., 2012).

The material here studied comes from the Cañadón del Loro locality, located north of the Chubut River (see Fig. 1A). The plant-bearing sediments of Cañadón del Loro locality are stratigraphically below the localities from the south of the Chubut River. In this section, the lower part of the Lefipán Fm. has more terrestrial sedimentary features, including well-developed paleosols and associated coaly layers, and probably represents a more proximal (fresh water dominated) location in the regional deltaic system. Based on the palynological content of nearby and stratigraphic equivalent sections (Barranca de los Perros locality, Baldoni and Askin, 1993), the age of the lower Lefipán Fm. at the Cañadón del Loro locality is estimated to be Maastrichtian (Late Cretaceous).

Four fossiliferous horizons were identified at the Cañadón del Loro locality (Fig. 1B), all of them highly prolific in yielding fossil
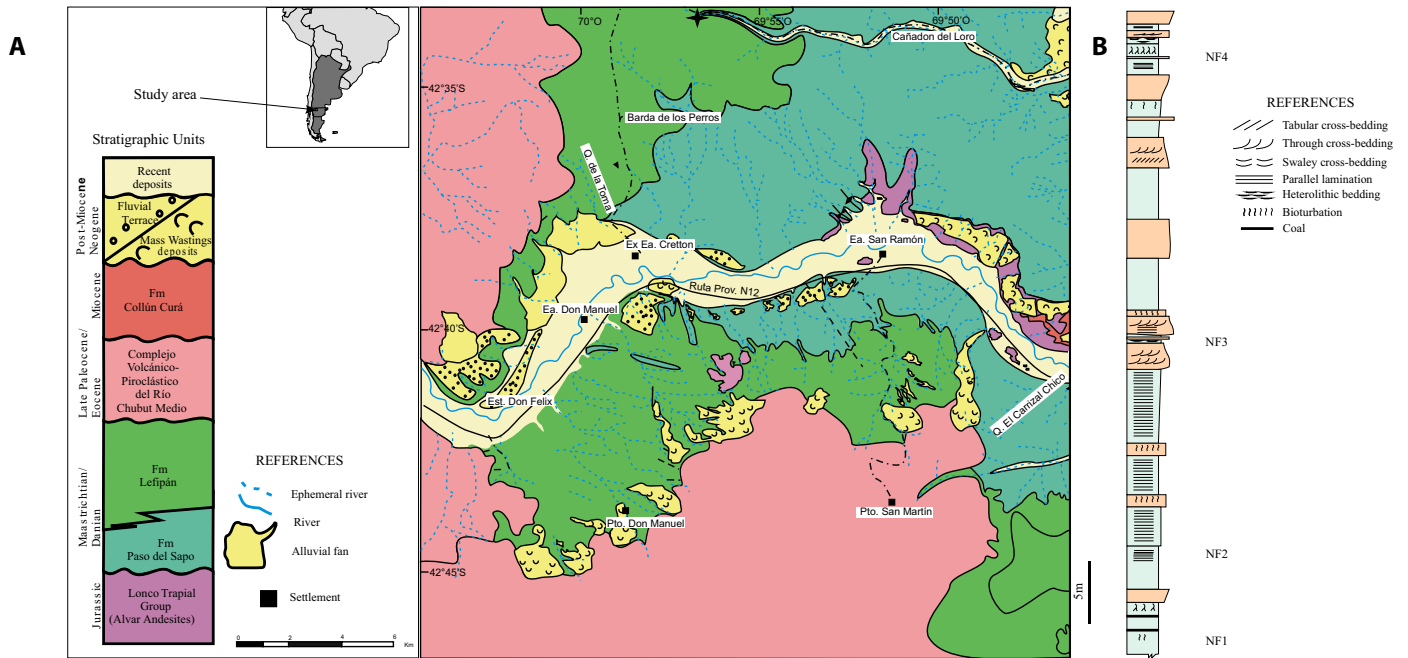
**FIGURE 1.** Geologic map and stratigraphic section. (A) Geologic map of study area (modified from Ruiz, 2007), Cañadón del Loro locality (Chubut Province, Argentina) marked with black star. (B) Partial stratigraphic section of lower portion of Lefipán Formation at Cañadón del Loro locality.

plants. In particular, Level 4 (Fig. 1B) has produced most of the araucarian remains herein studied. Associated with this level, two quarries were excavated: 4A and 4B. Level 4A is nearly 1 m thick, and it is dominated by angiosperms, while Level 4B (*La Huella*) is strongly dominated by the araucarian leaves and seed complexes here described. Level 4B is 15 cm thick with a highest fossil concentration layer of 7 cm and underlies a sand level with two types of dinosaur footprints. Interestingly, the best-preserved specimens of Level 4B were found immediately below the footprints. Level 4A yields, in addition to the araucarian material, a diverse angiosperm assemblage and fern remains, as well as leafy branches and isolated cone scale complexes of another type of conifer. This second conifer shows affinity to Cupressaceae, comprising multi-seeded cone scale complexes with seeds positioned distally and needle-like leaves. The cupressaceous conifer was also found at the other three fossiliferous levels represented by both leafy branches and cone scale complexes in clear association. The levels where the described fossils come from comprised by clayey siltstones, suggesting a low-energy depositional environment (N. R. Cúneo, personal observation) that allowed the preservation of delicate structures such as epidermal patterns of the leaves and the papery wings of the cone scale complexes.

## Fossil preparation and illustration

The fossil remains are preserved as impressions and compressions in clayey siltstones, occasionally with cuticular remains or some epidermal patterns impressed on the sedimentary surface. Fossils were prepared using standard mechanical techniques; macroscopic images of the specimens were taken with a Canon EOS 7D camera and a Canon EF-S 60 mm macro lens (Canon Corp., Melville, NY, USA) under halogen lighting projected at different angles to maximize observation of venation details (Kerp and Bomfleur, 2011).

The description of epidermal patterns is based on in situ leaf cuticular remains, cuticles extracted by bulk maceration (to obtain additional specimens), and observation of leaf impressions with no cuticle preserved but with retained impression of cellular details. Scanning electron microscope images were taken with a low vacuum scanning electron microscope (LVSEM) at Aluar Aluminio Argentino (Puerto Madryn, Chubut Province, Patagonia, Argentina).

Images obtained were processed with Photoshop Lightroom 5 (Adobe, San José, CA, USA) for exposure and white balance and with Photoshop CS5 (Adobe) for focus stacking (Bercovici et al., 2009) and plate assemblage. All specimens are housed at the Paleobotanical Collection of the Museo Paleontológico Egidio Feruglio, Trelew, Chubut Province, Patagonia, Argentina (hereafter MPEF-Pb).

## Statistical analyses

For testing the significance of differences between two morphological groups in a set of leaf morphological characters a multivariate analysis of variance (MANOVA) was applied. Four morphological variables (leaf length, leaf maximum width, apex angle, and distance between the leaf base and its maximum width) were selected as dependent variables and the shape group (ovate-lanceolate or lanceolate, see Results) was set as main factor.

Univariate normality was tested for each variable with Shapiro–Wilks tests and with graphic approaches (error frequency histograms and QQ-Plots). Multivariate normality (MVN) was tested with two analytical methods: Mardias's and Royston's MVN test, according to recommendations of Korkmaz et al. (2014). Homogeneity of variance–covariance matrices were verified with Box's M-test (Box, 1949). The statistic regarded for confirmation or rejection of the null hypothesis was Pillai's trace (Pillai, 1955;

Olson, 1974). We considered a level of significance of 95% (α = 0.05). All analyses were performed in R environment (R Core Team 2016), using stats (R Core Team 2016), biotools (da Silva, 2017), MNV (Korkmaz et al., 2014), lattice (Sarkar, 2008), psych (Revelle, 2016), Hmisc (Harrell and Dupont, 2016), MASS (Venables and Ripley, 2002), and mvoutlier (Filzmoser and Gschwandtner, 2018) packages.

The analyzed data set and the correspondent R script are available in Appendices S1 and S2 (see the Supplemental Data with this article).

## RESULTS

The results of the MANOVA show significant differences between the ovate-lanceolate and lanceolate leaf shape groups ($F_{4, 9}$ = 22.08; $P < 0.0005$). Therefore, subsequently, both leaf types were treated separately along the study. Nevertheless, these two leaf morphologies are assumed to belong to a single dimorphic species (see Discussion).

### Systematic palaeontology

**Family**—Araucariaceae Henkel and Hochst., 1865

**Genus**—*Araucaria* de Jussieu, 1789

**Type species**—*Araucaria araucana* (Molina) K.Koch, 1873

**Species**—*Araucaria lefipanensis* sp. nov. Andruchow Colombo, Escapa, Cúneo & Gandolfo
(Figs. 2–6; Appendices S3 and S4, see Supplemental Data)

**Etymology**—The specific epithet refers to the Lefipán Formation where the type material of this species was collected.

**Holotype**—MPEF-Pb 8297 (Fig 2A). Leafy branch. Level 4, Cañadón del Loro locality, Lefipán Formation, Cañadón Asfalto Basin, Chubut Province, Argentina.

**Paratypes**—Leafy branches. MPEF-Pb 5799, 5821, 5825, 5827, 8285, 8287-8288, 8291, 8294-8300, 8303-8306, 8311, 8314, 8316-8318, 8320, 8321, 8323, 8325, 8327, 8328, 8333, 9210-9213, 9216, 9219, 9221, 9223, and 9229. Isolated leaves. MPEF-Pb 5817, 5818, 8286-8287, 8289-8290, 8292-8294, 8299, 8308, 8310, 8312, 8315, 8319, 8326, 8329-8330, 8332, 9214-9215, 9217-9218, 9220, 9222, 9224-9228, 9230-9248, and 9250. Cuticle remains. MPEF-Pb 8331-8332. Cone scale complexes. MPEF-Pb 5810, 5826, 8299, 8301, 8307, 8309, 8313, 8322, and 9252-9272.

**Geographic occurrence**—Cañadón del Loro, Chubut Province, Argentina

**Stratigraphic occurrence**—Levels 3 and 4, lower Lefipán Formation (Maastrichtian), Cañadón Asfalto Basin

**Diagnosis**—Shoots bearing helically arranged, imbricated leaves; leaves dimorphic, multiveined, sessile, with entire margin and acute apex, lanceolate to ovate-lanceolate, abaxially keeled, 11.3–35.3 mm long, 4.7–12.4 mm wide. Stomata arranged in parallel discontinuous rows aligned with major axis of the leaf; stomatal apparatuses with ovate contour, four to five subsidiary cells. Cone scale complexes heart-shaped, length 14.9–18.3 mm, maximum width 11.5–20.0 mm, ligulate, with a bract tip; central body of complex cuneate in outline, woody in appearance and with longitudinal striations; lateral wings thin and slightly asymmetric; each complex bearing a single central inverted seed; seed 8.7–10.9 mm long, 4.2–5.9 mm wide.

**Description**—The vegetative remains are represented by impressions and compressions of foliar branches (Figs. 2 and 3) and of isolated leaves (Fig. 4). Several specimens are three-dimensionally preserved, and so the arrangement of the leaves on the branches is perceivable (Figs. 2 and 3).

**Leaves**—Foliar branches are up to 7.8 cm wide, including leaves (Fig. 2A). Leaves usually cover the entire central axis, although in a few specimens the leaves are only partially preserved and a portion of the central axis can be observed (Fig. 2D, 2E). Twigs are straight, up to 3.9 mm wide (mean: 3.0, SD: 0.8 mm, *n*: 3), and bear spirally arranged leaves showing helical phyllotaxy (Figs. 2A–F, 3A–D). The leaves are highly imbricated with a degree of superposition varying between 15–70% (mean: 41%, SD: 20%, *n*: 9, Figs. 2, 3) and show an insertion angle of 26–63º (mean: 40.8º, SD: 10.2º, *n*: 12, Fig. 2A, E). At the apical region of the foliar branches, the leaves are densely packed with small leaf insertion angles, resulting in a drop-like structure (Fig. 2B).

