# A new araucarian fossil species from the Paleogene of southern Argentina



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**Abstract.** A new Araucariaceaea from the Paleogene of Tierra del Fuego Province, Argentina is described. *Araucaria pararaucana* sp. nov. has imbricate, ovate-lanceolate leaves with an acute apex, characterized by the presence of discontinuous and longitudinally oriented stomatal rows separated by epidermal cells, which may be slightly sinuous. Stomatal guard cell surface is granular. These fossil leaves are compared with the extant sections *Bunya*, *Intermedia* and *Araucaria*. Their anatomical characters along with the external morphology suggest a close affinity with the extant southern Patagonian species *A. araucana* (Molina) K. Koch. The record of this new late Eocene species provides more evidence for a probable unique representation of Section *Araucaria* in the area during the Tertiary.

**Resumen.** Una nueva especie fósil de *Araucaria* del Paleógeno de Tierra del Fuego, Argentina. Se describe una nueva especie de Araucariaceae del Paleógeno de Tierra del Fuego, Argentina. *Araucaria pararaucana* sp. nov. se caracteriza por sus hojas imbricadas, ovado-lanceoladas con un ápice agudo. Sus caracteres anatómicos permiten una estrecha comparación con las actuales secciones *Bunya, Intermedia* y *Araucaria*. La presencia de hileras discontinuas de estomas orientados longitudinalmente, separadas por células epidérmicas que pueden ser algo sinuosas, la superficie granular de las células de cierre, junto con la morfología externa nos permiten compararla con la especie *Araucaria araucana* (Molina) K. Koch, actualmente restringida a la Patagonia austral. Esta especie del Eoceno tardío es una nueva evidencia de la exclusiva representación de la Sección *Araucaria* durante el Terciario en el área.

Key words. Gymnosperms. Araucariaceae. *Araucaria*. Cuticle. Paleogene. Argentina Palabras clave. Gimnospermas. Araucariaceae. *Araucaria*. Cutícula. Paleógeno. Argentina

### Introduction

Araucariaceae is a coniferous family now confined to the Southern Hemisphere, where the genus *Araucaria* de Jussieu is a characteristic member of the South American forests from southern Brazil and western Patagonia (represented by *A. angustifolia* (Bertol.) O. Kuntze and *A. araucana* (Molina) K. Koch, respectively), New Caledonia, Australia, Norfolk Island and New Guinea. The fossil record of *Araucaria* leaves in southern South America is scarce and includes Jurassic, Cretaceous and Tertiary species (Berry, 1928, 1938; Calder, 1953; Del Fueyo

and Archangelsky, 2002; Menéndez and Caccavari, 1966).

The fossil specimens described here were collected from Tertiary deposits at Sloggett Bay in Tierra del Fuego Province, Argentina (figure 1). The presence of fossil plants in the Sloggett Formation was reported originally by Andersson (1907). Palynological assemblages recovered from this unit suggest a Late Eocene-Early Oligocene age for the sequence (Olivero *et al.*, 1998). Podocarpaceae, Nothofagaceae and Proteaceae dominate the palynoflora with subordinated ferns of the Lophosoriaceae, Dicksoniaceae, Schizaeaceae, Pteridaceae, Athyriaceae, Polypodiaceae and Cyatheaceae (Olivero *et al.*, 1998). Also, pollen grains of *Araucariacites australis* Cookson were identified, indicating the presence of the Araucariaceae (Olivero *et al.*, 1998).

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### Material and methods

The studied specimens were collected from the AMGHB2-0002-7014/07\$00.00+.50

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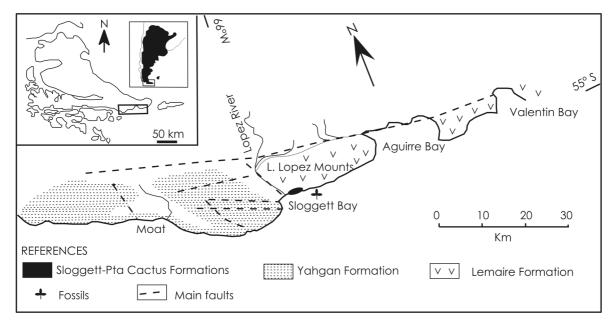


Figure 1. Location map (after Olivero et al., 1998) / mapa de ubicación (tomado de Olivero et al., 1998).

