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ARTICLE

Araucarian leaves and cone scales from the Loreto Formation of Río de Las Minas, Magellan Region, Chile[1]

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Abstract: Cone scales and leaves of the Araucariaceae are reported from the Loreto Formation in Río de Las Minas, Punta Arenas, Chile. Two types of cone scales including one new species, ***Araucarites alatisquamosus*** are recognized. They are similar to *Araucaria* section *Eutacta*. Two types of leaves are assigned to *Araucaria nathorstii* Dusén, and one new type is distinguished in the specimens from the type locality of *A. nathorstii.* A narrow leaf type is identical to Dusén's "Blätter der sterilen Zweige (leaves of sterile shoot)" of *A. nathorstii*, and a broad leaf type is identical to his "Blätter der fertilen Zweige (leaves of fertile shoot)". Both types show characters of leaves of section *Araucaria* as suggested by earlier studies. A smaller leaf type differs from the original description of *A. nathorstii*, and consists of small appressed leaves with the obtuse apex and stomatal orientation that are the characteristic of the section *Eutacta*. The occurrence of leaves and cone scales similar to section *Eutacta* suggest the presence of araucarians close to this section in southernmost South America during the Eocene–early Oligocene, and provide evidence for the wide distribution and diversity of genus *Araucaria* relatives in South America during the Paleogene.

Key words: Araucaria, conifer, *Eutacta*, Paleogene, Patagonia.

Résumé : On rapporte la présence d'écailles de cônes et de feuilles d'Araucariaceae dans la formation de Loreto au Rio de Las Minas, Punta Arenas, Chili. On trouve deux types d'écailles de cônes y compris celles d'une nouvelle espèce, ***Araucarites alatisquamosus***. Elles sont similaires à celles de la section *Eutacta* d'*Araucaria*. Deux types de feuilles sont assignés à *Araucaria nathorstii* Dusén et un type nouveau se distingue chez les spécimens de la localité type d'*A. nathorstii*. Un type de feuille étroite est identique à celui d'*A. nathorstii* de Dusén « Blätter der sterilen Zweige » (feuilles d'une pousse stérile) alors qu'un type de feuille large est identique à celui du « Blätter der fertilen Zweige » (feuille d'une pousse fertile). Les deux types présentent les caractères foliaires de la section *Araucaria* comme le suggèrent des études précédentes. Un type de feuille plus petite diffère de celui originalement décrit chez *A. nathorstii* et il consiste en de petites feuilles apprimées dont l'apex obtus et l'orientation des stomates sont caractéristiques de la section *Eutacta*. La présence de feuilles et d'écailles de cônes similaires à celles de la section *Eutacta* suggère la présence d'araucariens proches de cette section dans l'extrême sud de l'Amérique du Sud durant l'Éocène et l'Oligocène précoce, et donne la preuve d'une distribution et d'une diversité larges des parents du genre Araucaria en Amérique du Sud pendant le Paléogène. [Traduit par la Rédaction]

Mots-clés : Araucaria, conifères, *Eutacta*, Paléogène, Patagonie.

Introduction

Araucaria Juss. (Jussieu 1789) of the Araucariaceae Henkel et W. Hochstetter (1865) is a typical Southern Hemisphere taxon distributed disjunctively in Australia, New Caledonia, New Guinea, and South America (Farjon 2010; Debreczy and Rácz 2011). This disjunctive distribution has been considered to be related to a break-up of the Gondwana supercontinent. There are 19 living species in four sections of

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Araucaria, including *Eutacta* Endl., *Bunya* Wilde and Eames, *Intermedia* White, and *Araucaria* Juss. In addition, Section *Yezonia* has been proposed for a fossil species *A. vulgaris* (Stopes et Fujii) Oshawa, H. Nishida et Nishida, which has *Brachyphyllum*-like shoots and *Eutacta*-like cone scales (Ohsawa et al. 1995). The center of diversity for living species is the Oceania region, where 17 of 19 species assigned to three sections, *Eutacta*, *Bunya*, and *Intermedia*, are distributed. In South America, only two species of section *Araucaria* (*Columbea*) are distributed in south Chile, Argentina, and southwestern Brazil.

South America is considered to have played an important role in the distribution of *Araucaria* (Del Fueyo and Archangelsky 2002). Three of four extant sections have been found as macrofossils such as leaves, shoots, and cone scales. Section *Araucaria* is represented by *A. cartellei* Duarte from the Lower Cretaceous of Brazil (Duarte 1993), *Araucaria grandifolia* Del Fueyo and Archangelsky from the Lower Cretaceous of Argentina (Del Fueyo and Archangelsky 2002), *A. pararaucana* Panti et al. (2007) from the Paleogene of Argentina, and *A. nathorstii* Dusén (1899) from the Paleogene–Noegene of Argentina and Chile (Berry 1928; Doktor et al. 1996; Fiori 1939; Hünicken 1995; Menéndez and Caccavari 1966). Section *Bunya* is represented by the seed cones *Araucaria mirabilis* (Spegazzini) Windhausen (1931) from the Jurassic of Argentina (Stockey 1978), although its relationship to section *Bunya* was not supported by recent phylogenetic analyses based on molecular and morphological data (Escapa and Catalano 2013). Section *Eutacta* is represented by cone-scales described as *Araucarites* species; *A. minimus* Archangelsky (1966), *A. baqueroensis* Archangelsky (1966), and *A. chilensis* Baldoni (1979) from the Lower Cretaceous of Argentina and Chile, and *Araucaria pichileufulensis* Berry (1938) from the Eocene of Argentina.

Araucarites Presl (in Sternberg 1820–1838) is a fossil genus reported worldwide, and designated by Zijlstra et al. (2000) as representing araucarian seed cones and cone scales. The existence of section *Yezonia* in South America could be inferred by the presence of the pollen cone *Notopeuen brevis* Del Fueyo (1991) containing *Araucariacites* pollen grains and attached to branches bearing *Brachyphyllum* leaves. A *Eutacta*-type cone scale, *Araucarites chilensis* Baldoni (1979) from the Lower Cretaceous of El Cóndor, Santa Cruz, Argentina is also associated with *Brachyphyllum feistemantelii* (Halle) Sahni, although the evidence of section *Yezonia* is still insufficient in the Southern Hemisphere.