Two slightly different leaf morphologies were identified, which were labeled as "lanceolate" and "ovate-lanceolate" shape groups (L-shaped and O-shaped groups respectively), there are also leaves with intermediate morphologies between L- and O-shape groups (Appendix S4).

The O-shaped group includes, as indicated by its name, ovate-lanceolate leaves (Figs. 2C–E, 3B, C, 4C–E, G, H), with entire margin and acute apex (its angle varies between 31.3° and 53.4°, mean: 39.6°, SD: 7.7°, *n*: 9; Fig. 4E, F). The leaves are thick in appearance (Figs. 3C, 4G, H). Leaf length is 11.3–22.3 mm (mean: 17.5 mm, SD: 3.9 mm, *n*: 9), and its maximum width is 4.7–12.7 mm (mean: 8.9 mm, SD: 2.5 mm, *n*: 9). The width/length ratio is 0.3–0.7 (mean: 0.5, SD: 0.1, *n*: 9), and the distance between the leaf base and the maximum width represents a 15–33% of the leaf length (mean: 21%, SD: 5%, *n*: 9). These leaves are sessile (Figs. 2D, E, 4C, D, G, H), have 55–68 parallel veins that maintain the same caliber through all of the length (Figs. 3C, 4D, E), and have a central abaxial keel extended from the base to the apex; the leaves are often folded over the keel when found on the branches (Figs. 2C, 3C).

The L-shaped group comprises lanceolate leaves (Figs. 2A, 2B, 2F, 3A, 3D, 4A, 4B, 4F), which are also thick in appearance (Figs. 2A, 2B, 2F, 3A, 3D) and have entire margins and acute apices (apex angle varies between 19 and 38.9°, mean: 27.7°, SD: 7.2°, *n*: 8; Fig. 4A, 4B). The leaf length is 19.5–35.3 mm (mean: 28.2 mm, SD: 5.2 mm, *n*: 8), although one specimen exhibited one leaf 47.0 mm long; leaf maximum width is 6.3–12.4 mm (media: 8.6 mm, SD: 2.3 mm, *n*: 8). The width/length ratio fluctuates between 0.2 and 0.4 (mean: 0.3, SD: 0.1, *n*: 8), and the distance between the leaf base and its maximum width represents a 16–35% of the leaf length (mean: 21%, SD: 7%, *n*: 8). The leaves have a central abaxial keel that extends from the base to the apex (Fig. 3A, D), and when found on the branches, the leaves are often folded over the keel (Figs. 2A, B, F, 3A, D); 21–46 veins have been counted or estimated (Figs. 2A, B, F, 3A, D, 4F).
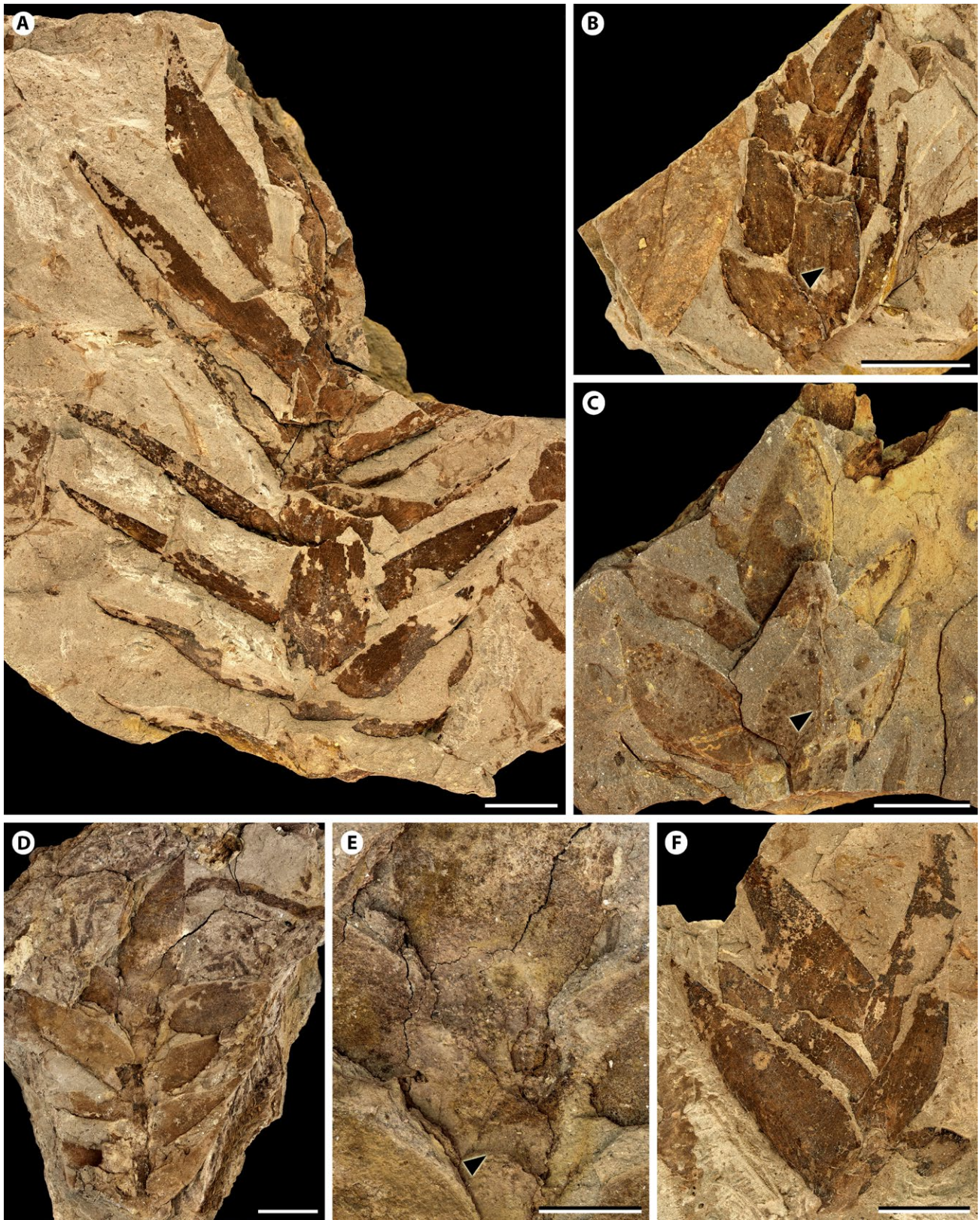
**FIGURE 2.** Leafy shoot diversity of *Araucaria lefipanensis* sp. nov. (A, B, F) L-shaped group. (C–E) O-shaped group. (A) Holotype MPEF-Pb 8297. (B) MPEF-Pb 8288 apical zone of a leafy shoot; abaxial keel of lower leaf indicated by arrowhead. (C) MPEF-Pb 8327, abaxial keel of lower leaf indicated by arrowhead. (D) MPEF-Pb 8316, general view of specimen showing portions of the naked branch. (E) MPEF-Pb 8316, detail of detached leaf base, indicated by arrowhead. (F) MPEF-Pb 8311. Scale bars A–D, F = 10 mm; E = 5 mm.
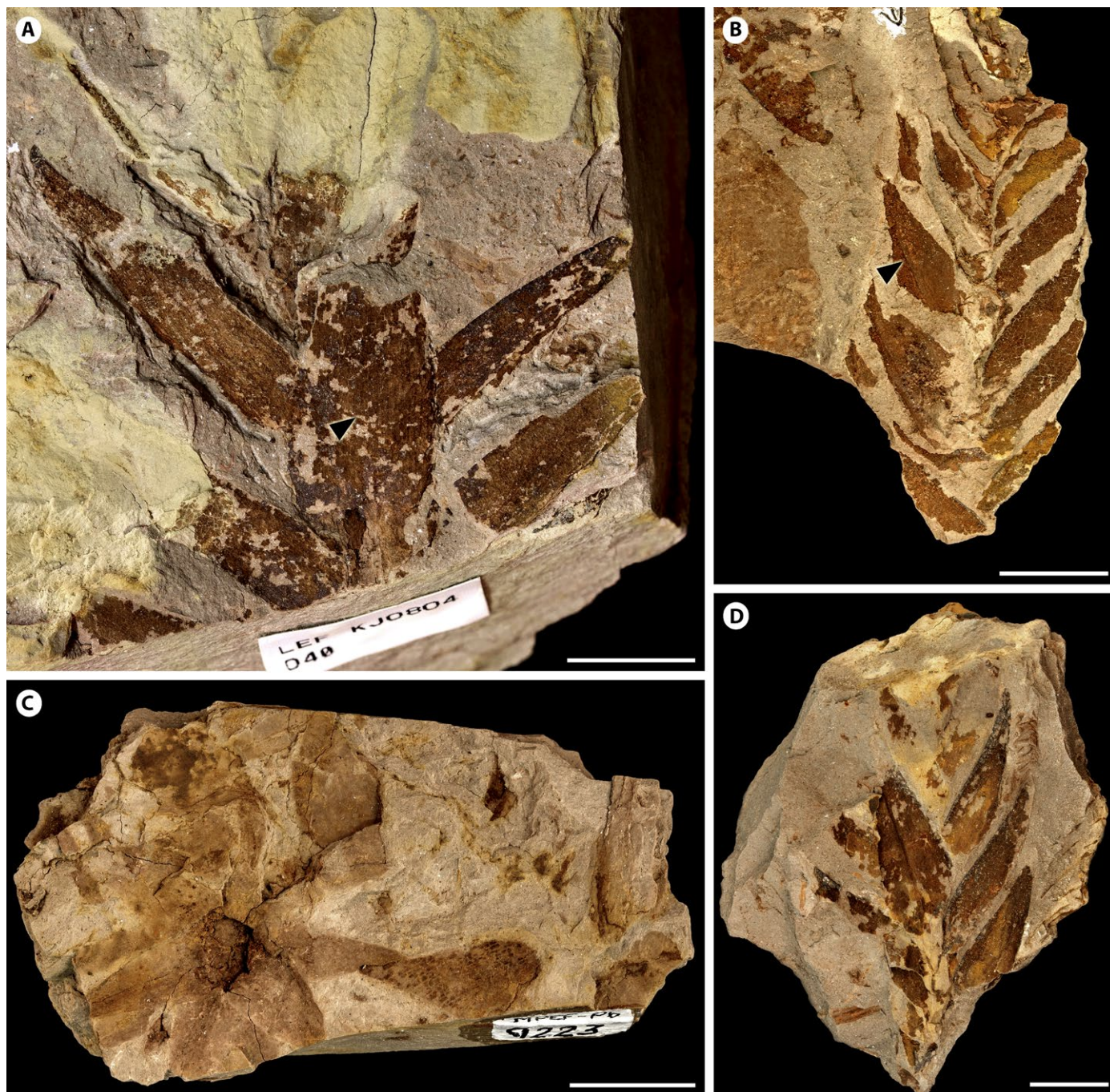
**FIGURE 3.** Leafy shoot diversity of *Araucaria lefipanensis* sp. nov. (A, D) L-shaped group. (B, C) O-shaped group. (A) MPEF-Pb 8296; arrowhead indicates zone with evident parallel venation. (B) MPEF-Pb 8291; arrowhead indicates abaxial keel. (C) MPEF-Pb 9223, transverse section of a leafy shoot showing the spirally arranged leaves. (D) MPEF-Pb 8328. Scale bars = 10 mm.

Isolated leaves of both morphological groups show several types of preservation at their bases (Fig. 4). Some of these leaves clearly show the leaf concave base (Fig. 4A–D, G), while others appear to have decorticated their branch when they detached (Fig. 4D, F–H).

*Cuticular patterns*—A few leaves of both morphological groups preserve epidermal patterns found as impressions on the rock (Fig. 4D, E). Several stomatal rows parallel to the leaf axis and occurring between adjacent veins were found (Fig. 4D, E). Stomatal apparatuses are ovate in outline (Fig. 4E). Also a few specimens, of both shape groups, preserve remains of carbonized cuticle on the leaves, which show similar features to those described below for bulk maceration specimens.

