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ABSTRACT

Premise of the study — The iconic conifer genus Araucaria, found worldwide during the Mesozoic, now has a relict, disjunct distribution between South America (two species) and Australasia (18 species). Australasian Araucaria Section Eutacta is the most diverse clade with 16 species, all but two of them endemic to New Caledonia. Fossils with affinities to Sect. Eutacta, with first appearances in the Jurassic, usually are represented by single dispersed organs, making it difficult to diagnose the section and test the generally post-Gondwanan (~20-25 Ma) molecular estimates of its crown age. Araucaria fossils thought to belong to Sect. Eutacta are abundant in early and middle Eocene Argentine caldera-lake deposits from Laguna del Hunco (~52.2 Ma) and Río Pichileufú (~47.7 Ma). The Laguna del Hunco flora was deposited during the Early Eocene Climatic Optimum, and the Río Pichileufú flora is from the earliest middle Eocene, deposited during the initial opening of the Drake Passage and start of climatic cooling. Araucaria pichileufensis Berry 1938 from Río Pichileufú was described as a member of Sect. Eutacta and later reported from Laguna del Hunco. Although there is increasing evidence of angiosperm species turnover between these floras, apparently related to decreasing rainfall, the diverse conifers found at Laguna del Hunco and Río Pichileufú are thought to represent the same set of species. However, the relationship of A. pichileufensis to Sect. Eutacta and the conspecificity of the Araucaria material among these floras have not been tested using modern methods.

Methods — We describe the type material of A. pichileufensis alongside large (n = 192) new fossil collections of Araucaria from Laguna del Hunco and Río Pichileufú, including the multi-organ preservation of Araucaria leafy branches, cuticle, ovuliferous
complexes, and pollen cones with in-situ pollen. We use a total evidence phylogenetic analysis to test for the nearest living relatives of the fossils.

**Key Results** — We improve the whole-plant concept for *Araucaria pichileufensis* at Río Pichileufú and recognize a new *Araucaria* species from Laguna del Hunco. Taxonomic analysis of characters, including those of an attached terminal pollen cone discovered from Río Pichileufú, establishes a relationship of both species to Sect. *Eutacta*. *Araucaria pichileufensis* resolves in the stem of Sect. *Eutacta*, and A. new species resolves in the crown of Sect. *Eutacta*, within the New Caledonian clade. The phylogenetic placement of both Eocene species within Sect. *Eutacta* confirms the taxonomic treatment, indicates the presence and survival of this group in Patagonia during initial separation from Antarctica, and adds to the Gondwanan connection of Patagonian fossil floras to Australasia.

**Conclusions** — The *Araucaria* fossils described here comprise one of the most complete representations of fossil *Eutacta* in the world, and they predate the molecular age estimates for the crown of the clade by ~30 million years. The differentiation of two *Araucaria* species is the first direct evidence of a change in the abundant conifer species between Laguna del Hunco and Río Pichileufú, adding to the signal of turnover between the two floras during the climate change and movement of landmasses that occurred from the Early Eocene Climatic Optimum to the earliest middle Eocene.

**Key Words** — *Araucaria*; Araucariaceae; conifers; EECO; Eocene; Laguna del Hunco; Patagonia; rainforest; Río Pichileufú; total evidence phylogeny
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PREFACE

This thesis is a manuscript intended for submission to the American Journal of Botany and is formatted for that journal. The manuscript includes three coauthors: Peter Wilf (Pennsylvania State University), and Ignacio Escapa and Ana Andruchow-Colombo (CONICET - Museo Paleontológico Egidio Feruglio, Trelew, Argentina). Peter Wilf participated in the taxonomic description, contributed feedback on drafts, provided funding for the project, and led nearly all the field trips resulting in the new collections. Ignacio Escapa participated in the taxonomic and phylogenetic analysis and provided the fossils from Museo Paleontológico Egidio Feruglio for study as the curator. Ana Andruchow-Colombo participated in the study of the fossil cuticle and phylogenetic analysis.
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recommendations expressed in this publication are those of the author and do not necessarily reflect the views of the National Science Foundation.
INTRODUCTION

Southern conifers are known for their diversity, ancient history, and dominant role in humid forests (Hill and Brodribb, 1999; McLoughlin, 2001; Archangelsky and Del Fueyo, 2010). Compared to angiosperms, the southern conifers occupy different ecological niches and are distinctive in their longevity, slow growth rates, and resilience to climate change (Enright and Ogden, 1995). The final breakup of Gondwana formed isolated biomes surrounded by oceans, resulting in warm, wet conditions that had a profound influence on the evolution and biogeography of southern conifers (Hill and Brodribb, 1999; McLoughlin, 2001; Archangelsky and Del Fueyo, 2010; Leslie et al., 2012; Kooyman et al., 2014). Differential evolutionary dynamics of Southern conifer lineages may be driven by the ratio of landmasses to ocean areas in the Northern versus Southern Hemispheres (Leslie et al., 2012). The well-documented fossil records of Australia and New Zealand trace the detailed history of the conifer lineages of those landmasses (e.g., Cookson and Pike, 1953; Hill, 1995; Pole, 1997, 1998, 2007, 2008; Hill and Brodribb, 1999; Brodribb and Hill, 2004), and southern South America also has an exceptional fossil record essential to the understanding of conifer evolution (e.g. Florin, 1940; Stockey, 1977; Archangelsky and del Fueyo, 1989; Villar de Seaone, 1998; Del Fueyo and Archangelsky, 2002; Escapa et al., 2008; Panti et al., 2012; Escapa and Leslie, 2017; Andrucho-Colombo et al., 2018). Of interest here, Eocene Patagonian fossil floras show the impact of South American isolation and climate change on the evolution and distribution of conifer genera.

Conifers previously described from well-studied Eocene fossil caldera lake deposits of Laguna del Hunco (~52.2 Ma), Chubut, Argentina, and Río Pichileufú (~47.7
Ma), Río Negro, Argentina (Figure 1), illustrate a biogeographic history of eastern (Australasian) and western (American) survival (Kooymen et al., 2014) after the separation of landmasses. *Papuacedrus* H.L.Li (Cupressaceae; Wilf et al., 2009), *Dacrycarpus* (Endl.) de Laub. (Podocarpaceae; Wilf, 2012), and *Agathis* Salisb. (Araucariaceae; Wilf et al., 2014) are conifer components of the Patagonian fossil floras, but today these genera are restricted to Australasia. Meanwhile, abundant *Retrophyllum* C.N.Page (Podocarpaceae; Wilf et al., 2017b) and *Araucaria* Juss. (Araucariaceae; Berry, 1938) from these fossil floras are examples of conifer genera that are extant in both South America and Australasia. Non-conifer fossil taxa also show evidence of the former Gondwanan connection of South America to Australasia (Zamaloa et al., 2006; Gandolfo et al., 2011; Carvalho et al., 2013; Knight and Wilf, 2013; Carpenter et al., 2014; Gandolfo and Hermsen, 2017; Wilf et al. 2019). More broadly, patterns of western survival are present as well; some Australian fossil taxa have living relatives that are only found in South America today (Barnes et al., 2001; Hill and Paull, 2003; Paull and Hill, 2008).