In contrast to abundant and diversified macrofossil records earlier than the Early Cretaceous, macrofossils except permineralized wood are very rare from the Late Cretaceous in South America (Panti et al. 2012). Only one species represented by cone scales, *Araucarites patagonica* Kurtz (1902) has been described from the Upper Cretaceous of Chile. However, it is designated as a *nomen nudum* by Hünicken (1971) because of its poor preservation and insufficient description. In the Paleogene, four species, *Araucaria araucoensis* Berry (1922), *A. pichileufulensis*, *A. pararaucana*, and *A. nathorstii* have been described from Argentina and Chile. Most of them are assigned to section *Araucaria* except for *A. pichileufulensis*, which is attributed to section *Eutacta*. Some authors suppose that sections *Bunya* and *Eutacta* had become extinct in South America at the end of Mesozoic (Veblen et al. 1995; Del Fueyo and Archangelsky 2002). To understand post-Cretaceous evolutionary history and biogeography of the genus *Araucaria* and its sections in South America, more fossil evidence is needed.

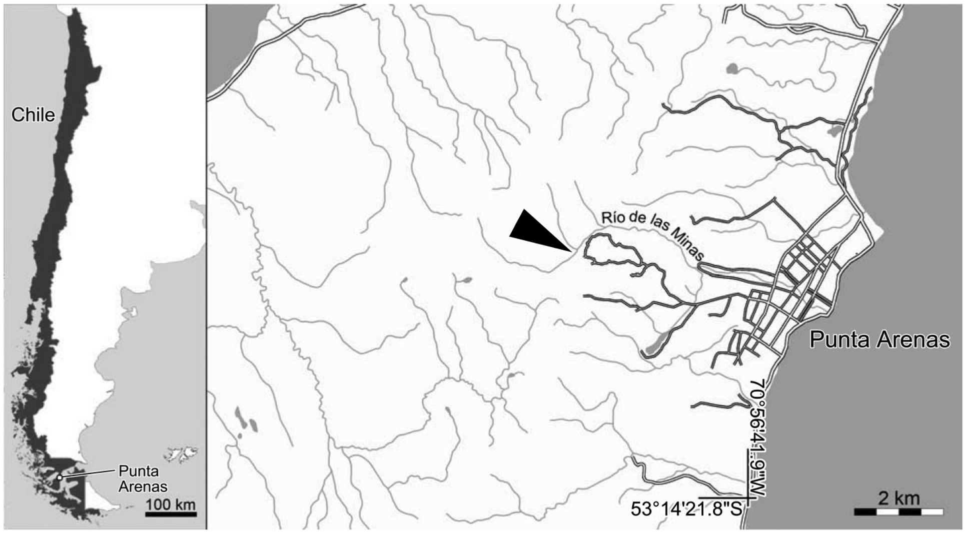
In this paper, we report newly collected araucarian fossils from the late Eocene to earliest Oligocene Loreto Formation which crops out along the river, Río de Las Minas north of Punta Arenas, Magellan Region, Chile. Two types of cone scales and three types of shoots and isolated leaves have been recognized. All are assignable to the genus *Araucaria*, including morphotypes comparable with *A. nathorstii* previously described from the same locality. The cone scales and one morphotype of shoot and leaf have features characteristic of section *Eutacta*, suggesting the possible coexistence of the section *Eutacta* with other section of *Araucaria* until the late Paleogene in South America.

Materials and methods

The fossils were collected from the Loreto Formation, which is exposed along the river Río de Las Minas, near Punta Arenas, Magellan Region, Chile (Fig. 1). The U–Th–Pb SHRIMP age of 36.48 ± 0.47 Ma is derived from the analysis of zircons obtained from the uppermost part of the Loreto Formation (Otero et al. 2012), thus the main part of the formation is thought to have been deposited in the late Eocene. This estimate is consistent with the age based on dinoflagellates (H. Kurita, personal communication, 2015).

The Loreto Formation mainly consists of sandstones and mudstones and several intercalated coal seams of variable thickness. Most of the formation was deposited in a shallow marine environment, because glauconites, as well as abundant elasmobranch fossils, are contained in the sandstones (Otero et al. 2012). Some deposits were formed in brackish environments, as indicated by herring-bone cross-stratification, typically formed by tidal currents. The araucarian remains were densely accumulated in a carbonaceous mudstone bed intercalated between sandstone beds of brackish origin, along with various forms of angiosperm leaves including *Nothofagus*. A leafy shoot of *Araucaria nathorstii* and some species of *Nothofagus* have been described previously from this locality (Dusén 1899). Some species of silicified woods including *Araucarioxylon* and *Nothofagoxylon* have also been reported recently (Terada et al. 2006).

Fig. 1. Map showing the fossil locality (arrowhead) based on Google Earth (© 2016 CNES/Astrium, Cnes/Spot Image, DigitalGlobe, Landsat, US Geological Survey and Google).



Organically preserved compressions of vegetative shoots, detached leaves and cone scales were collected by the authors during repeated field studies at the locality in 2005, 2007, 2008, and 2016. The fossils were stored in glycerin alcohol solution (glycerin–ethanol = 1:1, *v*/*v*) to prevent rapid disorganization due to desiccation. Specimens were photographed using a Pentax K-5 IIs camera with a smc Pentax-D FA Macro 50 mm lens attaching a polarizing filter. Cuticles were prepared using Schultz's solution (e.g., Kerp and Krings 1999) followed by diluted sodium hydroxide or using commercial bleach (sodium hypochlorite solution) until the cuticles were cleared. Either lower or upper cuticles, or both, were removed, rinsed with deionized water, and mounted in glycerine jelly. Cuticular features were examined with an optical microscope (Nikon Optiphot and Leica DMR) and photographed using Nikon DS-Fi1 and Leica MC170HD microscope cameras.

All specimens examined are deposited in the National Museum of Nature and Science, Tokyo, except for the holotype specimen of the new species (specimen No. SGO.PB 1577), which will be deposited in the Paleontology Section of the Museo Nacional de Historia Natural, Santiago, Chile.

Results

Araucarian cone scales

Two types of morphologies were identified from abundant specimens of detached cone scales. One is designated here as a new species of *Araucarites*, and the other as *Araucarites* sp.

Systematic Palaeontology

Family *Araucariaceae* Henkel and W. Hochstetter, 1865

Araucarites Presl 1838

Araucarites alatisquamosus sp. nov. Ohsawa et H. Nishida. Figures 2A(2)–2A(6).

HOLOTYPE: SGO.PB 1577, Museo Nacional de Historia Natural, Santiago, Chile.

PARATYPES: NSM PP-12151, NSM PP-12152, NSM PP-12153.