Cuticular fragments obtained from bulk maceration (Fig. 5) show stomata arranged in discontinuous parallel rows (Fig. 5A, F), which are oriented mostly parallel to slightly oblique to the long axis of the leaf (Fig. 5A, B, F), while perpendicular orientations are rare or absent. On the external cuticle epidermal cells outlines are
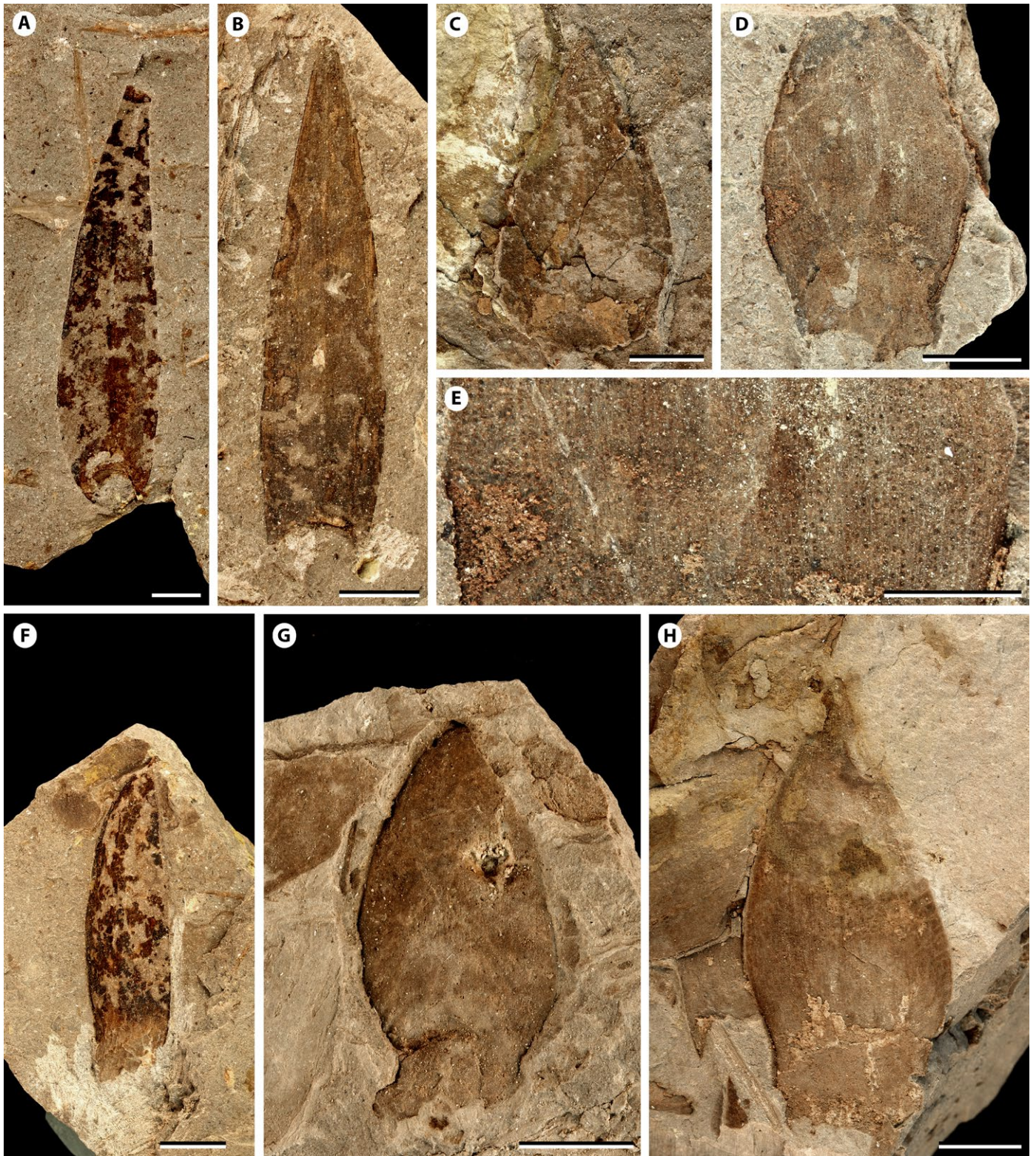
**FIGURE 4.** Isolated leaf diversity with varying abscission zones of *Araucaria lefipanensis* sp. nov. (A, B, F) L-shaped group. (C–E, G, H) O-shaped group. (A) MPEF-Pb 8310. (B) MPEF-Pb 8329. (C) MPEF-Pb 8308. (D) MPEF-Pb 8287, general view. (E) MPEF-Pb 8287, leaf detail showing venation and stomatal discontinuous rows. (F) MPEF-Pb 8319. (G) MPEF-Pb 9230. (H) MPEF-Pb 9233. Scale bars A–D, F–H = 5 mm; E = 2.5 mm.
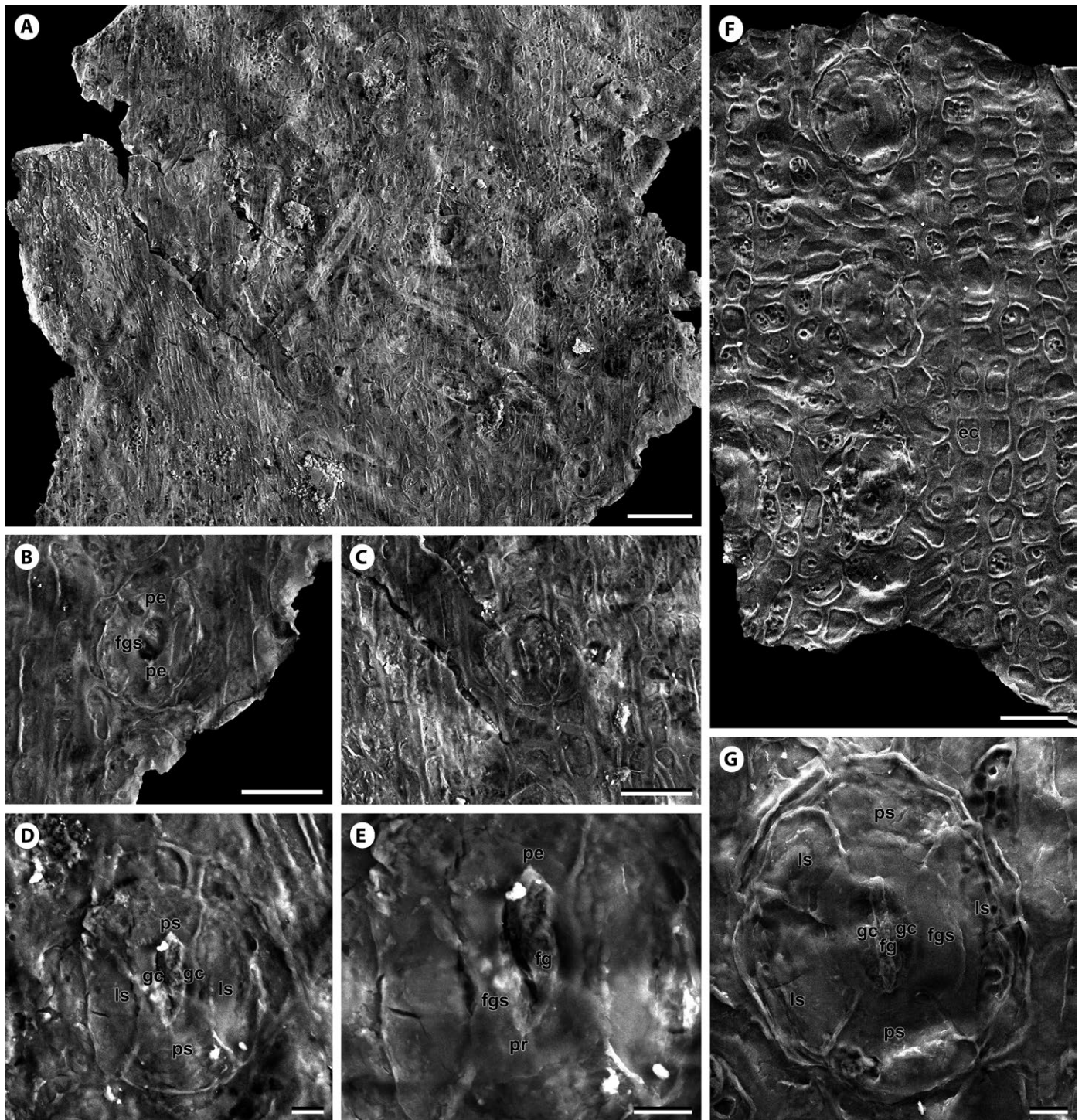
**FIGURE 5.** Cuticles of *Araucaria lefipanensis* sp. nov. under LVSEM, MPEF-Pb 8331 h III and IV; A–E, MPEF-Pb 8331 h III; F, G, MPEF-Pb 8331 h IV. (A) Middle portion of one cuticular fragment showing several stomatal rows and epidermal cell rows. (B–G) Detail of different stomata showing the typical morphology with four subsidiary cells, two lateral and two polar. (B) Stomata showing polar extensions. (E) Detail of the granulose cuticle that extends into the stomatal aperture. (F) Detail of a stomatal row and surrounding epidermal cells. (G) Detail of the first stoma of the previous image, one of the few stomata showing five subsidiary cells, three lateral and two polar. Abbreviations: ec, epidermic cell; er, external ridge; fg, flanges among guard cells; fgs, flanges between guard and subsidiary cells; gc, guard cell; ls, lateral subsidiary cell; pe, polar extensions; pr, polar ridge; ps, polar subsidiary cell. Scale bar A = 100 µm; B, C, F = 50 µm; D, E, G = 10 µm.
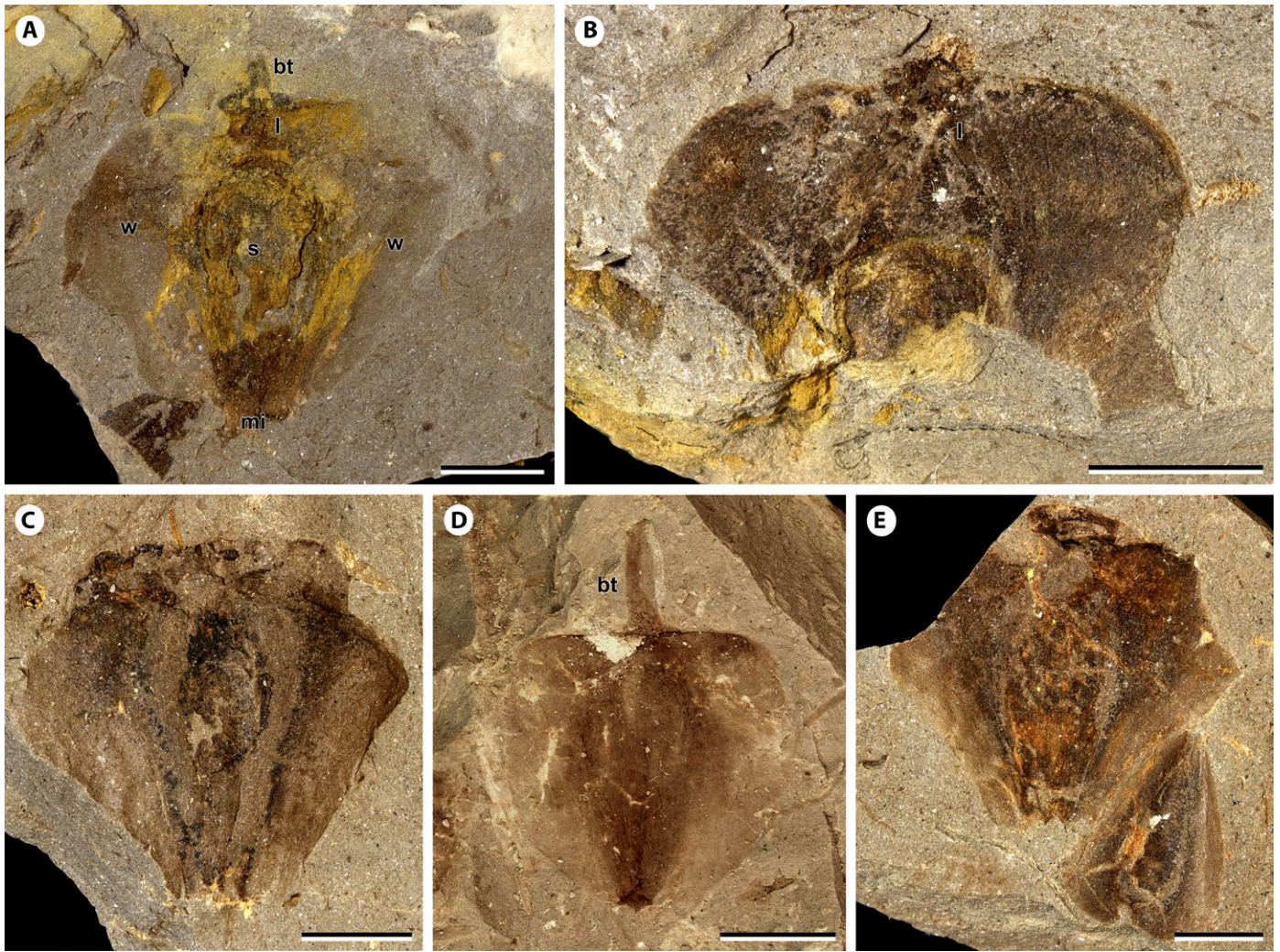
**FIGURE 6.** Isolated cone scale complexes of *Araucaria lefipanensis* sp. nov. (A) MPEF-Pb 8307. (B) MPEF-Pb 8322. (C) MPEF-Pb 8313. (D) MPEF-Pb 9252. (E) MPEF-Pb 5826. *Abbreviations:* bt, bract tip; l, ligule; mi, micropyle; s, seed; w, cone scale complex wing. Scale bar A = 10 mm; B–F = 5 mm.