**Geological context**— The survival patterns of the taxa in the Eocene Laguna del Hunco and Río Pichileufú floras are related to their deposition during critical intervals of global climatic and tectonic change. Laguna del Hunco is a highly diverse 52.2 Ma Gondwanan flora from the Early Eocene Climatic Optimum (EECO), the longest period of sustained warmth in the Cenozoic (~53-49 Ma; Zachos et al., 2001; Lauretano et al., 2018). In the greenhouse world, the westernmost edge of a frost-free, trans-Antarctic mesothermal rainforest biome reached into southern South America via a close connection between Patagonia and Antarctica (Wilf et al., 2009, 2013; Wilf, 2012;
Kooyman et al., 2014). The highly diverse 47.7 Ma early middle Eocene Río Pichileufú flora (Berry, 1925; Wilf et al., 2005; Wilf, 2012) was present in Patagonia during a period of initial climatic cooling and drying following the EECO (Pearson et al., 2007; Hollis et al., 2012; Bijl et al., 2013) when the earliest separation of South America and Antarctica was underway (Lawver et al., 2011). Comparison of the Laguna del Hunco and Río Pichileufú floras as a whole (see Table 1) yields evidence of some turnover in the angiosperms, suggesting a shift in the paleoenvironment (Wilf et al., 2013, 2019); however, until now there has been no detection of a significant change in species composition of the prevalent conifers between the two localities. Further investigation of the *Araucaria* species from the Laguna del Hunco and Río Pichileufú floras may provide new evidence for turnover and survival of the iconic southern conifer lineage between the early and middle Eocene.

**Araucariaceae fossil record**—The family Araucariaceae includes the genera *Araucaria, Agathis,* and *Wollemia* Jones, Hill & Allen. Within Araucariaceae, two sister clades are recognized and widely accepted through phylogenetic analyses based on morphological data and molecular sequences (Gilmore and Hill, 1997; Stefanovic et al., 1998; Kunzmann, 2007; Liu et al., 2009; Leslie et al., 2012; Escapa and Catalano, 2013; Escapa et al., 2018): *Araucaria,* and the agathoid clade, comprised of the sister genera *Agathis* and *Wollemia.* In comparison with *Araucaria,* the agathoid clade is less completely represented in the fossil record but does include the Early Cretaceous anatomically preserved seed cones of the stem agathiods *Emwadea microcarpa* Dettman, Clifford & Peters and *Wairarapaia mildenhalli* Cantrill & Raine from Australia and New Zealand, respectively (Cantrill and Raine, 2006; Macphail, 2007; Dettmann et al., 2012;
Macphail et al., 2013). Although once limited to occurrences in Australasia (Chambers et al., 1998; Hill et al., 2008; Pole, 2008; Jordan et al., 2011), fossil Agathis species are now known with multiple organ preservation from the early Paleocene (Escapa et al., 2018) and the early and middle Eocene (Wilf et al., 2014) of Patagonia, including Agathis zamunerae of the Laguna del Hunco and Río Pichileufú floras. Of the family, Wollemia has the most elusive fossil record, with no reliable fossils (Chambers et al., 1998).

*Araucaria* has a famously rich fossil history worldwide that contrasts with the genus’ modern, fragmented southern range (Stockey, 1982, 1994; Hill and Brodribb, 1999; Kershaw and Wagstaff, 2001; Panti et al., 2012; Kooymen et al., 2014). During the Mesozoic, *Araucaria* was most diverse and was present throughout the northern and southern hemispheres (Stockey, 1982, 1994; Kunzmann, 2007). The oldest definitive fossil occurrence is *Araucaria mirabilis* (Spegazzini) Windhausen, which has petrified ovuliferous cones with exceptional preservation of ovules, embryos, and seeds from Middle Jurassic (172-162 my; Pankhurst et al., 2000) deposits of the La Matilde Formation, Cerro Alto, Santa Cruz, Argentina (Spegazzini, 1924; Windhausen, 1931; Stockey, 1975, 1978). After the Mesozoic, possibly as a result of southern preferential survival following the Cretaceous-Paleogene mass extinction event, the range of *Araucaria* contracted to the Southern Hemisphere (Kunzmann, 2007; Wilf et al., 2013).

*Araucaria* macrofossils from the Cenozoic are known from Chile, Argentina, Antarctica, Australia, and New Zealand (Berry, 1938; Cookson and Duigan, 1951; Hill, 1990; Pole, 1992; Troncoso and Romero, 1993; Hill and Brodribb, 1999; Panti et al., 2012; Ohsawa et al., 2016; Shi et al., 2018).
**Living Araucaria**—*Araucaria* has a disjunct distribution and includes 20 species (Farjon, 2010; Mill et al., 2017). Section *Eutacta* accounts for most of the diversity within *Araucaria*, with 16 Australasian species. With the exceptions of *A. heterophylla* (Salisb.) Franco (Norfolk Island, Australia) and *A. cunninghamii* Mudie (Australia and New Guinea), Section *Eutacta* is confined to the island of New Caledonia (de Laubenfels, 1972, 1988; Farjon, 2010). Some molecular phylogenetic studies have weakly resolved relationships within Sect. *Eutacta* due to the genetic similarity of the New Caledonian taxa (Setoguchi et al., 1998; Stefenon et al., 2006), which are inferred to have diversified recently following the re-emergence of the island ca. 37 Ma (Aitchison et al., 1995; Pelletier, 2007). Subsequent studies split the New Caledonian *Eutacta* into three clades that respectively correspond phenotypically to large-leaved species, small-leaved coastal species, and small-leaved interior species (Gaudeul et al., 2012; Escapa and Catalano, 2013; Ruhsam et al., 2015). Section *Bunya* is represented by a single Australian species, *A. bidwilli* Hook, and Section *Intermedia* is limited to *A. hunsteinii* K. Schum., a single species in Papua New Guinea (de Laubenfels, 1988; Farjon, 2010).

*Araucaria* Section *Araucaria* is the only non-Australasian group, with two South American species, *A. araucana* (Molina) K. Koch (southern Argentina and Chile) and *A. angustifolia* (Bertol.) Kuntze (northern Argentina, Brazil, and Paraguay; Farjon, 2010).

*Araucaria* trees are often dominant and emergent in moist temperate, subtropical, and tropical angiosperm-conifer forests, so they are often thought to indicate fossil rainforests (Kershaw and Wagstaff, 2001). However, extant *Araucaria* have a wider range of moisture tolerances than many of the other southern conifers, and they are better adapted to drought compared to *Wollemia* (Baker et al., 2015). Sect. *Araucaria* occupies
subtropical to temperate-antarctic floral zones in South America (Golte, 1993). In the Andes, *Araucaria araucana* grows in seasonally wet and dry seasons in a transition zone between a Mediterranean climate to the north and a more temperate and cool climate to the south (Farjon, 2010). New Caledonian Sect. *Eutacta* is adapted to grow in very nutrient poor ultramafic to calcareous substrates, ranging from sea level to high altitudes, and is found either in dense, humid forests or maquis shrublands (Farjon, 2010; Gaudeul et al., 2012). *Araucaria cunninghamii* in New South Wales and Queensland, Australia, is the most dry-adapted of the *Eutacta* lineage, ranging into drier areas of subtropical and warm temperate rainforests, and is most common in dry vine forests and thickets with rainfall between 630-1100 mm (Enright, 1995; Harden, 2006). In contrast, the *A. cunninghamii* var. *papuana* Lauterb. in New Guinea is found in lower to upper montane forests (Enright, 1995; Farjon, 2010) with average annual rainfall of about 1400–5700 mm (Gray, 1973).