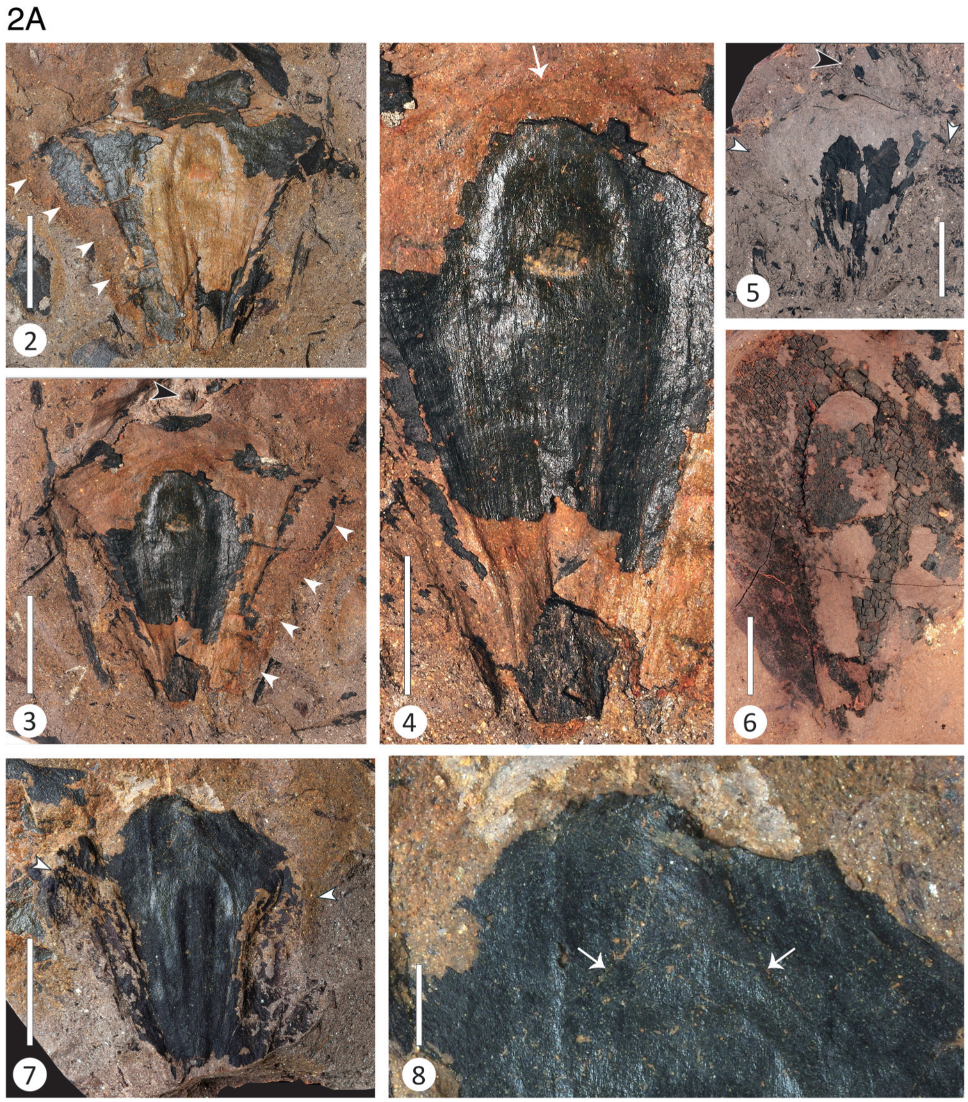
TYPE LOCALITY AND HORIZON: Loreto Formation, Río de Las Minas area near Punta Arenas, Magellan Region, Chile. Late Eocene – early Oligocene.

ETYMOLOGY: Species epithet, *alatisquamosus* originates from a Latin *alatus* for "winged" and *squamosus* for "scaly".

DIAGNOSIS: Fossil detached cone scales composed of cuneate bract, 32–33 mm long by 30–34 mm wide. Delicate wings expanded laterally up to 5–6 mm from each side of woody central zone of cone scale. Bract spine short, 3 mm long. Single oval seed embedded in ovuliferous scale, 18–24 mm long by 5–5.5 mm wide. Ovuliferous scale surrounding seed, oval, 7.6–8.0 mm at the widest portion. Ovuliferous scale tip rounded, about 2 mm from distal end of seed.

DESCRIPTION: Detached cone scales consist of a cuneate bract and an attached ovuliferous scale (Figs. 2A(2) and 2A(3)). The cone scale is winged, 32–33 mm long by 30–34 mm wide at the widest portion including lateral wings. The central part of the cone scale is woody and thick. The delicate wings, which are often degraded, expand laterally up to 5–6 mm on each side of the woody central zone. The bract has distal rounded corners from which it tapers to form a distinct shoulder, and terminates in a short apical spine up to 3 mm long (Figs. 2A(3) and 2A(5)). A single seed is embedded in the ovuliferous scale tissue (Figs. 2A(4) and 2A(6)). The seed is approximately 18–24 mm long by 5.0–5.5 mm wide, and broadest near the distal end, sometimes represented by a circular imprint (Fig. 2A(4)). The ovuliferous scale, 7.6–8.0 mm at widest portion, surrounds the seed, and its tip is rounded (Fig. 2A(4)).

Fig. 2A. ***Araucarites alatisquamosus*** sp. nov. (2–6). (2) Cone scale of holotype specimen. White arrowheads on the left indicate the edge of lateral wing. The right hand side of the structure was not preserved. SGO.PB 1577a. Scale bar = 10 mm. (3) Counter part of Fig. 2. White arrowheads on the right indicate the edge of lateral wing. Black arrowhead points to the apex of scale, the lower portion of which was curved and not preserved. SGO.PB 1577b. Scale bar = 10 mm. (4) Close-up of (3) showing seed with circular imprint and ovuliferous scale (white arrow). Scale bar = 5 mm. (5) Cone scale of paratype specimen. Black arrowhead indicates the apex of the scale. Two white arrowheads indicate distal rounded corner of scale. NSM PP-12152. Scale bar = 10 mm. (6) Close-up of a paratype specimen showing seed and ovuliferous scale. NSM PP-12153. Scale bar = 5 mm. **Fig. 2A**. (7 and 8) *Araucarites* sp. (7) Cone scale. Two white arrowheads indicate distal rounded corner of scale. NSM PP-12154. Scale bar = 5 mm. (8) Close-up of cone scale in (7), showing the triangular tip of ovuliferous scale (white arrows). NSM PP-12154. Scale bar = 2 mm. [Colour online.]