obscure and stomatal plugs were not observed. Internally, cuticles show from two to five epidermal cells (Fig. 5F) separating adjacent stomata in a row, and between five and 11 rows of normal epidermal cells between stomatal rows (Fig. 5A–C, F). Stomatal apparatuses are rounded to polygonal in outline (Fig. 5B–D, F–G), 63.9–90.8 μm long (mean: 77.7 μm, SD: 9.0 μm, *n*: 12), and 37.0–75.3 μm wide (mean: 55.6 μm, SD: 8.9 μm, *n*: 12). Stomatal size (only considering the guard cells) ranged between 26.2–36.8 μm (mean: 32.1 μm, SD: 4.1 μm, *n*: 6) long and between 14.1–21.4 μm (mean: 18.5 μm, SD: 2.9 μm, *n*: 6) wide. Four subsidiary cells are common (two lateral and two polar, Fig. 5B–D). One stomatal apparatus with five subsidiary cells was observed (Fig. 5G), in which the fifth subsidiary cell appears to be the consequence of a lateral subsidiary cell division, due to its position (Fig. 5G). Outer flanges of subsidiary cells are uniformly thickened in both lateral and polar subsidiary cells (Fig. 5B, G). Subsidiary cell cuticle surface appears to be rugose and sometimes granulose (Fig. 5G). Flanges between guard cells and subsidiary cells are thick and irregular to smooth in appearance (Fig. 5D, G). Cuticle on guard cells surface appears to be granular in texture (Fig. 5G). The flange between guard cells is also granular, with—in some cases—pronounced pointed polar extensions

that show a middle polar ridge (Fig. 5B, 5E, 5G). Epidermal cells are generally rectangular, although polygonal cells are common (Fig. 5F). The epidermal cells within stomatal rows measure 8.9–20.6 μm (mean: 14.9 μm; SD: 4.5 μm; *n*: 7) wide and 17.4–27.5 μm (mean: 24.1 μm; SD: 3.5; *n*: 7) long; while epidermal cells between stomatal rows measure 11.5–18.0 μm (mean: 14.7 μm, SD: 2.8; *n*: 5) wide and 23.4–31.0 μm (mean: 26.2 μm; SD: 3.4 μm; *n*: 4) long. Epidermal cell flanges seem to be thick and straight at both LVSEM and epifluorescence light microscopy (Fig. 5F).

*Reproductive organs*—Isolated cone scale complexes are cuneate to heartshaped (Fig. 6B–F), 14.9–18.3 mm (mean: 16.7 mm, SD: 1.3, *n*: 7) long; their minimum width, located at the base of the cone scale complex, is 2.2–7.2 mm (mean: 4.4 mm, SD: 1.9 mm, *n*: 7), and their maximum width is 11.5–20.0 mm (mean: 15.2 mm, SD: 3.3, *n*: 8). The maximum width is localized at the distal zone of the cone scale complex, approximately at two thirds of its total length (Fig. 6B–F). The apex of the bract is mucronate, and the length of the bract tip is 1.8–2.7 mm (mean: 2.1 mm, SD: 0.5 mm, *n*: 3; Fig. 6B, E). The central body of the complex has a cuneate outline, with a distal widening adjacent to the end of the lateral wings, it is woody in appearance

and has longitudinal striations (Fig. 6B, 6.4–6). The lateral wings are slightly asymmetric and thin with a membranous appearance (Fig. 6B, D–F), their maximum width varies between 1.6–3.3 mm (mean: 2.5 mm, SD: 0.6 mm, *n*: 8). Each complex bears only one central, inverted seed that occupies a high proportion of the central body surface (Fig. 6B–F). Seed length varies between 8.7–10.9 mm (mean: 9.9, SD: 0.8 mm, *n*: 7), and its maximum width between 4.2–5.9 mm (mean: 4.9 mm, SD: 0.6 mm, *n*: 8). At the adaxial surface of some of the complexes, a ligule can be distinguished immediately distal the chalazal end of the seed (Fig. 6B, C, F).

## DISCUSSION

### Taxonomic assignment and comparisons

*Araucaria lefipanensis* is assigned to the genus *Araucaria* (Araucariaceae) based on numerous reproductive and vegetative characters such as single-seeded cone scale complexes with well-developed wings, and broad, multiveined, ovate-lanceolate to lanceolate leaves with parallel-oriented stomata arranged in discontinuous rows.

Both leaves and cone scale complexes show enough diagnostic characters to be independently assigned to *Araucaria*, and although these two types of organs were not found in organic connection, they occur intimately associated at the same level. This close association is especially strong in the quarry 4B (*La Huella*, see Materials and Methods) where the araucarian reproductive and vegetative remains—obtained from a 7 cm layer—strongly outnumbered all other taxa. Furthermore, both organs are characterized by diagnostic araucarian features, while no other remains found at any level of the Cañadón del Loro locality, nor in any locality of the Lefipán Formation, show araucarian affinities. Thus, we propose that both organs were produced by the same plant, and consequently, the definition of *Araucaria lefipanesis* is based on dimorphic leaves and cone scale complexes.

The araucarian affinity of the leafy shoots is supported by macromorphological characters such as the helical phyllotaxy and the presence of sessile, keeled, multiveined leaves with an ovate to lanceolate outline (Carrière, 1855; Seward and Ford, 1906; Wilde and Eames, 1952; de Laubenfels, 1988; Page, 1990; Farjon, 2010). Besides, when leaves are found isolated, their bases are not always noticeable, since in many specimens leaves appear to have detached together with part of the branch cortex (Fig. 4). These differences in leaf base preservation suggest that *A. lefipanensis* lacked a mechanism of natural dehiscence, in agreement with what is observed among the extant members of the genus *Araucaria* (de Laubenfels, 1988; Page, 1990; Farjon, 2010), which retain their leaves even on old branches and trunks. The placement of these remains within *Araucaria* is strongly supported by numerous cuticular features as well. Among them, the arrangement of the stomata in discontinuous rows, their predominantly parallel orientation respect with the leaf major axis, the presence of 4–5 subsidiary cells, and the presence of polar extensions (Stockey and Taylor, 1978a; Stockey and Ko, 1986).

Other conifer genera that produce leaves comparable to *A. lefipanensis* are *Nageia* (Podocarpaceae), *Agathis* and *Wollemia* (Araucariaceae), as they all produce broad, multiveined leaves (Seward and Ford, 1906; de Laubenfels, 1969, 1972, 1988; Page, 1990; Farjon, 2010). Nevertheless, *Wollemia* possesses strap-shaped leaves with rounded apices (Chambers et al., 1998; Farjon, 2010) and has stomata with usually six subsidiary cells and prominent polar extensions (Chambers et al., 1998). In addition, although *Wollemia nobilis* stomata are mostly oriented parallel to the long axis of the leaf, it has a higher proportion of oblique and transversal orientations (Chambers et al., 1998). On the other hand, *Agathis* and *Nageia* produce petiolate leaves (Seward and Ford, 1906; de Laubenfels, 1969, 1972, 1988), whereas leaves of *Araucaria lefipanensis* lack a petiole. Furthermore, *Agathis* species usually show oblique or transverse stomatal orientations, prominent, bilobed polar extensions, Florin rings (absent in *Araucaria* species), and epidermal cells that are quadrangular but not as elongated as those in *Araucaria* (Stockey and Atkinson, 1993). Another difference between *Araucaria* and *Agathis* is the range of variation of the subsidiary cell number. Although four subsidiary cells is most common among species of both genera, many species of *Agathis* have a wider variation in this feature, with three to nine subsidiary cells sometimes present (Stockey and Atkinson, 1993), while in *Araucaria* species the natural variation ranges between four and six (Stockey and Ko, 1986). *Nageia* species differentiate from *A. lefipanensis* in having decussate phyllotaxy, stomata with Florin rings, usually two to four subsidiary cells that show a narrow rectangular outline, and guard cells with prominent polar extensions (de Laubenfels, 1969, 1988; Hill and Pole, 1992; Stockey, 1994; Sun, 2008; Jin et al., 2010).

The vegetative remains assigned to *Araucaria lefipanensis* show robust morphological similarities with the broad-leaved araucarians (*Araucaria* sections *Araucaria*, *Intermedia*, and *Bunya*), which have been recurrently found as forming a monophyletic group in both DNA and combined phylogenetic analyses (Setoguchi et al., 1998; Liu et al., 2009; Escapa and Catalano, 2013). These similarities between *A. lefipanensis* and the members of the broad-leaved clade include the presence of multiple veins, the leaf shape, and the stomatal morphology and organization (Seward and Ford, 1906; Wilde and Eames, 1952; Stockey and Ko, 1986; de Laubenfels, 1988; Farjon, 2010). Among the broad-leaved sections, the one that shows the strongest similarities with the Lefipán vegetative organs is the Australian species *A. bidwillii* (section *Bunya*). *Araucaria lefipanensis* and *A. bidwillii* have similar leaf dimorphism, with some leaves ovate-lanceolate in outline and others lanceolate (Table 1, Fig. 7; Seward and Ford, 1906; Offler, 1984; Stockey and Ko, 1986; Farjon, 2010). Leaves of *A. lefipanensis* are also similar to those of the South American section *Araucaria*. The South American section contains two species: the Brazilian-Argentinian-Paraguayan *A. angustifolia*, whose narrow lanceolate leaves resemble those of the L-shaped morphology of *A. lefipanensis*; and the Patagonian *A. araucana*, which bears ovate-lanceolate leaves that are more similar to the O-shaped morphology of *A. lefipanensis* (Table 1; Carrière, 1855; Seward and Ford, 1906; Farjon, 2010). *Araucaria* section *Intermedia* has leaves that are more triangular-lanceolate than those of *A. lefipanensis* (Table 1; Seward and Ford, 1906; Offler, 1984; Farjon, 2010). All the members of the sections *Araucaria*, *Intermedia*, and *Bunya* show a similar cuticular micromorphology with stomata oriented parallel to the long axis of the leaf, organized in discontinuous rows having 4–6 subsidiary cells (Stockey and Ko, 1986), features that *A. lefipanensis* share with members of these sections.