*Araucaria* species are large, monoecious (rarely dioecious: Sect. *Araucaria*) evergreen trees that are recognizable for their characteristic candelabra-shaped, pyramidal, or columnar crowns (Farjon, 2010). The sections of *Araucaria* are separated based on distinct morphological differences among the leaves, pollen cones, ovuliferous complexes, and germination modes (Endlicher, 1847; Florin, 1931; Wilde and Eames, 1952; Stockey, 1982; Stockey and Ko, 1986), and the sections have also been confirmed as monophyletic in molecular studies (Setoguchi et al., 1998; Escapa and Catalano, 2013). The leaves are spirally arranged on branches and can be monomorphic (Sects. *Araucaria* and *Bunya*) or differentiated into juvenile and adult forms in Sections *Intermedia* and *Eutacta* (Wilde and Eames, 1952; de Laubenfels, 1972, 1988; Farjon,
2010). In section *Eutacta*, juvenile leaves are acicular, straight or falcate, and spreading (Fig. 2A, 2F), whereas adult leaves are broad, imbricate, adpressed, and incurving (Fig. 2C, 2H; de Laubenfels, 1953, 1972, 1988; Farjon, 2010). In *Eutacta*, an intermediate stage between the dimorphic leaf forms is common (Fig. 2B, 2G); as the leaves mature, they generally grow wider while maintaining the same profile (de Laubenfels, 1953). Bud scales or terminal buds are absent in the genus *Araucaria*, and the apex of a leafy branch consists of a cluster of incompletely formed leaves (Fig. 2C; de Laubenfels, 1988).

Leaves are multi-veined (Sects. *Araucaria*, *Bunya*, and *Intermedia*) or univeined (Sect. *Eutacta*), entire or very slightly toothed, and amphistomatic (Wilde and Eames, 1952; de Laubenfels, 1972; Stockey and Ko, 1986; de Laubenfels, 1988; Farjon, 2010). Stomata lack Florin rings, and cuticular features such as stomatal orientation, size, and the number of subsidiary cells are also diagnostic for the sections and species (Florin, 1931; Stockey and Taylor, 1978; Stockey and Ko, 1986).

*Araucaria* pollen cones are subtended by a cluster of sterile basal bracts, which are modified leaves that are triangular with pointed apices and emerge directly at the base and overlap the cone body (Fig. 2E; Farjon, 2010). The pollen cones are usually erect and linear initially, curving after shedding pollen, and the size range of pollen cones varies by species. *Eutacta* is the only section with terminal pollen cones (Fig. 2C; de Laubenfels, 1988), which are axillary in the other sections. The seed cones of *Araucaria* consist of hundreds of spirally arranged, overlapping ovuliferous complexes (Fig. 2I). When mature, the seed cones shatter and disperse the individual ovuliferous complexes (Fig. 2J), which consist of the bract, scale, and seed. Seed cones are terminal in Sect. *Eutacta* and axillary in the other sections. The ovuliferous complex shape varies by species and within a single
cone can vary in size depending on the position within the cone. Ovuliferous complexes have a single embedded seed in the center, often extend laterally as thin to woody wings, and have a narrow spine that projects above the convex thickened apical margin, termed the apophysis (Fig. 2J, K). Scales are partially fused with the bract, and the scale apex terminates in a free tip, termed a ligule, which is distal to the seed and reaches the apophysis (Fig. 2K; de Laubenfels, 1988). There is usually one ovule per scale, and the seed coat is fused with the scale (de Laubenfels, 1988). Sect. Araucaria has large, dense, nut-like ovuliferous complexes that lack wings; Sect. Intermedia has large, thin, samara-like ovuliferous complexes; and Sect. Bunya has thick, woody ovuliferous complexes and is the only section with a large, round, dehiscent seed (Wilde and Eames, 1952; Farjon, 2010). As shown in Figure 2J, Sect. Eutacta has small, samara-like ovuliferous complexes, with broad lateral bract margins that are thin and papery (de Laubenfels, 1988).

Molecular age and biogeographic origins of Araucaria—The molecular age estimates of the divergence of Araucariaceae and its clades are at odds with the rich fossil record (Biffin et al., 2010; Crisp and Cook, 2011; Leslie et al., 2012; Escapa and Catalano, 2013; Escapa et al., 2018). Despite the widely accepted fossil evidence of Araucaria from the Middle Jurassic, including the famous petrified seed cones of Araucaria mirabilis, molecular clock estimates generally suggest that the living genera within Araucariaceae radiated during the Late Cretaceous to Cenozoic (Biffin et al., 2010; Crisp and Cook, 2011; Kranitz et al., 2014). The young molecular age estimates for the family led to the interpretation of the numerous Jurassic and Early Cretaceous records of Araucaria as stem lineages, rather than members of the crown genus (Biffin et al.,
2010; Crisp and Cook, 2011; Escapa and Catalano 2013). However, the Early Cretaceous fossil records of agathioid clade members *Emwadea microcarpa* and *Wairarapaia mildenhalli*, combined with the substantial Jurassic fossil record of *Araucaria* (Stockey, 1994; Cantrill and Raine, 2006; Kunzmann, 2007; Dettmann et al., 2012), indicate that both sister lineages of Araucariaceae were present by the Albian. Therefore, the fossil record shows a minimum age of the Araucariaceae crown as Albian (113-100.5 Ma; Escapa et al., 2018), compared with the molecular estimates of ca. 36 Ma (Crisp and Cook, 2011), ca. 65 Ma (Biffin et al., 2010), or ca. 138-60 Ma (Kranitz et al., 2014).

A Mesozoic age of Araucariaceae has further implications for the molecular age estimates of the internal nodes within *Araucaria*, which are also frequently at odds with the fossil record. The molecular estimates of the crown age of Sect. *Eutacta* have usually been calculated as post-Gondwanan, placed at ca. 20 Ma (Biffin et al., 2010), ca. 22.8 Ma (Leslie et al., 2012), or between ca. 51 and ca. 9 Ma (Kranitz et al., 2014). Still, an ovuliferous complex from the Lower Jurassic of Massachusetts (ca. 190 Ma; Axsmith et al., 2008) may be a possible first occurrence of Sect. *Eutacta* and could represent a minimum age of the lineage. Kranitz et al. (2014) reported that using the Lower Jurassic *Eutacta* scale to date the node for the crown of either the family, the genus, or *Eutacta* gave implausible results that exceeded the age of the oldest known land plants. Not only is the selection of well-dated fossils with confident assignments to Araucariaceae and its clades critical to obtaining more harmonious age estimates, but attention to the selection of the nodes the fossils are used to calibrate and the methodology used for calibration should also be under scrutiny (Bromham, 2003; Magallón, 2004; Gandolfo et al., 2008; Ho and Phillips, 2009; Sauquet et al., 2012; Magallón, 2014; Wilf and Escapa, 2015).
The biogeographic origins of Sect. *Eutacta*, and more broadly the floras of the whole Southern Hemisphere, in the context of overwater dispersal vs. vicariance are debated (Pole, 2001; Sanmartín and Ronquist, 2004; Sanmartín et al., 2006; Waters and Craw, 2006; Gaudeul et al., 2012, 2014; Kranitz et al., 2014; Wilf and Escapa, 2015). The young molecular age estimates align with long-distance dispersal as the dominant pattern, implying that most extant lineages evolved after the separation of Gondwana and were later dispersed over water to expand their ranges (Crisp and Cook, 2009, 2013). In contrast, the fossil record often supports the idea that vicariance and continental movement, rather than dispersal, was a central mechanism in the biogeography and evolution of Southern Hemisphere plants; fossil ages provide direct evidence that many southern lineages, including some southern conifers, evolved in Gondwana prior to the separation of landmasses (as summarized by Wilf and Escapa, 2015).