COMPARISONS: The cone scale described here is closely similar to *Araucaria* because of its woody, winged bracts, free ovuliferous scale tip, with a single seed embedded in ovuliferous scale tissue, which is retained at maturity (Stockey 1982). *Araucarites* was designated as representing araucarian seed cones and cone scales by Zijlstra et al. (2000), and the isolated cone scales with araucarian affinities have been assigned to *Araucarites* (Zijlstra et al. 2000). Thus we assigned our specimen to *Araucarites* Presl. ***Araucarites alatisquamosus*** sp. nov. is characterized by its large size, prominent but fragile lateral wings that are narrower than the main seed body, and ovuliferous scale that has a rounded tip. In the genus *Araucaria*, the ovuliferous scale is vestigial in section *Araucaria* (van der Ham et al. 2010). *Araucarites alatisquamosus* differs from cone scales of section *Araucaria* by having prominent wings. The cone scales of section *Bunya* are characterized by thick and rigid lateral wings and a prominent woody tip of the ovuliferous scale (van der Ham et al. 2010). The lateral wings of *Araucarites alatisquamosus* are thin and delicate in contrast to those of section *Bunya*. The cone scales of section *Intermedia* are relatively large, with a narrow central woody portion and broad papery wings that are broader than the central woody portion (Wilde and Eames 1948; van der Ham et al. 2010). *Araucarites alatisquamosus* is composed of a relatively wide central woody portion and prominent lateral wings that are narrower than the central woody portion. In these features, *Araucarites alatisquamosus* is most similar to the cone scales of section *Eutacta*.

A large number of fossil araucarian cones have been described worldwide. They are assigned to either *Araucarites* or *Araucaria* (Stockey 1994; Kunzmann 2007). In South America and the Antarctic Peninsula, many species are described from the Jurassic to the Eocene (Panti et al. 2012). Among the described species, *Araucaria pichileufulensis*, *Araucarites baqueroensis*, *A. antarcticus* (Gee) Birkenmajer et Ociepa (2008) from the Jurassic of Antarctica, *A. chilensis*, *A. citadelbastionensis* Cantrill and Falcon-Lang (2001) from the Albian of Alexander Island, *A. minimus*, and *A. phillipsi* Carruthers (1869) are characterized by prominent lateral wings. Of these, *A. antarcticus*, *A. chilensis*, *A. citadelbastionensis*, *A. minimus*, and *A. phillipsi* are much smaller than our new species. *Araucaria pichileufulensis* and *Araucarites baqueroensis* are most closely comparable with our new species, sharing large cone scales with prominent lateral wings. *Araucaria pichileufulensis* was established based on leafy shoots and isolated cone scales. The cone scales are kite-shaped with broad lateral wings, 27.5 mm long × 30 mm wide including lateral wings. *Araucaria pichileufulensis* is distinguished from *Araucarites alatisquamosus* by having a prominent triangular tip rather than a rounded tip on the ovuliferous scale and its slightly smaller size. *Araucarites baqueroensis* is represented by isolated cone scales 20–30 mm long × 20 mm wide. Seeds are 10–15 mm × 4–5 mm, and embedded in the ovuliferous scale with a rounded tip (Archangelsky 1966). Cone scales of *Araucarites alatisquamosus* are much larger than those of *A. baqueroensis*.

Araucarites sp. (Figs. 2A(7) and 2A(8)).

MATERIAL STUDIED: NSM PP-12154.

NOTE: The fossil is a detached cone scale consisting of a cuneate bract and an attached ovuliferous scale (Fig. 2A(7)). The cone scale is 12 mm long × 12 mm wide at the widest point including the lateral wings. The central part of the cone scale is woody and thick. Delicate wings expand laterally up to 3 mm on each side of the woody portion of the bract. The bract has distal rounded corners from which it tapers to form a distinct shoulder. The apical spine is not preserved in the specimen we observed. The seed is long and oval, 7.6 mm long × 1.6 mm wide, and is broadest near the distal end (Fig. 2A(7)). The free ovuliferous scale tip is distinct, triangular, and 1.8 mm long × 2.8 mm wide at base (Fig. 2A(8)).