Sloggett Formation at Sloggett Bay, the type locality of the stratigraphic unit (Caminos et al., 1981). Olivero et al. (1998) recognized two members in the sequence; the lower Gris Member consists of massive carbonaceous mudstones cut by conglomerate and pebbly sandstone channels. The plant remains are found in thin, black banks with abundant mudstone matrix inside this member, which represents a fluvial system with humid and vegetate areas (Caminos et al., 1981; Zanettini and Zapettini, 1988; Olivero et al., 1998). Besides the araucarian remains, the paleobotanical association includes angiosperm leaves that will be analysed in a forthcoming paper. The upper Bayo Member is a major complex of lenticular conglomerates and sandstones grading laterally and vertically to heterolithic mudstones and coal measures (Olivero et al., 1998).

The organically preserved leaf remains were examined under light microscope and with scanning electron microscope (SEM). Cuticles were prepared by soaking leaf fragments in nitric acid; small amounts of 10% nitric acid were successively added until the fragments were cleared, followed by sodium hypochlorite (20%). Material for SEM observation was sputter-coated with gold-palladium (40%-60%) and examined in a microscope Phillips XL 30 at the Museo Argentino de Ciencias Naturales B. Rivadavia. Twenty stomata and epidermal cells were measured for each sample and the averages were calculated (table 1).

All specimens were photographed using a Coolpix 4500 camera adapted to a Nikon stereomicroscope and an Olympus microscope. The speci-AMEGHINIANA 44 (1), 2007

mens studied are stored in the Paleobotanical Collection of the Museo Argentino de Ciencias Naturales B. Rivadavia (BAPb) together with the thin sections (BAPbPm).

### Systematic paleontology

Family Araucariaceae Henkel and Hochst., 1865

Genus Araucaria de Jussieu, 1789

Section Araucaria Wilde and Eames, 1952

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

# *Araucaria pararaucana* sp. nov. Figures 2.A, C-G and 3

**Holotype.** BAPb 13544 (BAPbPm 476). **Other material studied.** BAPb 13541 (BAPbPm 473), BAPb 13542 (BAPbPm 474), BAPb 13543 (BAPbPm 475).

Etymology. From Latin par: equal, like.

**Type locality and horizon.** Sloggett Bay, Tierra del Fuego Province, Argentina. Sloggett Formation, Gris Member, Late Eocene-Early Oligocene.

**Diagnosis.** Leaves imbricate, ovate to lanceolate, with acute apex and length/width ratio about 2.5. Leaves amphistomatic, more stomata occur on one surface. Stomata in parallel, discontinuous rows; elliptical to sub-rounded, most oriented parallel to leaf margin, oblique and horizontally oriented stomata rare. Subsidiary cells four; five and six occur. Cuticle

Sample	Leaf dimensions (μm)	Stomatal dimensions (µm)	Epidermal cell dimensions Av. Polar x Av. Lateral(μm)	
	Length x Width	Av. Polar x Av. Lateral	Between stomatal bands	Within stomatal bands
BAPB 13541 (BAPb Pm 473)	circa 17x7	67x54	26x29	20x34
BAPB 13542 (BAPb Pm 474)	59x24	73x45	50x21	27x37
BAPB 13543 (BAPb Pm 475)	55x21	86x59	46x25	25x46
BAPB 13544 (BAPh Pm 476) Holotype		85 x 60	54 x 22	26 x 35

**Table 1.** Leaf dimensions and internal cuticular features for the samples analyzed / dimensiones de las hojas y caracteres cuticulares internos de las muestras analizadas.