The post-Gondwanan molecular ages of *Araucaria* Sect. *Eutacta* and the idea of long-distance dispersal need to be tested using Gondwanan fossils with potential affinities to *Eutacta*. Section *Eutacta* is thought to be one of the oldest sections of the genus and was once found worldwide (Stockey, 1982; Axsmith et al., 2008). Mesozoic fossils attributed to *Eutacta* are frequently based on isolated ovuliferous complexes (i.e., Seward, 1903; Archangelsky, 1966; Bose and Maheshwari, 1973; Pole, 1995; Cantrill and Falcon-Lang, 2001; van der Ham et al., 2010), which usually cannot diagnose the lineage with confidence. When multiple organs are recovered from Mesozoic localities and considered together, mosaic evolution has been observed; for example, the late Cretaceous *A. lefipanensis* Andruchow Colombo, Escapa, Cúneo & Gandolfo exhibits *Eutacta*-like ovuliferous complexes but has broad, multi-veined foliage that is most
similar to the other three sections of *Araucaria* (Andrucho-Colombo et al., 2018). Stockey (1994) suggested that rapid evolutionary rates during the Mesozoic could account for the apparent mosaic of characters within a fossil species and difficulty in assigning fossils to the living sections. Two fossil species described from isolated foliage with preserved cuticular features from the Lower Cretaceous of Australia are some of the only Mesozoic leaves confidently assigned to *Eutacta* (Cantrill, 1992; Stockey, 1994). However, the three other Cretaceous species with *Eutacta*-like foliage described by Cantrill (1992) exhibit mosaic evolution with cuticular characters common among *Eutacta*, the other sections of *Araucaria*, and even *Agathis* (Stockey, 1994). The oldest, most complete Mesozoic record that is likely to represent *Eutacta* with multi-organ preservation includes small, terminal pollen cones on leafy twigs (*Brachyphyllum mamillare* Lindley & Hutton) and ovuliferous complexes (*Araucarites phillipsii* Carruthers) from the Jurassic of Yorkshire, UK (Kendall, 1949; Harris, 1979). Associated foliage and pollen cones (questionably assigned to *Brachyphyllum feistmantelii* (Halle) Sahni) and ovuliferous complexes (*Araucarites chilensis* Baldoni) that bear similarities to *Eutacta* are also known from the Jurassic-Cretaceous boundary interval in Argentina (Baldoni, 1979). Even with multi-organ preservation, there is still no consensus on whether the Jurassic fossils are assignable to either the stem or crown group of Sect. *Eutacta* (Stockey, 1994; Leslie et al., 2012).

The majority of Cenozoic fossil records of *Araucaria* Sect. *Eutacta* from Australia, New Zealand, Antarctica, and South America are also reported based on single organ preservation, such as an isolated ovuliferous complex, leafy branch, or dispersed cuticle specimen (Table 2). Although their affinities to the section are more reliable than
the Mesozoic fossils due to better preservation, the lack of multiple organs still makes it
difficult to be certain of a fossil’s phylogenetic position with respect to the stem or crown
Coal Seam of Australia (Cookson and Duigan, 1951), is one of the only Cenozoic
*Eutacta* species that includes three-organ preservation of ovuliferous complexes, leaves,
and a fragment of a pollen cone.

**Araucaria pichileufensis**—Of interest here, the Río Pichileufú site from the early
middle Eocene of Río Negro, Argentina is the type locality for *Araucaria pichileufensis*,
initially described based on one ovuliferous complex and five leafy branch fossils (Berry,
1938). Berry (1938) noted the probable relationship of *A. pichileufensis* to Sect. *Eutacta*
based on the characters of the ovuliferous complexes and thought that the leafy branches
most resembled either Australian *A. heterophylla* or New Caledonian *A. columnaris* (J.R.
Forst.) Hook (both Sect. *Eutacta*). Florin (1940) agreed with Berry’s interpretation of the
characters of the ovuliferous complexes, but he found the leafy branch morphologies of
*A. pichileufensis* to be most comparable with *A. columnaris*, *A. subulata* Vieill. (New
Caledonia), and *A. cunninghamii* (Australia and New Guinea; all three are extant species
of Sect. *Eutacta*).

Modern excavations at Río Pichileufú (Wilf et al., 2005, 2017b) have significantly
increased the sampling of *A. pichileufensis*, including the discovery of previously
undescribed pollen cones (fossil material shown in Figs. 3-10). The discoveries of a
pollen cone attached to a leafy branch, in situ fossil pollen, and fossil leaf cuticle increase
the number of characters that can be used to diagnose the fossils to a living section of
*Araucaria*. The use of a total evidence phylogeny has the potential to further test
affinities to Sect. *Eutacta* suggested in the early 20th century (Berry, 1938; Florin, 1940). Notably, fossil *Araucaria* from Laguna del Hunco, which has never been formally studied, is also thought to represent *A. pichileufensis* in the absence of any previously observed differences among this material. The Laguna del Hunco *Araucaria* fossil material also includes preservation of leafy branches, ovuliferous complexes, and pollen cones (Wilf et al., 2005, 2014, 2017b).

This paper will (1) investigate whether modern taxonomic treatment and new fossil material of *Araucaria pichileufensis* supports identification to Section *Eutacta*; (2) test the conspecificity of the *Araucaria* fossils from Laguna del Hunco and Río Pichileufú; and (3) evaluate the systematic placement of the fossils within the *Araucaria* clade using a total evidence phylogenetic analysis. We will also explore the implications of these results for the biogeographic history of *Araucaria* Sect. *Eutacta* and for floral turnover in Patagonia in the context of the isolation of South America and global cooling.
MATERIALS AND METHODS

Localities— The Araucaria pichileufensis fossils presented here are found at Río Pichileufú, Río Negro, Argentina, and fossils of Araucaria new species are found at Laguna del Hunco, Chubut, Argentina. Both the Río Pichileufú and Laguna del Hunco localities are fossiliferous caldera lake deposits of the Eocene La Huitrera Formation (Petersen, 1946; Aragón and Romero, 1984; Aragón and Mazzoni, 1997; Iannelli et al., 2017). Berry initially interpreted the two sites to be Miocene in age and similar in species composition (Berry, 1925, 1938). Over the past two decades, significant field collections have resulted in numerous revisions and descriptions of fossil plants, insects, ichnotaxa, and vertebrates from Río Pichileufú and Laguna del Hunco, summarized previously (Wilf et al., 2009, 2013, 2014). Paleomagnetic stratigraphy at Laguna del Hunco revealed two paleomagnetic reversals within the 170 meters of section, and three tuffs that interbed the 28 fossil quarries have been radiometrically dated (Wilf et al., 2003, 2005; Wilf 2012). At Laguna del Hunco, abundant Araucaria fossils are found above and below volcanic ash 2211A, which yields sanidine crystals with an $^{40}$Ar-$^{39}$Ar age of 52.22± 0.22 Ma (Wilf et al., 2005, 2017a). The other two ashes produce similar ages, so the working age for the Laguna del Hunco flora is 52.2 Ma (early Eocene, Ypresian; Wilf et al., 2017a). A. new species is found in quarries LH2, LH4, LH6, LH13, LH15, LH20, LH22, LH23, LH25, LH27, LH28, LH29, and LH30 (Wilf et al., 2003, 2005; Gandolfo et al., 2011; new quarries from the 2019 field season include LH30, which is at the same level as LH6, and LH29, which is in the lower section, close to LH13). A. new species is most abundant in the LH13 and LH27 quarries (see Systematics section).
At Río Pichileufú, three tuffs containing sanidines produced concordant $^{40}\text{Ar} - ^{39}\text{Ar}$ ages, resulting in a combined age of $47.74 \pm 0.05$ Ma (Wilf et al., 2005, Wilf 2012); these tuffs are located just above the fossiliferous strata, which include abundant Araucaria fossils. The age of the Río Pichileufú flora is thus most likely earliest middle Eocene (Ypresian/Lutetian boundary is 47.8 Ma, as updated at www.stratigraphy.org; Gradstein et al., 2012). The Araucaria pichileufensis fossils reported here were found at quarries RP1–3 (Wilf et al., 2005), and at a new quarry from the 2017 field season, RP4, which is at the same stratigraphic level as RP3.