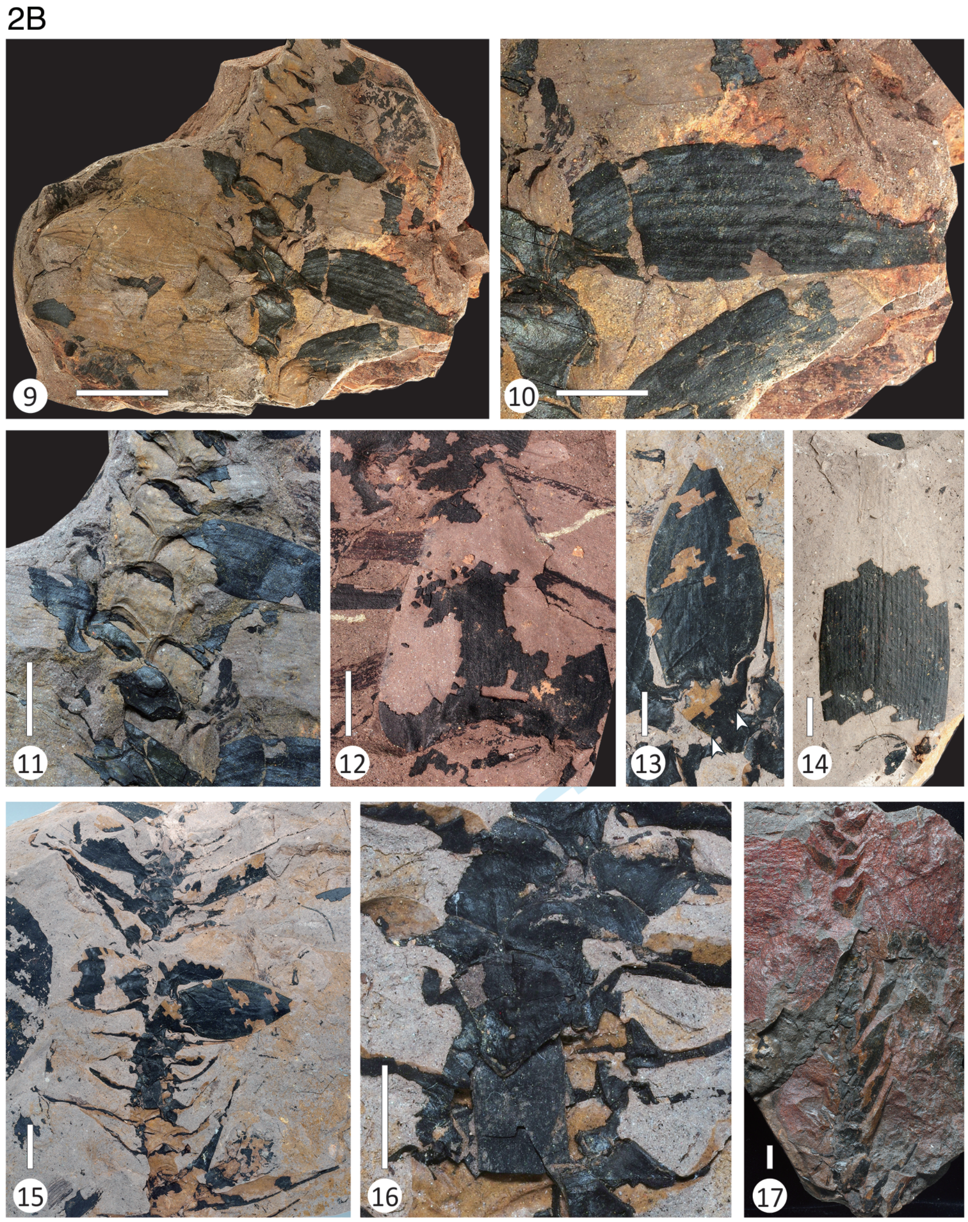
COMPARISONS: *Araucarites* sp. is characterized by prominent lateral wings and a triangular ovuliferous scale tip. As is the case with *Araucarites alatisquamosus*, this *Araucarites* sp. is similar to the cone scales of section *Eutacta*. Besides the smaller size, *Araucarites* sp. differs from *A. alatisquamosus* in the presence of a triangular ovuliferous scale tip. Among the *Araucarites* species described from South America and the Antarctic Peninsula, *A. antarcticus*, *A. chilensis*, *A. citadelbastionensis*, *A. minimus*, and *A. phillipsi* Carruthers (1869) are characterized by small size and prominent lateral wings. However, cone scales of *A. minimus* and *A. phillipsi* are much smaller than those of the *Araucarites* sp. described here, and do not have the triangular ovuliferous scale tip (Archangelsky 1966; Arrondo and Petriella 1980). Cone scales of *Araucarites antarcticus* are slightly larger than those of *Araucarites* sp., and the seed is broad-oval in outline (Birkenmajer and Ociepa 2008), in contrast to the elongate oval seed of *Araucarites* sp., *Araucarites chilensis* has cone scales as long as those of the *Araucarites* sp. described here. However, its lateral wings are not as wide as those of the *Araucarites* sp., and the cone scale is no more than 8 mm wide (Baldoni 1979) instead of the 12 mm in *Araucarites* sp. The *Araucarites* sp. described here closely resembles *A. citadelbastionensis* in size, and in having broad wings and triangular ovuliferous scale tip. Considering that *A. citadelbastionensis* is described from the Lower Cretaceous (as opposed to the late Eocene – early Oligocene) of Coal Nunatak, Alexander Island, Antarctica, the *Araucarites* sp. cone scales may represent a different species. However, it is premature to conclude whether or not *Araucarites* sp. is conspecific with *A. citadelbastionensis* until further information has been compiled for our *Araucarites* sp.

Araucarian leaves

Araucaria nathorstii was described by Dusén for impression/compression shoots and leaves from the same locality and formation as our specimens (Dusén 1899). Specimens used for the original description show great variation in form, and Dusén (1899) described them as "Blätter der sterilen Zweige (leaves of sterile shoot)" and "Blätter der fertilen Zweige (leaves of fertile shoot)". Leaves of his sterile shoots are lanceolate with fine longitudinal ridges (Dusén 1899, Plate XII, fig. 3), while those of the fertile shoots are ovate, broadly lanceolate or sometimes almost triangular with dense longitudinal ridges (Dusén 1899, Plate XII, figs. 4–10). However, one leaf specimen of his fertile shoot (Dusén 1899, Plate XII, figs. 11 and 12) is smaller and has sparse longitudinal ridges. In our specimens, we distinguished three leaf types, some attached on shoots. These are a narrow type comparable to the vegetative-shoot leaves of Dusén, a broad type comparable with the fertile-shoot leaves, and a smaller type similar to the small fertile-shoot leaf with sparse ridges. The smaller type is quite different from the two forms of *A. nathorstii*, and we conclude that it should be distinguished from *A. nathorstii*. Here we report the narrow and the broad types of *A. nathorstii*, and a new leafy shoot that we describe as *Araucaria* sp.

Araucaria nathorstii Dusén 1899 (Figs. 2B(9)–2C(26)).

Fig. 2B. *Araucaria nathorstii*. (9–17). (9) Shoot of narrow type. NSM PP-12155. Scale bar = 10 mm. (10) Leaf of narrow type. NSM PP-12155. Scale bar = 4 mm. (11) Close-up of stem showing leaf scars. NSM PP-12155. Scale bar = 4 mm. (12) Isolated leaf of broad type with triangular outline. NSM PP-12158. Scale bar = 4 mm. (13) Ovate leaf attached to the stem. White arrowheads indicate position of leaf attachment. NSM PP-12156. Scale bar = 5 mm. (14) Isolated leaf of broad type with ovate outline. NSM PP-12161. Scale bar = 5 mm. (15) Shoot of broad type. NSM PP-12156. Scale bar = 10 mm. (16) Close-up of stem showing leaf scars. NSM PP-12156. Scale bar = 5 mm. (17) Shoot of broad type. NSM PP-12157. Scale bar = 10 mm. [Colour online.]