of the guard cells is granular. Epidermal cells are rectangular to quadrangular between stomata rows, irregular around stomata; outlines slightly sinuous. **Description.** The holotype BAPb 13544 corresponds to a complete, ovate-lanceolate leaf with a broad base (figure 2.E). It seems to have been thick and coriaceous. Leaves are amphistomatic, with more stomata in one surface (in the fossil specimens the abaxial and adaxial surfaces could not be differentiated). Stomata are arranged in parallel and discontinuous rows (figure 3.D), they are elliptical to sub-rounded in shape (figure 3.B), sometimes with perpendicular orientation of the stomata to the leaf margin. Cuticle of the guard cells surface is granular (figure 3.C). The common subsidiary cell number is four, but five and six were observed. Epidermal cells are rectangular to quadrangular between stomata rows and irregular around stomata. Their outlines are slightly sinuous.

A second smaller specimen (BAPb 13543) has a length/width ratio of 2.6. This specimen shows stomata densely arranged in one surface. Oblique and horizontally oriented stomata occur less frequently in some leaf fragments (figure 2.F). The complete leaf of sample BAPb 13542 (figure 2.C) is similar to the holotype and preserves the acute apex, with a length/width ratio of 2.4.

All the specimens analyzed are detached leaves except the sample BAPb 13541, which shows imbricate leaves, arranged in a tight helix (figure 2.A). They are preserved without the apex. At high magnification the stomata can be observed arranged in rows parallel to leaf margins. Stomata are sparser on one surface (figure 2.D) and subsidiary cells have a different shape giving them a more sub-rounded shape (figure 3.E). They are mostly oriented parallel to the leaf margin but oblique and horizontally oriented stomata are observed less frequently (figure 2.G). The most common subsidiary cell number is four, but five and six were observed as in the holotype, and result from the division of both lateral and

polar subsidiaries (Stockey and Ko, 1986). Epidermal cells are rectangular to quadrangular between stomata rows and irregular around stomata as in the holotype. Their outlines are slightly sinuous (figure 3.A) but usually these margins are masked by the cuticle thickness that partially covers the inner wall surface.

# Discussion and comparisons

Wilde and Eames (1952) classified the genus Araucaria into four extant Sections: Araucaria (= Columbea), Bunya, Eutacta and Intermedia. This classification, based on morphological characters, agrees with the rbcL phylogeny proposed by Setoguchi *et al*. (1998), who suggested that the number of cotyledons, position of the pollen cone and cuticular micromorphologies are phylogenetically informative. Among the cuticular characters, stomatal orientations to long axis of leaf and stomatal distribution have resulted useful to split Section Eutacta from the other sections as a clade (Setoguchi et al., 1998). That section is characterized by stomata mostly oblique or perpendicular, distributed in two bands or groups and the prominent polar extensions of the guard cells. The other three sections constitute another clade (with stomata in discontinuous rows), which divides into two clades, one of them including the two South American species (A. araucana and A. angustifolia). Moreover, an analysis of the evolutionary trend in stomatal orientation showed that parallel orientation arose in the ancestor of sections Araucaria, Bunya and Intermedia (Setoguchi et al., 1998) and is also present in Wollemia adult leaves (Chambers et al., 1998).

Therefore, our species characterized by discontinuous rows of stomata parallel to the leaf margin, can be compared with the sections *Bunya*, *Intermedia* and *Araucaria* (adult leaves of *Wollemia* differ in having prominent extensions of the guard cells). According to the descriptions of Stockey and Ko (1986), this