Laguna del Hunco and Río Pichileufú are both highly diverse, angiosperm-dominated floras with more than 100 species found at each locality (Wilf et al., 2005). Many taxa from these floras that have been recently described or assessed (Table 1) have nearest living relatives in Australasian, southeast Asian, South American, and African subtropical and montane tropical rainforests (e.g., Barreda et al. 2010; Barreda et al. 2012; Wilf et al., 2014). The paleoenvironments of Eocene Laguna del Hunco and Río Pichileufú are interpreted as mesothermal rainforests from southern middle paleolatitudes of ca. 46–47°S (Morley, 2000; Wilf et al., 2005, 2013). Elevated species richness from these floras is probably linked to aseasonal rainfall and frost-free winters at the time (Wilf et al., 2009).

Modern systematic work on the floras to identify taxonomic affinities of specimens from the large new collections and to reassess the original affinities put forth by Berry (1925, 1938) has also led to the comparison of species from Laguna del Hunco and Río Pichileufú. Table 1 summarizes the taxa that have been studied systematically in
recent years, or can otherwise be considered reliable, and their presence and absence between the two localities. Many of the tropical to subtropical angiosperm genera whose living relatives are found in Australasia and Southeast Asia are found at Laguna del Hunco but not present at Río Pichileufú (Wilf et al., 2013), for example, *Eucalyptus* L'Hér. (Myrtaceae; Gandolfo et al., 2011), *Gymnostoma* L.A.S.Johnson (Casuarinaceae; Zamaloa et al., 2006), *Castanopsis* (D.Don) Spach (Fagaceae; Wilf et al., 2019), and several others (Table 1). In addition to the numerous angiosperms found only at Laguna del Hunco, there is no record of the fern *Todea amissa* or the cycad *Austrozamia stockeyi* at Río Pichileufú (Carvalho et al., 2013; Wilf et al., 2016). The disappearance of taxa that prefer warm and everwet environments in Patagonia by ~47.7 Mya may demonstrate a critical turning point in the character of the flora that could be correlated to the first stages of opening of the Drake Passage and climatic cooling and drying by Río Pichileufú time. Still, some angiosperms are known from both Laguna del Hunco and Río Pichileufú, including *Atherospermophyllum guinazui* (Knight and Wilf, 2013) and some species of proteaceous leaves (González et al. 2007).

Gymnosperms have a higher survival rate than angiosperms between Laguna del Hunco and Río Pichileufú. *Ginkgoites patagonicus* and a high diversity of rainforest conifers are present at both localities, including species of *Acmopyle* Pilg., *Podocarpus* L’Hér. ex Pers., *Agathis*, *Papuacedrus*, *Dacrycarpus*, *Retrophyllum*, and *Araucaria* Section *Eutacta*, studied here (as summarized by Wilf et al., 2017b). The newly described *Huncocladus laubenfelsi*, an extinct podocarp related to *Phyllocladus* represented by a single specimen from Laguna del Hunco (Andruchow-Colombo et al., 2019), is the only Laguna del Hunco conifer taxon that is not present at Río Pichileufú. Otherwise, the
conifers are thought to be congruent at species level between the two localities; however, that interpretation may be biased by the smaller sample size and less complete representation of fossil organs at Río Pichileufú (Wilf et al., 2017b). Although the conifer diversity is almost consistent across the sites, most conifers are less abundant at Río Pichileufú than Laguna del Hunco (Table 1). Among the conifers present at Río Pichileufú and Laguna del Hunco, most require high moisture, subtropical to tropical rainforest environments today (Brodribb and Hill, 1998, 2004; Brodribb, 2011; Wilf et al., 2009, 2014, 2017b; Wilf, 2012); however, some extant Australasian Araucaria species are relatively drought-tolerant, such as A. cunninghamii (Sect. Eutacta), which thrives in the dry rainforests of Australia (Enright, 1995; Harden, 2006; Baker et al., 2015).

**Fossil repositories, preparation, and imaging** — The historic Río Pichileufú type and cohort collections of Araucaria pichileufensis (Berry 1938) discussed here are housed at the Paleobotanical Division of the Smithsonian Institution, National Museum of Natural History (USNM). The remainder of the Patagonian fossils reported here were collected during expeditions based out of the Museo Paleontológico Egidio Feruglio (MEF, Trelew, Chubut, Argentina; repository acronym MPEF-Pb) from 1999-2019 and the Museo Paleontológico de Bariloche (BAR, San Carlos de Bariloche, Río Negro, Argentina) in 2017. The total collection of fossil Araucaria analyzed here includes 136 specimens from Laguna del Hunco and 56 specimens from Río Pichileufú. Fossils collected since 2002 from Río Pichileufú are housed at BAR and the fossils collected since 1999 from Laguna del Hunco are housed at MEF.

Type and cohort Araucaria pichileufensis collections (26 specimens) were loaned from the USNM to be examined at the Paleobotany Laboratory, Pennsylvania State
University (PSU). Material from BAR was loaned to MEF, and the rest of the collections were prepared, imaged, and analyzed at MEF. Preparation of fossils to remove extraneous matrix was done using airscribes in the laboratory. Macroimages were taken using a Nikon D90 camera with 60 mm macro lens (Nikon, Melville, New York, USA), a polarizing filter, and low angle light. Fossils were also extensively examined using reflected light microscopy (at MEF, Nikon Eclipse 50i compound microscope; at PSU, Nikon Eclipse LV100 compound microscope and Nikon SMZ-1500 binocular scope), and images of fine details and cellular details were taken using an attached camera (at MEF, Nikon DSFi3 with an L4 control unit; at PSU, Nikon DS-Ri1 and NIS Elements BR software). For observation of fossil cuticle and pollen, a Nikon C-SHG1 epifluorescence illumination unit was used on the MEF Eclipse microscope, and an X-Cite 120 epifluorescence illumination unit (EXFO Electro-Optical Engineering, Quebec City, Quebec, Canada) was used on the PSU Eclipse microscope and camera set up. Images of multiple depths of field were stacked using Adobe Photoshop CC (version 20.0.1; Adobe Inc., San Jose, California, USA). Images were loaded into Photoshop as layers, and Photoshop tools Auto-Align and Auto-Blend were used to create the stacked images. For composite photos that did not fit in one field of view, overlapping lateral image panels were combined into a single image using the Photomerge tool in Photoshop.

Cuticle from Laguna del Hunco was coalified, so attempts were made with both bleach (NaClO 5%) and chromium trioxide (CrO$_3$ 20%) to remove coal and expose underlying cuticle. Chemical treatments were performed after separating in situ cuticle fragments from the fossils with tweezers and were performed in situ in a well created with modeling clay to avoid cuticle fragmentation during removal. The cuticle treatments
were unsuccessful, but it was still possible to make in situ observations of the unprepared cuticle using epifluorescence.