Species of section *Eutacta* produce leaves that differ greatly from those described here in both macro and micromorphological features. *Araucaria* section *Eutacta* species show relatively small,

**TABLE 1.** Comparisons of leaf morphology and cuticle among *Araucaria lefipanensis* and adult morphology of extant *Araucaria* species.

| Character | A. lefipanenis | Section *Araucaria* | | Section *Bunya* | Section *Intermedia* | Section *Eutacta* |
| | | A. araucana | A. angustifolia | A. bidwillii | A. hunsteinii | |
| --- | --- | --- | --- | --- | --- | --- |
| Shape | Ov. lanc.-Lanc. | Ov. lanc. | Lanc. | Ov. lanc.-Lanc. | Tr. lanc. | Squamiform |
| Length (mm) | 11.3–35.3 | 25–60 | 15–50 | 10–50 | 50–100 | Up to 20 |
| Width (mm) | 4.7–12.7 | 15–30 | 3–20 | 3–15 | 12–20 | Up to 12 |
| Width/Length | 0.2–0.7 | 0.2–0.4 | 0.2–0.4 | 0.3 | 0.1–0.3 | Varying |
| Maximum width position | Varying | Almost at the leaf base | Near the middle | Near the middle | Near the middle | Varying |
| Type II leaf dimorphism[a] | Present | Absent | Absent | Present | Absent | Present |
| Stomatal orientation[b] | Mostly parallel | Mostly parallel | Mostly parallel | Mostly parallel | Mostly parallel | Oblique or perpendicular |
| Epidermal cell outlines | Straight | Straight | More or less straight | More or less sinuous | More or less sinuous | Varying |

*Notes:* Lanc. = lanceolate; Ov. = ovate; Ov. lanc. = ovate-lanceolate; Tr. lanc. = triangular-lanceolate.
[a]Leaf dimorphism characterized by two distinct leaf shapes that do not necessarily differ in size.
[b]Stomatal orientation is considered with respect to the major axis of the leaf. Data from Farjon (2010) and Stockey and Ko (1986).
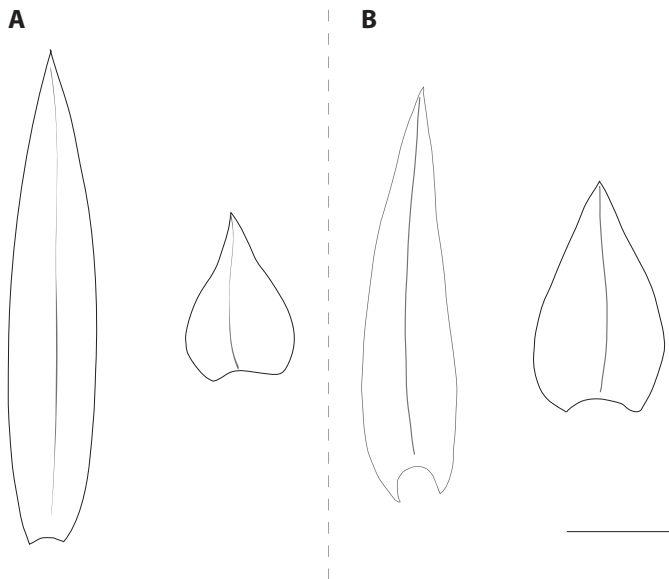


**FIGURE 7.** Dimorphism comparison between *Araucaria bidwillii* Hook. and *Araucaria lefipanensis* sp. nov. (A) *Araucaria bidwillii*. Leaf silhouettes of two specimens from the Kew Royal Botanical Gardens Herbarium. Left, a lanceolate, elongated leaf (L-shaped morphology, specimen K000961232); right, a shorter, ovate-lanceolate leaf (O-shaped morphology, specimen K000961233). (B) *Araucaria lefipanensis* sp. nov. leaf silhouettes. Left, L-shaped leaf morphology (MPEF-Pb 8310; Fig. 3.1); right, O-shaped leaf morphology (MPEF-Pb 8308; Fig. 3.3). Scale bar = 10 mm.

single-veined leaves and stomata arranged in rows within two lateral bands located at both sides of the central vein (Carrière, 1855; Wilde and Eames, 1952; de Laubenfels, 1972; Offler, 1984; Stockey and Ko, 1986; Farjon, 2010). Also, the species within this section exhibit stomata oblique or perpendicularly oriented in relation to the leaf major axis (Stockey and Ko, 1986).
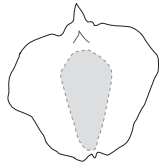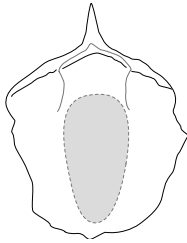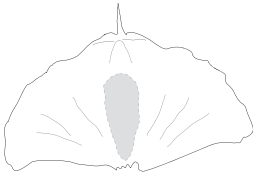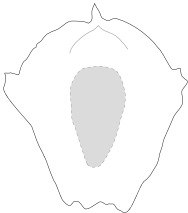
In terms of the reproductive organs, the species from Lefipán has ligulate, winged cone scale complexes with a single, unwinged central seed, which are diagnostic of the genus *Araucaria* (Seward and Ford, 1906; Wilde and Eames, 1952; de Laubenfels, 1972, 1988). These cone scales are also comparable to those of the genera *Agathis* and *Wollemia*. However, both *Agathis* and *Wollemia* produce single, winged seeds that are adaxially positioned on the cone scale

complexes, and which are not embedded in the ovuliferous scale tissues (Seward and Ford, 1906; Florin, 1951; de Laubenfels, 1988; Chambers et al., 1998; Page, 1990; Owens et al., 1997; Farjon, 2010). Also they lack the characteristic *Araucaria* distal ligule (Seward and Ford, 1906; Florin, 1951; Whitmore, 1980; Chambers et al., 1998; Farjon, 2010).

The cone scale complexes of *A. lefipanensis* are more similar to those of extant species of *Araucaria* section *Eutacta* in their general outline as well as in the thin, papery appearance of the wings of the complex (Table 2; Dickson, 1863; Carrière, 1855; Seward and Ford, 1906; Wilde and Eames, 1952; de Laubenfels, 1972). Interestingly, the members of the broad-leaved clade (*Araucaria* sections *Intermedia*, *Bunya*, and *Araucaria*) produce variable cone scale complexes (Table 2; Seward and Ford, 1906; Wilde and Eames, 1952; Farjon, 2010). *Araucaria* section *Intermedia* has cone scale complexes with papery-thin, well-developed wings. However, the cone scale complexes of this section are fan-shaped, differing from the more cuneate complexes of *A. lefipanensis* and *Eutacta* species (Table 2; Wilde and Eames, 1952; de Laubenfels, 1988; Farjon, 2010). Furthermore, the wings of the cone scale complexes of *Araucaria* section *Intermedia*, contrary to what happens in at least some species of the section *Eutacta* (e.g., *A. cunninghamii*), are vascularized (Haines, 1983b). Species of the section *Araucaria* have cone scale complexes with extremely reduced wings and a prominent rounded ligule (Table 2; Carrière, 1855; Dickson, 1863; Seward and Ford, 1906; Wilde and Eames, 1952). Cone scale complexes of *Araucaria* section *Bunya* have woody, vascularized wings and seeds that can be shed at maturity, neither of which was observed in the cone scale complexes of *A. lefipanensis* (Table 2; Wilde and Eames, 1948, 1952; Florin, 1951). The cone scale complexes of *A. lefipanensis* are generally smaller than in extant species (Table 2).

There are also major differences between *Araucaria lefipanensis* and other fossil species previously described within the genus *Araucaria* and the fossil genus *Araucarites* for the mid-late Mesozoic and Cenozoic (Tables 3–6). Several of these species have similar leaf morphology to *A. lefipanensis* (Tables 3, 4), but only a few of them have reported dimorphism (Table 4; see also section *Leaf morphological variation and seasonality*). Among previously described dimorphic species only *Araucaria alexandrensis* Cantrill and Falcon-Lang (2001) from the late Albian of Alexander Island (Antarctica) shows a similar size to the Lefipán species'. It has long, leafy branches that bear two different leaf sizes, but unfortunately

**TABLE 2.** Comparisons of cone scale complexes among *Araucaria lefipanensis* and extant *Araucaria* species.

| Character | A. lefipanensis | Section *Araucaria* | | Section *Bunya* | Section *Intermedia* | Section *Eutacta* |
| | | A. araucana | A. angustifolia | A. bidwillii | A. hunsteinii | |
|---|---|---|---|---|---|---|
| Shape (Not to scale) | | | | | | |
| OC maximum width (mm) | 14.9–18.3 | 15–20 | 20 | 60–80 | 70–90 | From 15 to 90 |
| OC total length (mm) | 11.5–20 | 40–50 | 50 | 80–100 | 50–60 | From 15 to 60 |
| Seed length (mm) | 9.9 | 35–50 | 40 | Up to 50 | 30 | 15–30 |
| Seed width (mm) | 4.9 | 10–15 | 15 | Up to 35 | 8 | 5–15 |
| Wings | Well-dev. | Ext. red. | Ext. red. | Well-dev. | Well-dev. | Well-dev. |
| Wing appearance | Thin | Thin | Thin | Woody | Papery-thin | Papery-thin |

*Notes:* Well-dev. = well developed; Ext. red. = extremely reduced. Data from Farjon (2010).

cuticular characters were not preserved (Tables 3, 4). The Antarctic species has been found in association with cone scale complexes referred to the fossil species *Araucarites wollemiaformis* that has a cuneate outline, a much more prominent bract tip, and is significantly larger than the cone scale complexes described here (Tables 5, 6).

*Araucaria bladenensis* Berry (Berry, 1908; Stults et al., 2012) from the middle and late Cretaceous of North America shows also dimorphic leaves of a similar length but generally wider than those of *A. lefipanensis* (Tables 3, 4). The disposition and orientation of the stomata, and the number and disposition of subsidiary cells are

**TABLE 3.** List of fossil species compared with *Araucaria lefipanensis* (Leaves)

| Species | Age | Formation | Locality | Reference |
|---|---|---|---|---|
| *Aa. cartellei* Duarte | Aptian | Santana Fm. | Crato, Ceará, BR | Duarte 1993 |
| *Aa. grandifolia* Feruglio | Early Albian | Punta del Barco Fm. | Ea. El Verano, Santa Cruz, AR | Feruglio, 1951; Del Fueyo and Archangelsky, 2002 |
| *Aa. seorsum* Cantrill | Mid to Late Albian | Unnamed [a] | Southern Victoria, AU | Cantrill, 1992 |
| *Aa. lanceolatus* Cantrill | Mid to Late Albian | Unnamed [a] | Southern Victoria, AU | Cantrill, 1992 |
| *Aa. acutifoliatus* Cantrill | Mid to Late Albian | Unnamed [a] | Southern Victoria, AU | Cantrill, 1992 |
| *Aa. carinatus* Cantrill | Mid to Late Albian | Otway Fm. | Southern Victoria, AU | Cantrill, 1992 |
| *Aa. otwayensis* Cantrill | Mid to Late Albian | Otway Fm. | Southern Victoria, AU | Cantrill, 1992 |
| *Aa. alexandrensis* Cantrill & Falcon-Lang | Late Albian | Neptune Glacier Fm. | Triton Point Member, AN | Cantrill and Falcon-Lang, 2001 |
| *Aa. chambersii* Cantrill & Falcon-Lang | Late Albian | Neptune Glacier Fm. | Triton Point Member, AN | Cantrill and Falcon-Lang, 2001 |
| *Aa. bladenensis* Berry | Mid and Late-Cretaceous | Black Creek and Eutaw Fm. | Alabama, N and S Carolina, US | Berry, 1908; Stults et al., 2012 |
| *At. ovatus* Hollick | Cenomanian | Magothy Fm. | Cliffwood, NJ, US | Hollick, 1897 |
| *Aa. desmondii* Pole | Cenomanian | Horse Range Fm. | Horse Range, NZ | Pole, 1995 |
| *At. marshalli* Edwards | Campanian | Unnamed | Bull's Point and Batley, NZ | Edwards, 1926 |
| *Aa. haastii* Ettingshausen | Late Cretaceous | Taratu Fm. | Shag Point and Malvern Hills, NZ | Bose, 1975 |
| *Aa. oweni* (Ettingsh.) Pole | Campanian | Taratu Fm. | Shag Point, NZ | Pole, 1995 |
| *Aa. lefipanensis* | Maastrichtian | Lefipán Fm. | Cañadón del Loro, Chubut, AR | This publication |
| *Aa. taierensis* Pole | Maastrichtian | Taratu Fm. | Kai Point Mine, NZ | Pole, 1995 |
| *Aa. fibrosa* Césari | Maastrichtian | Snow Hill Island Fm. | Cape Lamb, AN | Césari et al., 2001; Césari et al., 2009 |
| *Aa. hastiensis* Hill & Bigwood | Mid-Late Eocene | Unnamed | Hasties, North-East TA | Hill and Bigwood, 1987 |
| *Aa. pararaucana* Panti | Late Eocene-Early Oligocene | Sloggett Fm. | Slogget Bay, Tierra del Fuego, AR | Panti et al., 2007 |
| *Aa. fimbriatus* Hill | Late Oligocene | Unnamed | Little Rapid River, North-Western TA | Hill, 1990 |
| *Aa. nathorsti* Dusén | Late Oligocene-Miocene | Ñirihuau Fm. | Pico Quemado, Río Negro, Argentina | Dusén, 1899; Berry, 1928; Menéndez and Caccavari, 1966; Falaschi et al., 2012; Ohsawa et al., 2016 |