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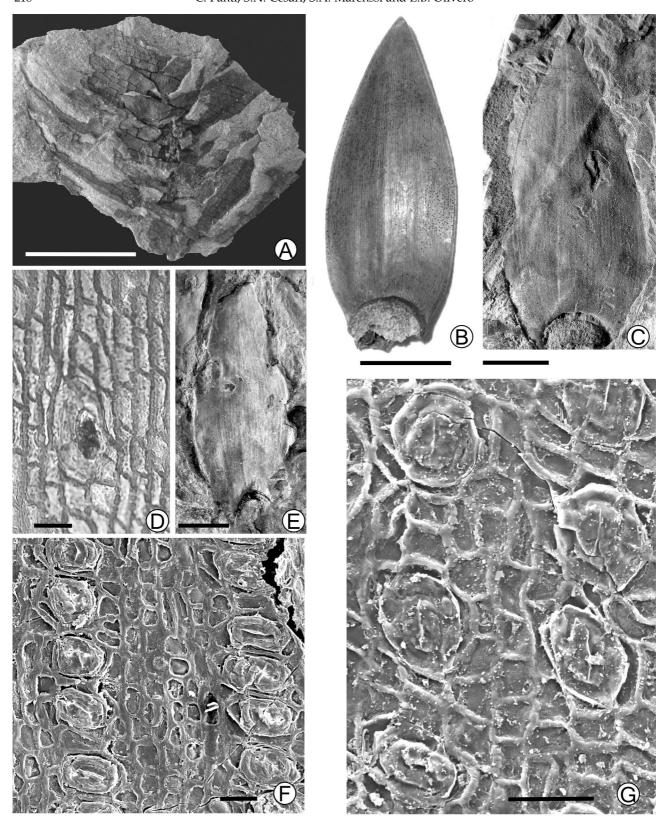
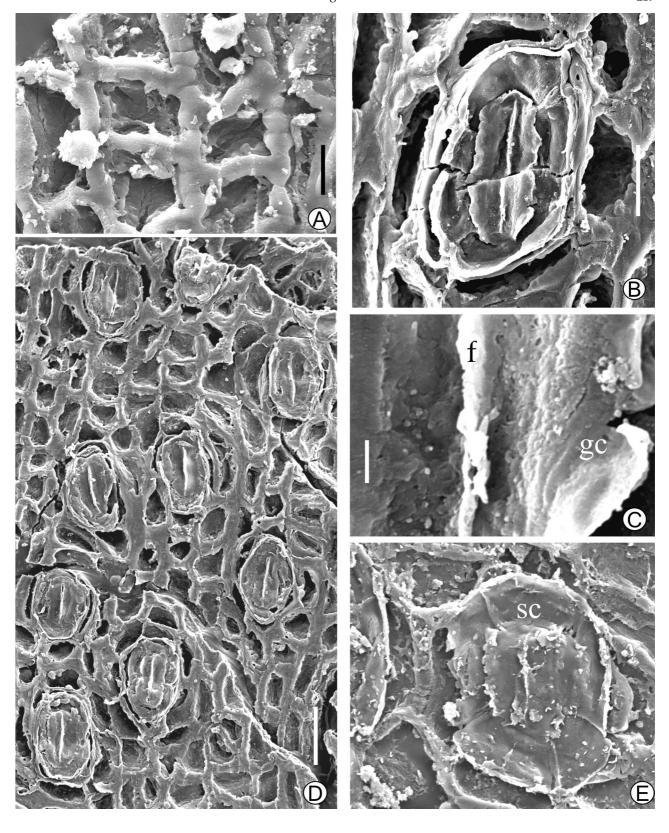


Figure 2. A, C-G, Araucaria pararaucana sp. nov.; A, Imbricate leaves in tight helix / hojas imbricadas en espiral apretada, BAPb 13541. B, Leaf of Araucaria araucana / hoja de Araucaria araucana. C, Complete leaf / hoja completa, BAPb 13542. D, Surface of cuticle with few stomata and slightly sinouous epidermal cells / superficie de la cutícula con pocos estomas y células epidérmicas algo sinuosas, BAPb Pm 473C. E, Holotype / holotipo, BAPb 13544. F, surface with densely packed horizontally oriented stomata / superficie con estomas densamente distribuidos y orientados horizontalmente, BAPb Pm 475. G, One surface of cuticle with longitudinally oriented stomata/ superficie de la cutícula con estomas con orientación longitudinal, BAPb 13541. Scale bar / escala gráfica, A-C, E = 1 cm, D, F-G = 50 μm.