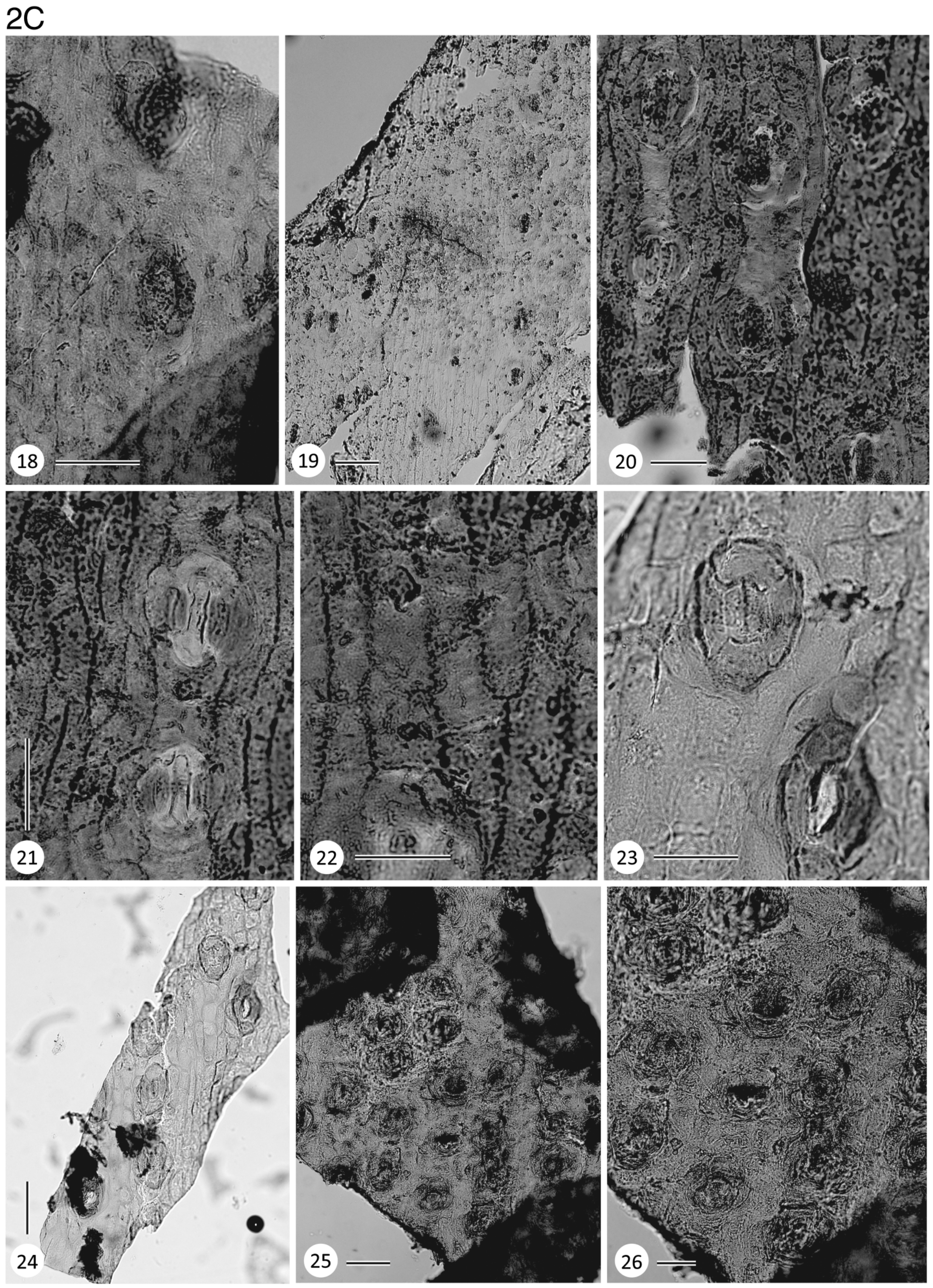
MATERIALS STUDIED: narrow type, NSM PP-12155; broad type, NSM PP-12156, NSM PP-12157, NSM PP-12158, NSM PP-12159, NSM PP-12160, NSM PP-12161, NSM PP-12162, NSM PP-12163, NSM PP-12164.

Notes on leaf types

NARROW TYPE LEAVES: (Figs. 2B(9)–2B(11), 2C(18)–2C(22)): One isolated shoot, up to 55 mm in width (Fig. 2B(9)), is identified as the narrow-type of *A. nathorstii*. The stem is 8 mm in diameter and shows rhomboidal and slightly curved scars 3.7–4.4 mm in horizontal and 3.0–3.8 mm in vertical dimensions (Figs. 2B(9) and 2B(11)). The shoot bears densely packed imbricate leaves (Fig. 2B(9)). The leaves are lanceolate, flat and not keeled, with an acute apex and a decurrent base (Fig. 2B(10)), 23–31 mm long by 6.5–8.1 mm wide at the widest point, tapering to the base, but not dramatically contracted at the very base. The leaf has entire margins and 7–9 longitudinal ridges, which probably correspond to the positions of veins.

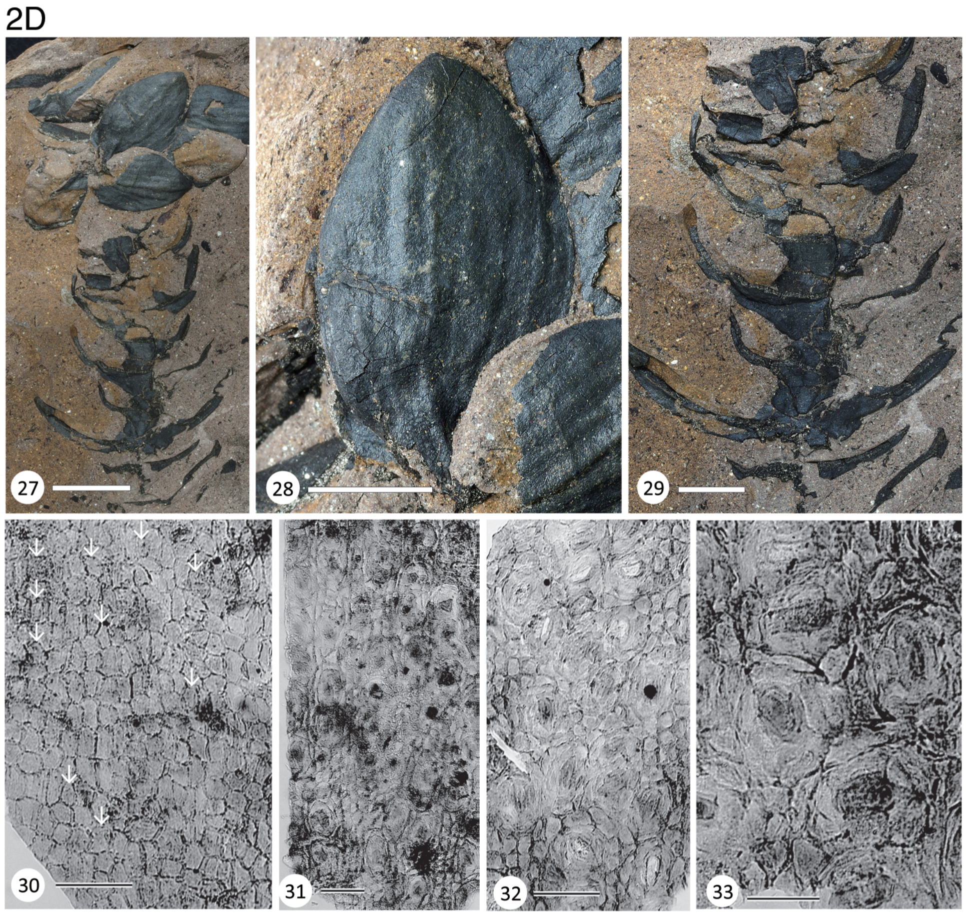
These leaves are amphistomatic, but stomata are sparse on the adaxial cuticle, where the epidermis is composed of mostly elongate rectangular cells (Fig. 2C(18)). The stomata are rare and arranged in indistinct rows. In