*Notes: Aa. = Araucaria; At. = Araucarites*; AN = Antarctica; AU = Australia; AR = Argentina; BR = Brasil; NJ = New Jersey; NZ = New Zealand; TA = Tasmania; US = United States.
[a]Otway Group, Zone D (Cantrill and Webb, 1987; Cantrill, 1992).

**TABLE 4.** Comparisons of leaf morphology and cuticle among *A. lefipanensis* and extinct *Araucaria* species.

| Species | Shape | Length (mm) | Width (mm) | Width/Length | Maximum width position | Foliar dimorphism | Stomatal orientation |
|---|---|---|---|---|---|---|---|
| *Aa. cartellei* | Lanc. | 48 | 10 | 0.2 | Near basal third of leaf | ? | — |
| *Aa. grandifolia* | Tr. lanc. | 70–80 | 10–20 | 0.2 | Near basal third of leaf | Absent | Mostly parallel |
| *Aa. seorsum* | Lanc. | 54–72 | 7–11 | ≅0.14 | Near middle | Absent | Mostly parallel |
| *Aa. lanceolatus* | Lanc. | 40–52 | 7–9 | 0.17 | Near basal third of leaf | Absent | Mostly parallel |
| *Aa. acutifoliatus* | Lanc. | 47–52 | 6–7 | 0.13 | Near basal third of leaf | Absent | Parallel to oblique |
| *Aa. carinatus* | Lanc. to Ov. | 4–17 | 2–12 | 0.7 | Near basal third of leaf | Absent | Oblique or perpendicular |
| *Aa. otwayensis* | Lanc. to Ov. | 20 | — | — | Near middle | ? | Mostly oblique |
| *Aa. alexandrensis* | Lanc. to Ov. | 20–30 | 8–12 | 0.4 | Near basal third of leaf | Present | ? |
| *Aa. chambersii* | Lanc. or Ov. lanc. | 45–105 | 8–15 | 0.15 | Near middle | Present | ? |
| *Aa. bladenensis* | Ov. lanc. | 10–30 | 8–20 | 0.7 | Near middle | Present | ? |
| *At. ovatus* | Ov. lanc. | Up to 38 | Up to 12.7 | 0.3 | Near middle? | ? | ? |
| *Aa. desmondii* | Ov. to lanc. | 14–20 | 10–11 | 1.4–1.8 | Near middle | ? | Mostly perpendicular |
| *At. marshalli* | Ov. to lanc. | | | | Near basal third of leaf | Present | ? |
| *Aa. haastii* | Lanc. | 25–75 | 10–18 | 0.3 | Near basal third of leaf | ? | Mostly parallel |
| *Aa. oweni* | Ov. lanc. | 20–35 | 9–16 | 2.2 | Near middle | ? | ? |
| *Aa. lefipanensis* | | | | | | Present | Mostly parallel |
|    O-shaped group | Ov. lanc. | 17.49 | 8.92 | 0.5 | Almost at leaf base | | |
|    L-shaped group | Lanc. | 28.37 | 8.51 | 0.3 | Near middle | | |
| *Aa. taierensis* | Ov. lanc. | 9–12 | 5–8 | 0.6–0.7 | Near third of leaf | Absent | Mostly parallel |
| *Aa. fibrosa* | Lanc. to Ov. | 55–40 | 25 | 0.5 | Near basal third of leaf? | ? | Mostly parallel |
| *Aa. hastiensis* | Ov. lanc. | 19 | 9 | 0.5 | Almost at leaf base | ? | Mostly parallel |
| *Aa. pararaucana* | Ov. lanc. | 57 | 22.5 | 0.4 | Near basal third of leaf | ? | Mostly parallel |
| *Aa. fimbriatus* | Lanc. | 19–23 | 6–8 | 0.3 | Near middle | ? | Mostly parallel |
| *Aa. nathorsti* | Ov. to Lanc. | 43 | 20 | 0.5 | Near basal third of leaf | Present | Mostly parallel |

*Notes: Aa. = Araucaria; At. = Araucarites; Lanc. = Lanceolate; Ov. = ovate; Ov. lanc. = ovate-lanceolate; Tr. lanc. = triangular-lanceolate.*

**TABLE 5.** List of fossil species compared with *Araucaria lefipanensis* (reproductive)

| Species | Age | Formation | Locality | Reference |
|---|---|---|---|---|
| *Aa. cutchensis* Feistmantel | Jurassic and Early Cretaceous | Mount Flora Fm., Cañadón Asfalto, and Jabalpur Series | Hope Bay, AN; Chubut, AR; SE of Chandia, IN; Makoia and Mount Potts, NZ | Halle, 1913; Arber, 1917; Frenguelli, 1949; Pant and Srivastava, 1968; Escapa et al., 2008 |
| *At. sehoraensis* Bose & Maheshwari | Mid-Late Jurassic? | Parsora Fm. | Sher River, Madhya Pradesh, IN | Bose and Maheshwari, 1973 |
| *At. minutus* Bose & Maheshwari | Mid-Late Jurassic? | Parsora Fm. | Sher River, Madhya Pradesh, IN | Bose and Maheshwari, 1973 |
| *Aa. indica* (Sahni) Sukh-Dev & Zeba-Bano | Late Jurassic-Early Cretaceous | Jabalpur Fm. | Madhya Pradesh, IN | Sukh-Dev and Zeba-Bano, 1976 |
| *Aa. minimus* Archangelsky | Early Cretaceous | Anfiteatro de Ticó Fm. | Bajo Grande, Santa Cruz, AR | Archangelsky, 1966 |
| *At. baqueroensis* Archangelsky | Early Cretaceous | Anfiteatro de Ticó Fm. | C. Testigo and other loc., Santa Cruz, AR | Archangelsky, 1966 |
| *At. chilensis* Baldoni | Early Cretaceous | Springhill Fm. | El Cóndor, Santa Cruz, AR | Baldoni, 1979 |
| *At. vulcanoi* Duarte | Early Cretaceous | Santana Fm. | Crato, Ceará, BR | Duarte, 1993 |
| *Araucarites* sp. Archangelsky | Early Cretaceous | Springhill Fm. | Pozo El Dorado, XI Región, CH | Archangelsky, 1976 |
| *At. citadelbastionensis* Cantrill & Falcon-Lang | Early Cretaceous | Neptune Glacier Fm. | Citadel Bastion, Alexander Island, AN | Cantrill and Falcon Lang, 2001 |
| *At. rogersii* Seward | Early Cretaceous | Kirkwood Fm. | Cape Province, SA | Seward, 1903; Brown, 1977 |
| *Aa. jeffreyi* Berry | Mid-Cretaceous | Black Creek and Eutaw Fm. | North Carolina, US | Berry, 1908 |
| Araucarian ovulate cone scales | Cenomanian | Winton Fm. | Queensland, AU | Dettman et al., 1992; McLoughlin et al., 1995 |
| *Aa.* scale type B Pole | Cenomanian and Campanian | Horse Range Fm. | Horse Range and Clutha Mouth, NZ | Pole, 1995 |
| *Aa. lefipanensis* | Maastrichtian | Lefipán Fm. | Cañadón del Loro, Chubut, AR | This publication |
| *Aa. bladenensis* asociated cone scales | Late Cretaceous | Eutaw Fm. | Ingersol Shale, Alabama, US | Stults et al., 2012 |
| *At. pichileufensis* Berry | Early Eocene | La Huitrera Fm. | Río Pichileufú, Chubut, AR | Berry, 1938 |
| *Aa.* cf. *Araucarites pichileufensis* Berry | Early Eocene | Huitrera Fm. | Pampa de Jones, Neuquén, AR | Wilf et al., 2010 |
| *Araucaria* sp. Wilf | Early Eocene | Ventana Fm. | Laguna del Hunco, Chubut, AR | Wilf et al., 2003 |
| *Aa. nathorsti* Dusén | Late Oligocene-Miocene | Ñirihuau Fm. | Pico Quemado, Río Negro, AR | Falaschi et al., 2012; Ohsawa, 2016 |

*Notes: Aa. = Araucaria; At. = Araucarites; AN = Antarctica; AR = Argentina; AU = Australia; BR = Brasil; CH = Chile; IN = India; NZ = New Zealand; SA = South Africa; US = United States.*

**TABLE 6.** Comparisons of *Araucaria lefipanensis* and extinct *Araucaria* and *Araucarites* species (reproductive)

| Species | Maximum width (mm) | Total length (mm) | Bract tip length (mm) | Seed length (mm) | Seed width (mm) | Wings | Wing appearance | Leaf association |
|---|---|---|---|---|---|---|---|---|
| *At. cutchensis* | 12.7–20.7 | 10–22.8 | 3.5–6.5 | 5.7–13.8 | 3.6–7.9 | Well-dev. | Thin | Linear squam. |
| *At. sehoraensis* | 11–13 | 13–20 | 1.2 | 10–12 | 6–9 | Well-dev. | ? | Not reported |
| *At. minutus* | 8–11 | 10–15 | 1 - 2 | 8–10 | 3–6 | Well-dev. | ? | Not reported |
| *Aa. indica* | 9–15 | 23–40 | 15 - 25 | 7–17 | 4–10 | Well-dev. | ? | Podozamites |
| *At. minimus* | 8 | At least 7 | 3 | 3.5–5 | 2–2.5 | Well-dev. | Thin | ? |
| *At. baqueroensis* | 20 | 20–30 | 3 | 10–15 | 4–5 | Well-dev. | Thin | ? |
| *At. chilensis* | 8 | 11 | 1 | 7 | 3.5 | Well-dev. | ? | *Brach.* |
| *At. vulcanoi* | 0.8 | 12.5 | | 8.4 | 3.6 | Well-dev. | ? | Broad and *Brach.* |
| *Araucarites* sp. | 8 | 11 | 1.89 | 7 | 3.5 | Well-dev. | ? | *Brach.* |
| *At. citadelbastionensis* | 11–15 | 7–12 | 2 | - | - | Well-dev. | Thin | Broad |
| *At. rogersii* | 25–30 | 20–30 | Not pres. | 23.9 | 8.6 | Well-dev. | Thin | *Brach.* |
| *Aa. jeffreyi* | ? | ? | ? | ? | ? | Well-dev. | Thin | Broad |
| Araucarian ovulate cone scales | 7–26 | 10–37 | <1–5 | ? | ? | Well-dev. | ? | Broad |
| *Aa.* scale type B | 15–22 | 17–22 | 2–5 | 14 | 4.7 | Well-dev. | Thin | Broad |
| ***Aa. lefipanensis*** | **15.2** | **16.7** | **2.1** | **9.9** | **4.9** | **Well-dev.** | **Thin** | **Broad** |
| *Aa. bladenensis* asociated cone scales | 6.4 (inc.) | 8.9 (inc.) | Not pres. | 5.3 | 2.2 | Well-dev. | Thick | Broad |
| *At. pichileufensis* | 30 | 27.5 | 3.19 | 15.76 | 7.08 | Well-dev. | Thin | Linear squam. |
| *Aa.* cf. *Araucarites pichileufensis* | 15.03 | 16.9 | 2.05 | 10.81 | 4.5 | Well-dev. | Thin | Without assoc. fol. |
| *Araucaria* sp. | 12.84 | 14.83 | Not pres. | 8.29 | 5.5 | Well dev. | Thin | ? |
| *Aa. nathorsti* | Up to 30 | 15 | Not pres. | ? | 9 | Reduced | ? | Broad |