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**Figure 3.** *Araucaria pararaucana* sp. nov., **A,** Detail of slightly sinuous wall of epidermal cells / *detalle de la pared ligeramente sinuosa de las células epidérmicas*, BAPb 13541. **B,** Oval stomata / *estoma oval*, BAPb 13544. **C,** Detail of guard cells of stomata, f: flange, gc: guard cell / *detalle de las células de cierre del estoma, f: reborde, gc: célula de cierre*, BAPb 13544. **D,** Subrounded stomata / *estoma subredondeado*, BAPb 13541. **E,** General view of discontinuous stomatal rows / *vista general de las hileras discontinuas de estomas*, BAPb 13544. Scale bar / *escala gráfica*, A= 4 μm, B, D= 10 μm, C= 1 μm, E= 50 μm.

clade shares the oval to rounded outline of the subsidiary cells and the absence of prominent polar extensions in the guard cells. Moreover, the analysis of the different species seems to suggest that sinuous epidermal cells are present in all these sections.

Although mature leaves of Section *Bunya* (*A. bidwillii*) are arranged radially around the branchlet and often imbricate, they are more elongate than our species. Cuticle of this Section shares similarities with *Araucaria pararaucana* sp. nov. such as the oval to rounded outline of the subsidiary cells but differs in the more sinuous epidermal cells and the more reticulate guard cell surface. Moreover, stomata are predominantly oriented parallel to the long axis of the leaf (Stockey and Ko, 1986).

In the same way, the species included in the Section Intermedia are characterized by prominent sinuous epidermal cell outlines and clearly reticulate guard cells surfaces (Stockey and Ko, 1986). Besides, adult leaves of that Section are lanceolate, narrow and have a similar number of stomata in both surfaces.

Our species is referred to section *Araucaria*, which includes large, lanceolate and imbricate leaves, represented by the extant species Araucaria araucana and A. angustifolia. A. araucana seems to be the most similar in both external and internal characters to the studied leaves. Silba (1986) characterized A. araucana leaves as scale-like, persistent on the trunk even to the base, ovate-lanceolate, 30-50 mm long by 8-25 mm wide, a surface marked with longitudinal lines, and bearing stomata on both faces (more in one surface). The extant and fossil species share the arrangement of the leaves in a tight helix and the same leaf shape (figures 2.B, C). Both species have discontinuous stomatal rows separated by epidermal cells that may be slightly sinuous (Stockey and Ko, 1986). They coincide in the shape and distribution of the stomata, which are characterized by globular or granular guard cell surface. In contrast, A. angustifolia has smaller leaves, sharply acute, keeled, with a distinct sinuous outline of the epidermal cells and the flange between the guard and subsidiary cells has a serrate edge.

Several fossil leaves have been described in Argentina, among them *Araucaria nathorstii* Dusén, reported by Menéndez and Caccavari (1966) from the Tertiary of Rio Negro Province, is the most similar to *A. pararaucana* sp. nov. by having ovate-lanceolate leaves, but their tips are more acute. The cuticular features in which they differ are more regular stomatal rows and the very rectangular epidermal cells in *A. nathorstii*. However, this species was originally described by Dusén (1899) for leaves without cuticle from Upper Oligocene-Lower Miocene strata of Punta Arenas (Chile). Later, the species was used by AMEGHINIANA 44 (1), 2007

Berry (1928) to describe impression of leaves from the Rio Negro Province. Our specimens might be similar to the original material described by Dusén (1899), but the absence of cuticle in the Chilean specimens prevents closer comparisons.

Araucaria pichileufensis Berry, another species described by Berry (1938) from the Eocene of Rio Negro province, is characterized by small pointed, triangular, falcate leaves without cuticle preserved. The size and falcate shape differ from those of *A. pararaucana* sp. nov.