Pollen was observed in situ in a single *Araucaria pichileufensis* cone specimen from Río Pichileufú. Because there are only three pollen cone specimens from the locality, and we did not want to destroy the specimen, separation of pollen from the cone for analysis under SEM was not attempted for this study. Observation of the pollen in situ was sufficient to observe the characters needed for the analysis.

**Extant material** — Living *Araucaria* Sect. *Eutacta* collections were examined, vouchered, and photographed from the Montgomery Botanical Center, Coral Gables, Florida, and vouchers are deposited at the Pennsylvania State University Herbarium (PAC; see Appendix A). In addition to the new collections, extant *Araucaria* species were examined and photographed, using the same macrophotography methods as above, from herbarium collections at the Harvard University Herbaria (HUH, Boston, Massachusetts, USA) and The Huntington Library, Art Collections, and Botanical Gardens (HNT, San Marino, California, USA). The late D. J. de Laubenfels donated part of his research collection to HNT in 2010. High-resolution images of herbarium sheets were also accessed online from Muséum National d’Histoire Naturelle, Paris (P; http://science.mnhn.fr/institution/mnhn/collection/p/item/search/form).

All images of fossil and herbarium specimens were annotated and organized using common keywords in Adobe Bridge CC (version 9.0.1.216; San Jose, California, USA) to allow for comparison of a unified set of morphological characters (after Wilf et al. 2017b). Full-resolution images of fossil specimens are deposited open-access at FigShare (doi: 10.6084/m9.figshare.c.4494374). Depending on the completeness of the specimens,
measurements of ovuliferous complexes included overall maximum width and position, total length, base width, central body maximum width and position, seed length, seed width and position, and spine length. For the leafy branches, the central axis width, total branch length and width, leaf length and height in profile view, leaf angle in profile view, leaf length and width in abaxial view, and leaf scar maximum length and width were measured when preserved. Pollen cone length and width, basal bract length and width, and microsporophyll length and width were measured. For the length of curved pollen cone specimens, measurements were estimated by a straight line from base to apex and found to be similar to lengths estimated by segmenting along the cone length.

Measurements of fossils were made virtually on scaled photographs using Adobe Photoshop and tested on specimens with calipers. *Araucaria* species taxonomy follows Farjon (2010), de Laubenfels (1974, 1988), and Mill et al. (2017).

**Phylogenetic analysis**— The two Eocene *Araucaria* species in this study were analyzed phylogenetically using a total evidence approach and a previously published matrix revised here (Escapa and Catalano, 2013; Escapa et al., 2018). This approach simultaneously combines (1) a morphological matrix for an ingroup composed of 32 living and 12 fossil species of Araucariaceae, including the two fossils analyzed here for the first time, and (2) a molecular dataset for the 32 living ingroup species and an outgroup of 306 species from the other five extant conifer families (Podocarpaceae, Sciadopiceae, Cupressaceae, Taxaceae, and Pinaceae). The morphological matrix comprises 53 discrete characters and 10 continuous characters (standardized in TNT during the analysis, using methods established by Goloboff et al., 2006), listed in Appendix B. Molecular data assembled by Escapa and Catalano (2013) and Escapa et al.
(2018) using GenBank to TNT (Goloboff and Catalano, 2012) includes 23 genomic regions, including plastid (16s, rbcl, matK, nadhF, nadhB, accD, atpB, atpF, nadhJ, psbB, psbD, psbE-psbJ, rpoB, rpl2, rpoC1, rps4, trnD-trnT, psbA-trnH, and rps12), nuclear (18S, 26S), and mitochondrial genomes (atpI, coxI). The complete Escapa et al. (2018) dataset can be downloaded online as their appendix S1 from the American Journal of Botany, and the edited morphological matrix used in the present analyses, including the scores for the two new fossil species analyzed here, is available in Appendix C and D of this thesis.

The fossils were first removed from the combined matrix to test the methodology on only the extant taxa; then fossils were included. Combined phylogenetic analyses of the dataset were run using equally weighted parsimony in TNT (Goloboff and Catalano, 2016). The analysis was run using Sectorial Search, Drift, and Tree Fusing, and the minimum length was found 30 times. Then, tree bisection-reconnection was used, and the strict consensus tree was calculated. The consensus tree was bootstrapped (standard sampling with replacement) for 500 replicates using absolute frequencies to show group support. Group support was also tested using jackknifing for absolute frequencies, with an independent probability of character removal of 0.36.

Support values are not reported for the resulting strict consensus tree. The addition of fossils to the analyses introduces uncoded characters, including the lack of genetic data and many morphologic characters that are not preserved in fossils, which lowers the overall support of the tree. The molecular-only support values were nearly identical to previous results for major clades, and as in similar prior studies the support values were much lower when fossils were included (Escapa and Catalano 2013; Escapa
et al. 2018). Within the historically problematic New Caledonian *Eutacta* clade, low support values are expected for the phylogeny, with or without the inclusion of fossils, due to the known genetic and morphologic similarities of the clade. Despite the low support values, including the fossils in the analysis resulted in the same topology for *Araucaria* that was found for the molecular-only phylogeny.
SYSTEMATICS

*Family*—Araucariaceae J. B. Henkel & W. Hochstetter, Synopsis der Nadelhölzer: xvii (1865).

*Genus*—*Araucaria* de Jussieu, Genera Plantarum: 413 (1789).

*Species*—*Araucaria pichileufensis* E.W. Berry, Geological Society of America Special Paper 12: 59 (1938).

*Lectotype, here designated*—USNM 40383e (Fig. 7A; Berry 1938: plate 11, figure 1), from the historic locality of Río Pichileufú, La Huitrera Formation, earliest middle Eocene, Río Negro Province, Argentina, exact collecting location unknown.

*Syntypes*—USNM 40383a (Fig. 3G; Berry 1938, pl. 11, fig. 5), USNM 40383b (Berry 1938: pl. 11, fig. 2), USNM 40383d (Fig. 3H; Berry 1938, pl. 11, fig. 6), USNM 40383f (Berry 1938, pl. 11, fig. 4), USNM 545203-545207, 545209-545222 (not figured by Berry; Fig. 3A, 3B; see Remarks). The syntype USNM 40383c (Berry 1938, pl. 11, fig. 3) is here excluded from the species.

*Other material here referred*—Río Pichileufú, La Huitrera Formation, middle Eocene, Río Negro Province, Argentina. Leafy branch segments of the subulate spreading leaf form: BAR 5608, 5612 (RP2); 5581 (RP3); 5576 (RP4); Leafy branch segments of the lanceolate adpressed form: BAR 5592, 5602 (RP2); 5579 (RP4); 4225, 5347 (unknown locality). Ovuliferous complexes: BAR 5591 (RP1); 5598 (RP2); 5580 (RP4); 4352 (unknown locality). Pollen cones: BAR 5618, 5619 (RP2); 5582 (RP4).
Emended description—Leafy branches (n=23; Fig. 3A-J) preserved as segments 2.5–25.3 cm long and 4.7–14.5 mm wide including foliage, ca. 0.6–1.9 mm wide without foliage. Leafy branch segments can be straight or slightly curved. The branch apex ends in a cluster of smaller, incompletely formed leaves (Fig. 3C, H; Fig. 5F).

Leaves are helically arranged and sessile. Individual leaves along the leafy branches are preserved either in a lateral profile view (Fig. 3A-E) or an abaxial view (Fig. 3G-J). Both views can occur on a single branch segment (Fig. 3E, F). The profile of the leaf in lateral view shows a combination of the abaxial and adaxial surfaces, which together approximates the height of the leaf. The abaxial view shows an approximation of the true width of the leaf, but the length is almost always underestimated due to imbrication obscuring the leaf base. Leaves are differentiated into longer, keeled, subulate spreading and shorter, adpressed lanceolate types and can vary continuously, or somewhat abruptly, in size and type along the branch segment (Fig. 3C, D, F). Leaf insertion angle measured on leaves preserved in lateral view varies from ca. 19–48°.