*Notes: Aa.* = *Araucaria*; *At.* = *Araucarites*; *Brach.* = *Brachyphyllum*; Inc. = incomplete; Linear squam. = linear squamiform; Not pres. = not preserved; Well-dev. = well developed; Without assoc. fol. = without associated foliage.

similar in both *A. bladenensis* and *A. lefipanensis*; however, these particular cuticular characters tend to be stable through the broad-leaved araucarian clade. Cone scale complexes associated with *A. bladenensis* were also described by Berry (1908) under the name *Araucaria jeffreyi* Berry (Tables 5, 6), which have a different general outline of those described for the new species. *Araucarites marshalli* Edwards (1926), from the Campanian of New Zealand also shows leaf dimorphism. It has leaves with slightly rounded apices that differ from the sharply acute apices of *A. lefipanensis* (Tables 3, 4). However, *A. marshalli* cone scale complexes are unknown.

Araucaria hastiensis Hill and Bigwood (Hill and Bigwood, 1987; Hill, 1990) from the mid-late Eocene of Tasmania and *A. fimbriatus* Hill (1990) from the late Oligocene of Tasmania (Table 3) have some similarities with *A. lefipanensis*. Both Tasmanian species show leaf size and shape similar to O- and L-shape groups of *A. lefipanensis*, respectively (Table 4). They also share with the Patagonian new species the presence of stomata oriented parallel to the major axis of the leaf, arranged in rows, with four subsidiary cells. Nevertheless, both *A. hastiensis* and *A. fimbriatus* show stomata with rectangular outlines, and elongated stomatal apparatuses (Hill and Bigwood, 1987; Hill, 1990) that differ from those observed in *A. lefipanensis*.

Leaves of *A. lefipanensis* also differ markedly from those of the previously known Patagonian fossil species *A. grandifolia* Feruglio, *A. pararaucana* Panti, and *A. nathorsti* Dusén (Table 3; Dusén, 1899; Berry, 1928; Feruglio, 1951; Menéndez and Caccavari, 1966; Del Fueyo and Archangelsky, 2002; Panti et al., 2007; Falaschi et al., 2012; Ohsawa et al., 2016). The Early Cretaceous *A. grandifolia* Feruglio has triangular-lanceolate leaves similar to those found in *Araucaria* section *Intermedia*, although Del Fueyo and Archangelsky (2002) classified this species as part of the section *Araucaria* because its leaves are more imbricated than those of the extant species of section *Intermedia*. *Araucaria lefipanensis* has ovate-lanceolate leaves that are smaller than those of *A. grandifolia* (Table 4; Feruglio, 1951; Del Fueyo and Archangelsky, 2002). The Eocene-Oligocene

species, *A. pararaucana* Panti, has a leaf morphology similar to that of the O-shaped morphology of *A. lefipanensis*, but differ in size, and stomatal orientation (Table 4, Panti et al., 2007). Finally, the Oligocene-Miocene *A. nathorstii* Dusén has leaves that are similar to the new species in shape and stomatal morphology, but that are larger, and associated cone scale complexes with a different general outline and degree of wing development (Table 4; Dusén, 1899; Berry, 1928; Menéndez and Caccavari, 1966; Falaschi et al., 2012; Ohsawa et al., 2016).

The cone scale complexes of *Araucaria lefipanensis* are unusual in comparison with other fossil cone scales of *Araucaria* and *Araucarites* (Tables 5, 6); they have a more heart-shaped outline than previously described species. Among the most similar cone scales in shape and size are *Araucarites cutchensis* Feistmantel (Feistmantel, 1876; Halle, 1913; Arber, 1917; Frenguelli, 1949; Pant and Srivastava, 1968) from the Jurassic and Cretaceous of Gondwana, *Araucarites baqueroensis* Archangelsky (1966) from the Early Cretaceous of Patagonia, *Araucaria* scale type B (Pole, 1995) from the Late Cretaceous of New Zealand, and *Araucaria* cf. *Araucarites pichileufensis* Berry (Wilf et al., 2010) from the early Eocene of Patagonia (Table 5). However, these species differ significantly in outline from *A. lefipanensis* cone scale complexes.

### Leaf morphological variation and seasonality

Among the vegetative specimens, two morphological groups were distinguished based on leaf shape and found to be significantly different in the statistical analyses performed (O and L groups, see Materials and Methods and Results). However, from a biological view, they may correspond either to a single taxon or to different natural taxa. Here we propose that both leaf morphologies belong to a single species with broad, multiveined, sessile leaves based on the fact that most of the leaf specimens were concentrated in a single fossiliferous layer (see geologic settings and comparisons),

which, in addition to the leaves, yielded a single morphotype of araucarian cone scale complexes. Furthermore, specimens with intermediate morphologies were also found, although in smaller proportion (Appendix S4). Only one type of *Araucaria*-like epidermal morphology was recorded in the macerated specimens, which show the same micromorphology than the (more poorly preserved) cuticles found in connection with both types of leaves of *A. lefipanensis*. This finding suggests that both groups also share cuticular characters, including the presence of 4–5 subsidiary cells, polar extensions, and quadrangular, elongated epidermal cells. Nevertheless, cuticular features in extant species of the broad-leaved clade (sections *Araucaria*, *Intermedia*, and *Bunya*) are conservative, sharing most of the gross micromorphological characters (Stockey and Ko, 1986). Additional information supporting the hypothesis of a single species are the continuous characters, like the sizes of the different epidermal structures, that vary in narrow ranges. In this respect, it is important to remark that continuous characters are potentially more informative than discrete features for resolving phylogenetic relationships among terminal nodes (Escapa and Pol, 2011) since they capture slighter variations, which are those that can be expected among closely related organisms.

The leaf shape differences described for *A. lefipanensis* are interpreted here as dimorphism. The presence of dimorphic leaves is a common feature in broad-leaved extant and extinct members of *Araucaria* (Seward and Ford, 1906; Berry, 1908; Cantrill and Falcon-Lang, 2001; Farjon, 2010). The araucarian broad-leaved clade has two kinds of leaf dimorphism. One consisting of only a change in leaf size (hereafter type I dimorphism), similarly to what occurs in the extant South American species *Araucaria angustifolia* (Bertol.) Kuntze, and in the extinct species *Araucaria bladenensis* Berry, *A. alexandrensis* Cantrill and Falcon-Lang, *Araucarites marshalli* Edwards, and *A. nathorstii* Dusén (Tables 3, 4; Dusén, 1899; Berry, 1908; Edwards, 1926; Berry, 1928; Menéndez and Caccavari, 1966; Cantrill and Falcon-Lang, 2001; Falaschi et al., 2012; Stults et al., 2012). The second type of dimorphism is characterized by two distinct leaf shapes (hereafter, type II dimorphism). This is found in the Australian *Araucaria bidwillii*, (Fig. 7; Stockey and Taylor, 1978a; Farjon, 2010; see the isolectotype of *A. bidwillii* K000961233 and the specimen K0009612332 from the herbarium of Kew Royal Botanical Gardens) and in the fossil species *A. chambersii* Cantrill and Falcon-Lang (2001) from the Late Cretaceous of Antarctica. The significant differences found between *A. lefipanensis* O- and L-shaped groups might indicate that the new species has the second type of dimorphism described above, with a similar morphological variation to *A. bidwillii* (Fig. 7). Furthermore, both O- and L-leaf morphologies have a wide range of sizes, suggesting that several stages of development were preserved at the Lefipán sediments. Therefore, we assume that the dimorphism here reported cannot be explained as different stages of a unique ontogenetic series.

Dimorphic leaves in the broad-leaved sections of *Araucaria* have been linked to seasonal variation (Cantrill and Falcon-Lang, 2001), and even though this has been proposed for variation in size (type I dimorphism), it is possible that changes in shape (type II dimorphism) are also developed as a response to seasonality. Both the paleoenvironment and paleoclimate have been reconstructed for the lower Lefipán Formation (Baldoni and Askin, 1993; Cúneo et al., 2008). These reconstructions suggest that during the Late Cretaceous the area was a warm to subtropical patchy forest, probably more open, warmer, and drier than the cool wet Weddellian forests of the more southern latitudes (Baldoni and Askin, 1993).

Based on angiosperm mean leaf area analysis (Wilf et al., 1998) and leaf margin analysis (Wolfe, 1993; Wilf, 1997), Cúneo et al. (2008) estimated for the latest Cretaceous Lefipán Fm., a mean annual precipitation of around 950 mm and mean annual temperature of $18.2 \pm 1.5°C$. Since the Late Cretaceous paleolatitude for Lefipán Fm. would have been somewhere near 45° S (Baldoni and Askin, 1993), both temperature and precipitation seasonality could be expected. The paleoclimate and paleoenvironment of the Lefipán Formation are comparable with that of nowadays natural niche of *Araucaria bidwilli* (Enright, 1995; Smith and Butler, 2002; Farjon, 2010), which grows in areas with a mean annual temperature of 18.5°C (Smith and Butler, 2002) and a mean annual rainfall—of the southern distribution areas of the species—that ranges from 900 to 1400 mm, with a dry season from April/May to September (Farjon, 2010).

### Mosaic evolution in araucarian conifers: the case for *Araucaria lefipanensis*?

Modern conifer systematics is dominated by molecular studies that do not include fossil species or that use them for node dating only, without their previous incorporation in the data matrix (e.g., Biffin et al., 2010; Lin et al., 2010; Mao et al., 2010; Crisp and Cook, 2011; Leslie et al., 2012; Yang et al., 2012). Because whole plant reconstructions are rare (e.g., Dilcher, 1991; Gee and Tidwell, 2010; Klymiuk et al., 2011; Bomfleur et al., 2013), conifer evolutionary studies based on morphology, or both morphology and molecular evidence, that include fossils are mostly based on anatomically preserved seed cones (Miller, 1976, 1988; Smith and Stockey, 2001; Gernandt et al., 2011; Rothwell et al., 2011; Escapa and Catalano, 2013; Smith et al., 2017). The use of this particular organ is understandable if we take into account that seed cones, among all the organs that conform the conifer bauplan, are often considered to have the highest number of characters retaining phylogenetic information (Miller, 1988; Rothwell et al., 2009; Spencer et al., 2015). Furthermore, most modern conifer families are characterized by unique sets of seed cone character states, whereas other organs, although better represented in the fossil record, tend to show higher levels of homoplasy (Kendall, 1947; de Laubenfels, 1953; Archangelsky, 1963; Harris, 1979; Miller, 1988). Because of their apparently less homoplastic nature in comparison with other organs, in absence of whole-plant reconstructions, seed cones are currently thought to be the most valuable single-organ substitute of the whole-plant concept when dealing with extinct conifers (Spencer et al., 2015).