Recently, Del Fueyo and Archangelsky (2002) emended *Araucaria grandifolia* Feruglio from the Lower Cretaceous of Patagonia. This species differs from *A. pararaucana* in having strongly-keeled, lanceolate leaves, with stomata only parallel to the leaf margin and epidermal cells with straight walls. *Araucarites santaecrucis* Calder, a species from the mid-Jurassic of Patagonia (Calder, 1953) has leaves that are rhomboidal and smaller than *A. pararaucana* sp. nov. with an incurved apex.

Several Antarctic Araucarian fossil species have been described recently, including Araucaria alexandrensis and Araucaria chambersii (Cantrill and Falcon-Lang, 2000) from the late Albian of Alexander Island. A. alexandrensis seems to be similar in shape and size to our species but differs in having concave and keeled leaves, while A. chambersii has leaves that are much larger with a narrowly acute apex and a base that is slightly contracted and twisted. A. sp. nov. leaves described from the Upper Cretaceous of Vega Island (Césari et al., 2001) seem to be similar externally to those of A. pararaucana sp. nov. but the stomatal rows are much more regular and are separated from each other by a constant number of epidermal cells which have straight walls instead sinuous epidermal cells. Araucaria imponens Dusén, from Seymour Island (Antarctica) differs in being a keeled leaf (Dusén, 1908).

Araucarian foliage from the Lower Cretaceous of Australia was studied by Cantrill (1992). He defined six species, four of them referred to Section *Eutacta* whereas *Araucaria seorsum* Cantrill and *A. lanceolatus* Cantrill have similarities to Section *Araucaria*. *A. seorsum* differs from our species in having leaves widely separated with broadly triangular bases and stomata with polar extensions prominent. On the other hand, *A. lanceolatus* have elongate leaves with rounded leaf apex and straight-walled epidermal cells.

The Tertiary araucarian fossils leaves described from Australia (Hill, 1990) present differences in size and shape from *A. pararaucana* sp. nov. *Araucaria lignitici* Cookson and Dungan, *A. readiae* Hill and Bigwood, *A. planus* Hill, *A. prominens* Hill and *A. uncinatus* Hill have very small leaves and stomata oriented obliquely, while *A. balcombensis* 

Selling, *A. hastiensis* Hill and Bigwood and *A. fimbriatus* Hill, show a stomata parallel orientation (a characteristic shared with *A. pararaucana*), but they are smaller and the epidermal cells walls are not sinuous (Hill, 1990).

The genus *Araucarioides* was defined by Bigwood and Hill (1985) to contain species which lack diagnostic characters of extant taxa of the Araucariaceae. The three species described by Bigwood and Hill (1985) from the Eocene of Tasmania differ from *A. pararaucana* sp. nov. in the stomatal orientation which is predominantly oblique to transverse distribution (Bigwood and Hill, 1985).

Finally, *Araucaria haastii* Ettingshausen from New Zealand, shares with *A. pararaucana* numerous characters like the stomata orientation, the number of subsidiary cells, flange of epidermal cells and the leaf shape, but the leaves are keeled (Bose, 1973).

### **Conclusions**

Although the pollen record including Araucariacites australis in the sequence suspected the presence of the family Araucariaceae in the flora of the Sloggett Formation, the discovery of well preserved leaves confirms the presence of these gymnosperms. The external and internal features of A. pararaucana sp. nov. allow us to include this new species in the Section Araucaria and anatomical characters compare with extant Araucaria araucana. Both taxa share the same leaf shape, arrangement and characteristics of the stomata and similar epidermal cell shapes. As suggested by Del Fueyo and Archangelsky (2002), Patagonia could be an important centre of development for Araucaria, since three of its four sections have been identified in the Mesozoic geological record. This new finding in the Late Eocene provides more evidence that during the Tertiary, Section Araucaria seems to be the unique representative in the region.

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