Fig. 2C. Cuticle of *Araucaria nathorstii* Dusén. (18–26). (18) Stomata of adaxial cuticle, showing four subsidiary cells. NSM PP-12155. Scale bar = 50 μm. (19) Abaxial cuticle, showing elongate rectangular normal cells and regular stomatal rows. NSM PP-12155. Scale bar = 100 μm. (20) Details of stomatal rows of abaxial cuticle. Stomatal apparatus in same row separated by 1–2 regular epidermal cells. NSM PP-12155. Scale bar = 50 μm. (21) Stomata in abaxial cuticle showing four subsidiary cells. NSM PP-12155. Scale bar = 50 μm. (22) Sinuous anticlinal walls of abaxial epidermal cells. NSM PP-12155. Scale bar = 50 μm. (23) Stomata of adaxial cuticle, and four subsidiary cells. NSM PP-12164. Scale bar = 50 μm. (24) Adaxial cuticle, showing three stomatal rows. Stomatal rows separated by 3–5 rows of elongate rectangular cells. NSM PP-12164. Scale bar = 100 μm. (25) Abaxial cuticle, showing stomatal rows, with stomata of variable orientation. NSM PP-12164. Scale bar = 100 μm. (26) Close-up of (25). Stomatal apparatus monocyclic, with 4–6 subsidiary cells. NSM PP-12164. Scale bar = 50 μm.



the abaxial cuticle, stomata are arranged in regular rows with the apertures orientated almost parallel to the leaf axis (Figs. 2C(19) and 2C(20)). The stomatal apparatus is elliptical, monocyclic and usually has four subsidiary cells (Figs. 2C(20) and 2C(21)). Stomata in the same row are separated by 1–2 rectangular epidermal cells. Interstomatal bands consist of 1–5 rows of elongate rectangular cells, excepting certain broad bands up to 15 cells wide. Anticlinal walls of the epidermis are obviously sinuous (Fig. 2C(22)).

Fig. 2D. *Araucaria* sp. (27–33). (27) Shoot and leaves. NSM PP-12166 a,b. Scale bar = 10 mm. (28) Close-up of (27), showing leaf. NSM PP-12166a. Scale bar = 5 mm. (29) Close-up of (27), showing sections of expanding leaves. NSM PP-12166b. Scale bar = 5 mm. (30) Adaxial cuticle consisting of quadrangular to irregular epidermal cells and few stomata (white arrowhead). Not all the stomata are recognized owing to poor preservation. NSM PP-12165. Scale bar = 100 μm. (31) Abaxial cuticle, showing irregular rows of stomata, separated by 1–3 rows of irregular or rectangular epidermal cells. NSM PP-12166. Scale bar = 100 μm. (32) Abaxial cuticle showing variably oriented stomatal apparatus. NSM PP-12165. Scale bar = 100 μm. (33) Close-up of (32), showing four subsidiary cells. NSM PP-12165. Scale bar = 50 μm. [Colour online.]



BROAD TYPE LEAVES: (Figs. 2B(12)–2B(17), 2C(23)–2C(26)): Several compressed shoots and isolated leaves are identified as the broad-type of *A. nathorstii*. The shoot is up to 60 mm wide, with the stem 9 mm in diameter (Figs. 2B(15)–2B(17)). The stem shows rhomboidal and slightly curved scars more than 6 mm in horizontal and 4.5–5.3 mm in vertical dimensions (Fig. 2B(16)). The shoot bears densely packed imbricate leaves. The leaves diverge at 55–72 degrees from the stem axis, and are ovate, concave, and not keeled, with an entire margin, an acute apex, and a decurrent base (Figs. 2B(12)–2B(14)), and are 28–40 mm long by 13–20 mm wide at the widest portion. The leaf base is narrower than the widest part, 9–13 mm wide, and not contracted. The leaves exhibit 25–30 dense vertical ridges, which probably correspond to vein positions or stomatal lines.

These wide leaves are amphistomatic. In adaxial cuticle, stomata are arranged mostly in regular rows with the apertures orientated almost parallel to the leaf axis (Figs. 2C(23) and 2C(24)). The stomatal apparatus is elliptical, monocyclic, and composed of mostly four but up to six subsidiary cells (Fig. 2C(23)). Stomata in the same row are separated by 1–2 rectangular epidermal cells. Interstomatal bands consist of 3–5 rows of elongate rectangular cells. The abaxial cuticle shows irregular rows of more densely aggregated stomata with the apertures orientated mostly parallel to, but sometimes oblique or perpendicular to the leaf axis (Figs. 2C(25) and 2C(26)). The stomatal apparatus is similar in morphology to that of the other cuticle observed. Stomata of the same row are usually continuous and (or) sometimes separated by 1–2 epidermal cells. Adjacent stomatal rows are separated by 1–2 rows of rectangular cells. Anticlinal walls of epidermal cells are usually smooth and not sinuous.

Araucaria sp. (Figs. 2D(27)–2D(33))

MATERIALS STUDIED: NSM PP-12165, NSM PP-12166.

NOTE: Two compressed shoots (NSM PP-12165 and NSM PP-12166) are 20–22 mm wide (Figs. 2D(27) and 2D(29)). Leaves resemble the small leaf of Dúsen's fertile branch of *A. nathorstii* (Dusén 1899, Plate XII, figs. 11 and 12). The shoot bears densely packed imbricate leaves. The leaves are ovate, appressed, concave, and have 7–9 rows of abaxial longitudinal ridges possibly corresponding to the internal leaf veins (Fig. 2D(28)). They are not keeled, but the middle ridge looks thicker than the lateral ones (Fig. 2D(27)). The leaf apex is obtuse and the base is decurrent. The leaves are entire, 11–13 mm long × 6–7 mm wide at the widest part. The leaf base is broad 2.5 mm wide.