Fossils with character state combinations not found in extant species may represent transitional stages in the evolution of a clade. Studying these is critical in order to understand cryptic homologies (Florin, 1951; Miller, 1988; Spencer et al., 2015) and to provide evidence for the assessment of whether hypothetical character state transitions are compatible or incompatible with the fossil record (Miller, 1988). When fossils with novel character state combinations are multiple-organ remains or, better still, whole-plant reconstructions, they are more relevant to evolutionary studies, since they might reveal changes occurring asynchronously in different organs (i.e., mosaic evolution). Evidences of mosaic evolution in the fossil record can help to elucidate the evolutionary history of a given plant group (e.g., Florin, 1951; Escapa et al., 2010; Bomfleur et al., 2013), since they may be providing information in areas of the phylogeny that are poorly sampled in terms of extant taxa (Donoghue et al., 1989;

Nixon, 1996; Spencer et al., 2015). Increased taxon sampling based on fossils, especially on those that show evidence of mosaic evolution, is particularly important in ancient lineages such as the conifers, whose evolutionary history goes back in time to the upper Paleozoic, and, consequently, whose extant families and genera are separated by long branches (Florin, 1951, 1963; Stockey, 1982; Kunzmann, 2007; Taylor et al., 2009; Leslie et al., 2012). In such cases, the taxon sampling automatically becomes extremely poor when only extant species are included in evolutionary studies, since there are extensive portions of the phylogenetic history of the group that are not sampled at all (Donoghue et al., 1989, Nixon, 1996). Therefore, the incorporation of fossil species with novel combinations of characters that occupy a transitional position within these large and poorly sampled areas, where a large number of changes may have occurred, provides information not only on the sequential order in which those changes arose, but also about the timing of these changes.
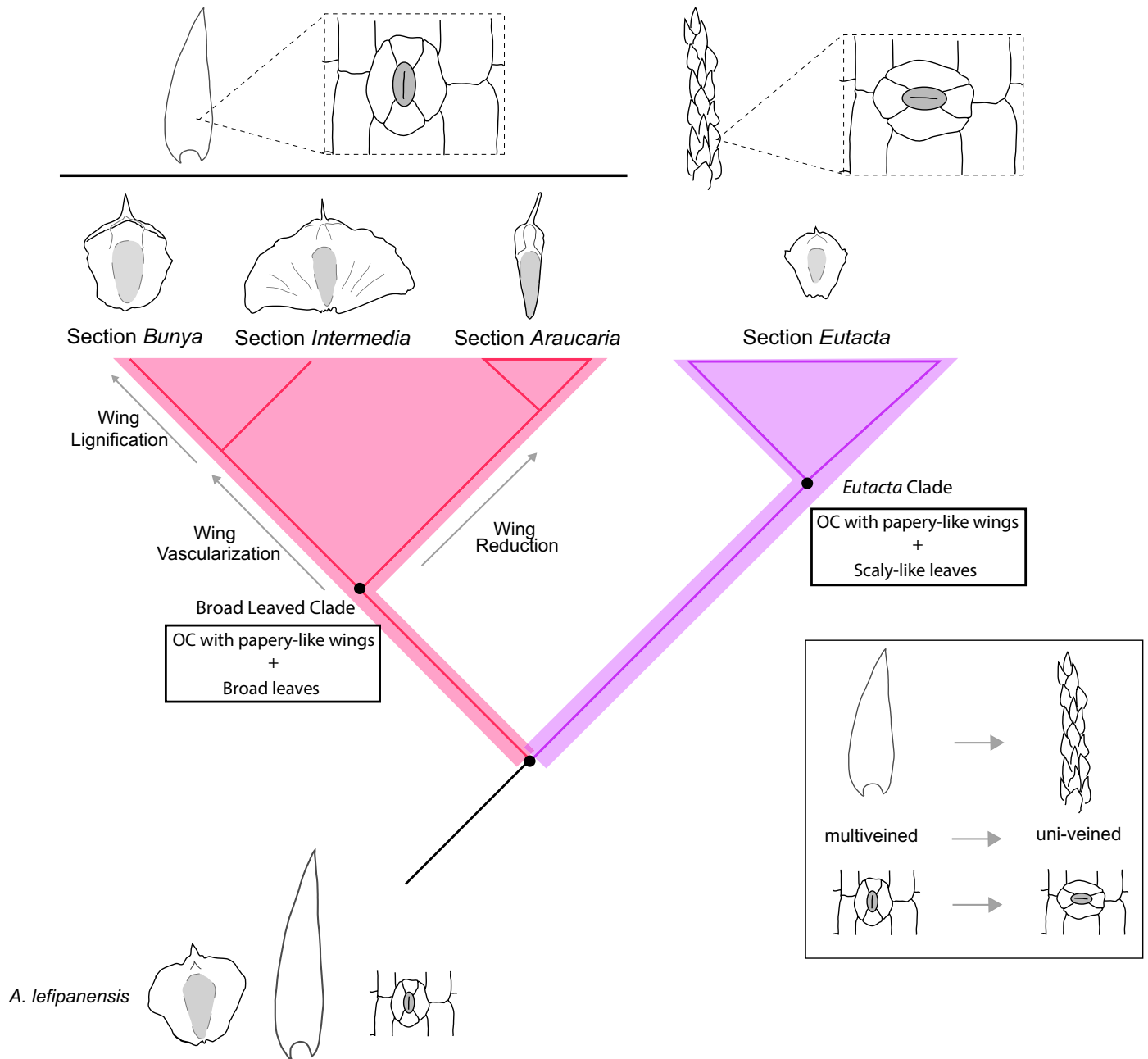


**FIGURE 8.** Character evolution of leaves and cone scale complexes of *Araucaria*. Phylogenetic hypothesis from Escapa and Catalano (2013); Broad-leaved clade (in pink) includes sections *Araucaria*, *Intermedia*, and *Bunya*; *Eutacta* clade (in lilac) includes species of section *Eutacta*. Reconstructed plesiomorphic features for both leaves and cone scale complexes specified at the nodes that define each of these clades; above the tree tips, diagrams of the mean features analyzed are presented. At bottom left, diagrams of the same features specified for the tree tips are shown for *Araucaria lefipanensis*. At bottom right are the character state changes expected for the *Eutacta* lineage if *A. lefipanensis* were positioned at its base. Finally, the grey arrows on the tree show a plausible evolutionary scheme for the cone scale complex wings of the broad-leaved clade.

The material here described—if as we hypothesize, belongs to the same biological species—provides evidence of mosaic evolution in *Araucaria*. Broad, sessile, multiveined leaves, characteristic of the clade formed by *Araucaria* sections *Araucaria*, *Intermedia*, and *Bunya*, are found together with cone scale complexes that are similar to those of extant species of *Araucaria* section *Eutacta* in both their general outline and the thin appearance of their wings. Hence, if they were not found associated, each organ would probably have been related with different sections of the genus.

According to the combined phylogenetic analysis of Escapa and Catalano (2013), when only considering extant species, the plesiomorphic configuration of the crown group of the genus *Araucaria* seems to be the papery-thin wing morphology for the cone scale complexes and a broad multiveined morphology for the leaves (Fig. 8). However, a rhomboidal (scale-like) morphology appears to be a more plausible basal leaf morphology when taking into account the oldest fossil record assigned to the genus or associated with it, as it is the case of several *Brachyphyllum* species (Kendall, 1949; Calder, 1953; Townrow, 1967; Harris, 1979; Gee and Tidwell, 2010; Falaschi et al., 2011; Sender et al., 2015). The reconstructed basal configuration for the crown group of the clade comprised by the species of section *Eutacta* would be thin-winged cone scale complexes and single-veined scale-like leaves (Fig. 8). Finally, for the crown group of the broad-leaved clade (sections *Araucaria*, *Intermedia*, and *Bunya*) the basal configuration for the leaves would be broad and multiveined (Fig. 8), especially if its fossil record is considered (e.g., Berry, 1908; Bose, 1975; Cantrill, 1992; Duarte, 1993; Cantrill and Falcon-Lang, 2001; Del Fueyo and Archangelsky, 2002). The basal configuration of the cone scale complex wings for this clade is papery-thin when considering only extant species, but when the fossil record is taken into account, the optimization of this character is ambiguous (Escapa and Catalano, 2013).

Regarding the previously discussed possible plesiomorphic configurations of the broad-leaved and *Eutacta* clades of the phylogeny recovered by Escapa and Catalano (2013), the new Patagonian species has two putative places within *Araucaria*. One would be at the base of the *Eutacta* clade. If this is the case, *A. lefipanensis* would be an autapomorphic basal species or, alternatively, broad leaves would be the basal configuration for the *Eutacta* clade, and they would go through a reduction in the evolution of the group to scaly, single-veined leaves, with oblique or transverse-oriented stomata, organized in parallel rows, arranged at both sides of the leaf mid-vein in two stomatal bands (Fig. 8). In this scenario, cone scale complexes would suffer virtually no change in the evolution of the clade (Fig. 8). In the second evolutionary scenario, *Araucaria lefipanensis* would be part of the broad-leaved clade. This scenario is supported by the high amount of features shared by leaves of the new Patagonian species and extant species of the genus, which include shape and attachment of leaves, presence of multiple veins, and cuticle morphology. Additionally, as mentioned above, the plesiomorphic configuration of the cone scale complex wing morphology for the broad-leaved clade is optimized as ambiguous, being compatible with a thin-winged basal species. The second scenario is also more compatible than the first one when taking into account the consistent evidence provided by the leaf morphology of the Cretaceous and Cenozoic fossil species assigned to both *Eutacta* and broad-leaved clades (e.g., Hill and Bigwood, 1987; Del Fueyo and Archangelsky, 2002; Panti et al., 2007).

Traditionally, the ancestral configuration of the seed cones of *Araucaria* was interpreted as showing heavy, woody-winged cone scale complexes (Wilde and Eames, 1948) because Jurassic members assigned to the genus show cone scale complexes with well-developed, woody wings (Kendall, 1949; Calder, 1953; Stockey, 1975, 1980; Axsmith et al., 2008). However, it is yet to be determined whether these species belong to the crown or stem group of the genus or even to the stem group of the family (Kunzmann, 2007). On the light of the total evidence analyses performed by Escapa and Catalano (2013), section *Bunya* is reconstructed to have the most derived cone scale complex morphology, including the woody, well-developed wings and seeds that shed at maturity (Wilde and Eames, 1952), which might have evolved sequentially in the broad-leaved clade, by an initial vascularization of the cone scale complex wings, as seen in section *Intermedia* (Haines, 1983b), and by further lignification (Fig. 8). In this context, *Araucaria lefipanensis* can be interpreted as having a derived configuration of leaf characters and a plesiomorphic configuration of cone scale complexes features (thin, well-developed wings), suggesting mosaic evolution.

## CONCLUSIONS

Remains of leaves and cone scale complexes from the Late Cretaceous of Patagonia were described and interpreted as belonging to a single new species, *Araucaria lefipanensis*. The leaf shape dimorphism in *A. lefipanensis* is consistent with the presence of this type of dimorphic leaves in the extant Australian *A. bidwillii* (section *Bunya*), which is native to subtropical forest with markedly seasonality and mean annual temperature and precipitation values similar to those reconstructed by Cúneo et al. (2008) for the Late Cretaceous portion of the Lefipán Formation.

The new Patagonian species shows a mosaic of character states, with broad, multiveined, sessile leaves typical of the broad-leaved clade (sections *Araucaria*, *Intermedia*, and *Bunya*; see Fig. 8), and cone scale complexes similar to those found in the *Eutacta* clade in both general outline and thin appearance of its wings (Fig. 8). Because of this mosaic of features, *A. lefipanensis* constitutes an interesting species to analyze in a phylogenetic context since it might provide information about the early evolution of either the broad-leaved or the *Eutacta* clades according to its phylogenetic position. Moreover, phylogenetic analyses including this and other fossil species based on compressions and impressions are necessary steps to better understand the evolution of the Araucariaceae. Definitely, including this kind of fossils implies the circumscription and discussion of systematically informative characters that can be identified in these preservation types, since previous studies that included fossils were based mostly in permineralized material (see discussion), and the inclusion of other types of preservations may give complementary information (e.g., Escapa and Leslie, 2017).

## ACKNOWLEDGEMENTS

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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