Subulate spreading foliage type (Fig. 3A-E): Leaves are divergent and spread from the branch at an average angle of ca. 33° (varies between 22–48°). Branches plus leaves with this foliage type are 8-14 mm wide. Leaf shape is subulate (awl-shaped; slender, but wider at base and tapering to a point). Seen in lateral view, leaves are abaxially keeled, varying from 3.3–10.2 mm long and 1.2–2.2 mm high, and vary between being somewhat linear (Fig. 3C-E, 5A) to slightly incurved (Fig. 3A, B). The leaf apex is acute and pointed. Leaves of the spreading type are usually only preserved in lateral view. Rhomboidal leaf scars along the branch are present where leaves have
broken off or detached (Fig 3E, MAPBAR 5576b) and measure ca. 1.8–2.6 mm wide and 0.9–3.6 mm long.

**Lanceolate adpressed foliage type** (Fig. 3F-J, 5B, F): Leaves are adpressed and densely packed on leafy branches that are 4.7–8.3 mm wide including the foliage. The angle of leaves to the branch is ca. 31° (varies between 19–32°). Leaf shape is lanceolate when viewed completely on the abaxial face and not covered by other leaves (Fig. 3F, G, I; Fig. 5B), and in lateral view, the leaves are recurved toward the central axis. In abaxial view, leaves are ca. 5 mm long (3.9–6.7 mm) and ca. 2.9 mm wide (2.2–4 mm). The apex is acute and incurved. Leaf scars (Fig. 5E) are ca. 2.3 mm wide (1.9–2.9 mm) and 2.4 mm long (2.1–2.7 mm).

**Cuticle remains** were observed on two specimens of the spreading foliage type as coaledified compressions. Stomata are arranged in parallel rows and mostly oriented parallel to the long axis of the leaf, with some oblique or perpendicular (Fig. 6E, F). Stomata are determined as amphistomatic based on fortunate preservation of stomata on a few adaxial leaf surfaces in addition to more easily observed abaxial surfaces (Fig. 6A). Stomatal apparatus, including subsidiary cells, are ca. 70 µm long and 60 µm wide. At least four subsidiary cells per stomate are observed, but the ability to differentiate cell wall locations between subsidiaries is limited by preservation quality. Guard cells are 25 µm long by 15 µm wide.

**Ovuliferous complexes** \((n=25; \text{Fig. 7A, C, E; Fig. 8A, C, E-H})\) are samara-like, with a central seed fused into the central body, surrounded on either side by broad lateral wings that are not always entirely preserved (Fig. 7E; Fig. 8A, G). The ovuliferous complex shape is broadly flabellate (fan-shaped), with a maximum width of ca. 28.9 mm
(23.4–33.4 mm) including the wing-like lateral extensions. The wings are bluntly rounded at the distal lateral margins. The average length of the ovuliferous complex is 24.6 mm (20.5–26.8 mm), and the position of the maximum width is ca. 50% of the total length (38–63%). The width of the base of the ovuliferous complex averages 9.4 mm (8.1–11.2 mm). The ovuliferous complex has a thickened central apical region, or apophysis, which projects in a convex triangular profile and ends in a ca. 2 mm long narrow tip or spine. The average maximum width at the apophysis is 15.4 mm (13.3–17.2 mm), and the maximum width of the apophysis is positioned at about 73% (59–80%) of the total length of the scale. A ligule is centered directly above the seed apex (Fig 8A, C, E). The ligule is long and triangular and is ca. 4.3–4.4 mm in length and 4.2–6.7 mm wide at its widest point. The apex of the ligule is located ca. 2 mm from the distal margin of the apophysis, where the spinose projection begins.

*Seeds* are inverted and embedded in the scale and are located in the center of the bract-scale complex. Seeds are obovate, narrowing to a point at the base, ca. 15.3 mm long and 6.4 mm wide at maximum width, located at ca. 73% of the total length of the seed. The base of the seed is ca. 2.3 mm (1.3–3.2 mm) from the base of the scale. Seeds are often striated (Fig 8A) and have amber casts within inferred resin duct locations (Fig. 8F, H).

*Pollen cones (n=3; Fig. 9A, B; Fig. 10A, C, F)* are terminal on leafy branches (Fig. 9A), solitary, cylindrical and often slightly curved, ending in a bluntly rounded apex. The one complete specimen (Fig. 9B) is 55 mm long and 7.4 mm wide; widths of the other specimens are 7.7 mm (Fig. 9A) and 8.3 mm (Fig. 10A). Terminal attachment is preserved on a single leafy branch (Fig. 9A). Basal bracts are longer and more triangular
than regular leaves, clustered and beginning immediately at the base of the cone body, and extending up to overlap the base of the cone body (Fig. 9B; 10A, F). The basal bracts are triangular, 6.4–8.6 mm long and 1.2–1.3 mm wide, and the apices are acute and pointed. Cuticle viewed on a basal bract of a pollen cone shows stomata oriented mostly parallel to the long axis of the bract (Fig. 10D), like the corresponding foliage. On a single preserved face of a cone (Fig. 10F), ca. 5-8 overlapping bracts are visible, suggesting that more than ten total were originally present around the entire base of the cone. Microsporophylls are helically arranged and imbricate. The microsporophyll laminae are peltate and rhombic with an acute, pointed apex, measuring ca. 1 mm by 1 mm (Fig. 10E). Stalks are not well preserved, and discernible pollen sacs are not preserved. Estimated number of microsporophylls per cone is ca. 800 (ca. 380 counted on a single face of the complete cone; Fig. 9B).

Pollen was found in situ in one pollen cone specimen (Fig. 10B, C). The pollen was observed in clumps along the microsporophyll stalks and inside the cone body under epifluorescence (Fig. 10B). The pollen grains are non-saccate, inaperturate, and spherical to sub-spherical, measuring about 60 by 55 µm (Fig. 10C). Due to the surrounding matrix and being observed in situ, it is not clear if the exine is sculptured or smooth.

Species—*Araucaria* (new species to be named) G. Rossetto, new species.

Etymology—(to be published with the formal naming of the species)

Holotype here designated—MPEF-Pb 10556 (Fig. 8B), ovuliferous complex from quarry LH27, Laguna del Hunco, Tufolitas Laguna del Hunco, La Huitrera Formation, early Eocene, northwest Chubut Province, Argentina.
**Paratypes**— Laguna del Hunco, Tufolitas Laguna del Hunco, La Huitrera Formation, early Eocene, northwest Chubut Province, Argentina. Leafy branch segments with acicular falcate foliage: MPEF-Pb 10589, 10593, 10594, 10596, 10597 (LH13); Leafy branch segments with ovate imbricate foliage: MPEF-Pb 10580, 10602 (LH6); 10605 (LH13); 10603 (LH22); 10606 (LH25); 10585, 10586, 10610, 10613, 10615 (LH27). Ovuliferous complexes: MPEF-Pb 10515 (LH6); 10533 (LH13); 10537, 10556, 10567, 10569 (LH27); 10531 (float). Pollen cones: MPEF-Pb 10617 (LH13); 10614, 10618 (LH27). Informal references to some of this material as *Araucaria pichileufensis* have appeared in several papers (e.g., Wilf et al., 2005, 2014).