The leaves of *Araucaria* sp. described here are amphistomatic, but the stomata are scarce on one adaxial cuticle, where the epidermis is composed of quadrangular to irregular cells (Fig. 2D(30)). On the abaxial cuticle (Figs. 2D(31) and 2D(32)), stomata are arranged in irregular rows with the apertures orientated in varying directions to the leaf axis. The stomatal apparatus is elliptical, monocyclic, and composed of mostly four but up to six subsidiary cells (Fig. 2D(33)). Stomata of the same row are separated by 1–3 irregular epidermal cells. Adjacent stomatal rows are separated by 1–3 rows of irregular or rectangular cells. Anticlinal walls of epidermal cells are sometimes slightly sinuous.

Discussion

Araucaria nathorstii was described by Dusén (1899) from the same locality where we made field collections. The narrow type described here is comparable with Dusén's sterile shoot, and the broad type with his fertile shoot. The broad type is the most typical form of *A. nathorstii* which subsequently has been described widely from southern South America and the Antarctic Peninsula (Berry 1928; Doktor et al. 1996; Fiori 1939; Hünicken 1995; Menéndez and Caccavari 1966; Panti et al. 2007; Troncoso 1986). The leaf of *Araucaria* sp. in this study is not identical with any of the leaves assigned to *A. nathorstii*, except a small leaf figured in the original description as one of the forms from a fertile *A. nathorstii* shoot.

In extant araucarian species, leaves often become dimorphic, with individuals displaying differences between the leaves produced by plants at juvenile and adult stages (de Laubenfels 1972; Stockey 1982), and in many cases the juvenile forms exhibit markedly narrower leaves (Farjon 2010). In *A. bidwillii* Hook and *A. angustifolia* (Bertol.) Kuntze, leaves vary a lot in length and width according to branch positions (Farjon 2010). Thus, the two leaf types of *A. nathorstii* might represent leaves of different growth stages or of leaves borne in different positions within the tree architecture. However, *Araucaria* sp. described here is quite different from other two types in having an obtuse apex and frequent stomata whose apertures are rather irregularly orientated with respect to the leaf axis, and probably deserves to be separated as a separate taxon.

Araucaria nathorstii has been assigned to section *Araucaria* based on gross morphology and cuticle characters (Dusén 1899; Menéndez and Caccavari 1966). The gross morphology of the narrow and broad leaf types of our specimens are congruent with those of the leaves of section *Araucaria*. Although *A. nathorstii* is attributable to section *Araucaria*, the absence of cone scales comparable with that section has yet to be fully explained.

On the other hand, the obtuse leaf apex and oblique or perpendicular orientation of stomata of this *Araucaria* sp. do not conform to what is expected for sections *Bunya*, *Intermedia*, or *Araucaria* (Stockey and Ko 1986). Frequent stomata oriented obliquely or perpendicular to the leaf axis are characteristic of section *Eutacta* (Stockey and Ko 1986), and some species of section *Eutacta* have adult leaves with an obtuse apex (Farjon 2010). Thus, this *Araucaria* sp. could be assigned to section *Eutacta*. Two types of *Araucarites* reported here are also similar to cone scales of section *Eutacta* in having thin lateral extensions. The co-occurrence of shoots and cone scales similar to section *Eutacta* suggests the presence of the section in southernmost South America until the late Eocene or earliest Oligocene.

Alternatively, it would also be possible that the features compared here to characterize *Eutacta* are plesiomorphic in genus *Araucaria* or its extinct stem group. Combined cladistics analysis of Araucariaceae by Escapa and Catalano (2013) clarified monophyly of *Eutacta*. Although only fossil permineralized cones were used for their analysis, they revealed 5 of 62 scored characters as unambiguous synapomorphies of the section. Among the five characters none were related to cone scales, but three were of leaves (No. 8, 45, and 47 in their score sheet). The leaves of *Araucaria* sp. described here share character 45 (rhomboidal or tetragonal leaves) and 47 (curved leaf apex). The lack of specimens showing cone-scale/shoot attachment and the absence of unambiguous synapomorphies for *Eutacta* cone scales bring up the possibility that our specimens could represent an extinct basal lineage or a stem lineage between section *Eutacta* and other sections. In either case, however, it is certain that the extant section *Eutacta* is a remnant of an *Eutacta*-like group, which would have been widely distributed in the Southern Hemisphere before the earliest Oligocene. Some reports of Cenozoic *Eutacta* from Australia and New Zealand emphasize a need of more extensive analysis including a wide range of fossil information to reconstruct the phylogeny and biogeography of *Eutacta* as well as the whole family (Hill and Bigwood 1987; Pole 2008).

The fossil record of section *Eutacta* is not abundant from the Paleogene or later of South America. It has been suggested that the fossil record of section *Eutacta* in South America may extend up to the Miocene, based on a leafy twig of *Araucaria* sp. from Matanzas, VI Región, Chile, which was assigned to section *Eutacta* based on external similarity to extant *Araucaria heterophylla* (Troncoso and Romero 1993). Precise description of the Matanzas specimen including cuticular anatomy, however, is required to confirm this as a representative of section *Eutacta* in South America.

Araucaria pichileufuensis from the Eocene of the Ventana Formation of Río Pichileufú, Río Negro, Argentina, is based on separate cone scales and leafy twigs (Berry 1938). Cone scales of *A. pichileufuensis* show prominent lateral wings characteristic of section *Eutacta*. However, the leaves of that species are acute, triangular, falcate, and thick, about 7 mm long × 2.5 mm in maximum width, and show intermediate characters between those of sections *Eutacta* and *Araucaria* (Berry 1938). The Ventana Formation, from which *A. pichileufuensis* originates, is dated as about 47.5 Ma by $^{40}Ar/^{39}Ar$ dating (Wilf et al. 2005); whereas, the Loreto Formation of Las Minas is dated about 36.5 Ma by U–Th–Pb dating (Otero et al. 2012). Thus, the araucarian remains from Río de Las Minas are younger than those from Río Pichileufú, and they are the youngest fossil record of the section *Eutacta* in South America. Our study reveals the co-occurrence of the relatives of sections *Araucaria* and *Eutacta* in Patagonia during the Eocene to early Oligocene, suggesting a wider distribution of section *Eutacta* or its stem group, and greater diversity of genus *Araucaria* in South America and the Antarctic regions during the Paleogene.

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