**Diagnosis**— Leafy branches are dimorphic with acicular falcate and ovate imbricate foliage types, stomata perpendicularly oriented to the long axis of the leaf. Ovuliferous complexes are narrowly flabellate-cuneate, with narrow, angular lateral extensions and ratios of maximum length to width close to one. Ovuliferous complex apophysis is rounded, and the ligule is a short, broad triangle.

**Description**— Leafy branches (*n*=36; Fig. 4A-J) are long and slender, with preserved segments 9.3 mm–24.5 cm long, 5 mm–12.5 mm wide with foliage, ca. 0.9–2.4 mm wide without foliage.

Leaves are helically arranged and sessile. Leaves are preserved in lateral (Fig. 4A-E, G) and abaxial views (Fig. 4F, H-J). Leaves are differentiated into acicular falcate and ovate imbricate types.

*Acicular falcate foliage type* (Figs. 4A-D; 5C, I): Leaves falcate, acicular incurved, 4.3–8.2 mm long and 1.2–2.3 mm high. Apex acute and pointed. The angle of
the leaf to the branch is ca. 29° (18–37°), and leafy branches with this foliage type are 6–12.5 mm wide. Leaf scars are ca. 2.5-2.7 mm long and 1.9 to 2.4 mm wide.

**Ovate imbricate foliage type** (Fig. 4E-J: Leaves are imbricate and tightly adpressed, average angle of insertion is 29° (ranges between 12–50°), and leafy branches with this foliage type are 5–11 mm wide. Leaves are broadly ovate (Fig. 5D). Viewed laterally, leaves are strongly incurved apically, 2.3–5.7 mm long and 1.1–3 mm wide. In abaxial view, leaves are ca. 4.2 mm long (3.4–6.5 mm) and ca. 3 mm wide (2.5–4.8 mm). Apex is acute to broad and incurved. Leaf scars are on average 2.5 mm long by 2.6 mm wide (ranging from 2.2 to 2.7 mm long and 2.4–3.4 mm wide; Fig. 4F, J; Fig. 5H).

**Cuticle remains** (Fig. 6B-D, G, H). were observed on seven specimens of both foliage types. Stomata are arranged in parallel rows and oriented mostly perpendicular to the long axis of the leaf, with some parallel or oblique (Fig. 6G, H). Stomata are determined as amphistomatic based on preservation of stomata on several abaxial and adaxial leaf surfaces (Fig. 6B-D). Stomatal apparatus, including subsidiary cells, are ca. 80 µm long and 65 µm wide. The number of subsidiary cells is not distinguishable due to coalification. Guard cells are ca. 50 µm long by 30 µm wide.

**Ovuliferous complexes** (n=64; Fig. 7B, D, F; Fig. 8B, D, I-K) are samara-like, narrowly flabellate to cuneate, maximum width ca. 18.9 mm (13.9–33.9 mm) including narrow, symmetrical lateral extensions that are angular at the lateral distal margins, rather than rounded. The average length of the ovuliferous complexes is 18.1 mm (13.3–24.5 mm), and the position of maximum width is ca. 62% (46–73%) of the total length. Some stomata were observed on the wings of ovuliferous complex specimens (Fig. 8I, J); these stomata are oriented in rows and are mostly perpendicular to the long axis of the
ovuliferous complex, like the corresponding foliage. The guard cells range from ca. 60 to 65 µm in length and ca. 25 µm wide. Width of the base of the ovuliferous complexes averages 6.5 mm (3.3–9.9 mm). The ovuliferous complex has a thickened central apical region, or apophysis, which projects in a convex rounded profile and ends in a ca. 1.7 mm long narrow tip or spine. The average maximum width at the apophysis is 11.7 mm, positioned at ca. 79% (66–89%) of the length of the scale. The ligule is present ca. 0.7–1.3 mm above the seed, showing where the scale terminates in a free tip above the seed (Fig. 8B, D). The ligule is a broad, low triangle that is 0.6–1.9 mm in height and 3.3–5.3 mm wide. The ligule apex is ca. 0.3–0.7 mm from the distal margin of the apophysis where the spinose projection begins.

Seeds are inverted and embedded in the center of the ovuliferous complex. Seeds are obovate, ca. 12.3 mm long and 5.3 mm wide at maximum, at ca. 76% of the total length of the seed. The base of the seed is located ca. 2 mm (1.2–4.4 mm) from the base of the scale. Seeds are often striated (Fig. 7F, Fig. 8B, D, K).

Pollen cones (n=7; Fig. 9C, D; Fig. 10G, H) are cylindrical and often highly curved, all found isolated. A complete specimen (Fig. 9D) is 86 mm long and 8.8 mm wide, but incomplete specimens can reach >105 mm in length and range from ca. 7.5–10 mm wide (Figs. 9C, 10H). Leaf-like bracts are clustered at the base of the cone and extend up to overlap the base of the cone body for the entire length of the bract (Fig. 10G, H). Basal bracts are triangular, 9–12.5 mm long and 0.3–0.5 mm wide, and the apex is acute and pointed (Fig. 10G). On a single preserved face of a cone, ca. 4-5 bracts are visible, suggesting more than ten total were present on the entire cone (Fig. 10H). Microsporophylls are helically arranged, imbricate, peltate (Fig. 10E), with a rhombic
external face and acute pointed apex, the face ca. 2 mm long by 1.7 mm wide. Stalks are thin and reflexed basally (Fig. 9C). Pollen sacs are not preserved. Estimated number of microsporophylls per cone is ca. 900 (ca. 450 counted on a single face of the complete cone (Fig. 9D).

**Remarks**—*Araucaria pichileufensis* and A. new species are discussed here, explaining the reasoning for assignment of both fossil species to the family, genus, and section. We compare the two fossils with one another, to other fossils, and the living species.

*Araucaria pichileufensis* types—We chose the ovuliferous complex as the lectotype because it is the organ that bears the most characters that distinguish the species, including the overall broadly flabellate shape, the wide, rounded lateral extensions, and the triangular apophysis. We excluded one syntype USNM 40383c (Berry 1938, pl. 11, fig. 3) from the species because we re-identified that specimen as *Daecrycarpus puertae* due to its small, bilaterally flattened leaves deployed in a single plane; juvenile leaves of *Araucaria* Sect. *Eutacta* are acicular, tetragonal in cross-section, and never twisted into a horizontal plane (de Laubenfels, 1988). The listed nonfigured specimens are also considered as syntypes because they were part of the original gathering that was studied by Berry (1938), as shown by their identification tags in his handwriting, and reside as a cohort collection to the figured types at the USNM.

**Assignment to Araucariaceae**— The foliage of extant Araucariaceae is spirally arranged or opposite-decussate on the branches and can be needle-like, scaly, or broad (de Laubenfels, 1988). The foliage of both fossil species (Fig. 3-5), which is spirally arranged and needle-like to scaly, conforms to this range of morphologies. The
ovuliferous complexes from this family, as in the fossils (Fig. 7, 8), have a single inverted seed and a bract that is fused with the scale. The presence of isolated fossil ovuliferous complexes that vary in size suggests that the scales of both fossil species were once arranged around an ovuliferous cone (Fig. 2I) and dispersed at maturity, as is characteristic of the extant family. Both *A. pichileufensis* and *A. new species* are also assigned to Araucariaceae based on cylindrical pollen cones (Figs. 9, 10) that have spirally arranged, imbricate, peltate microsporophylls and bear subtending basal bracts (de Laubenfels, 1988; Gilmore and Hill, 1997).

**Assignment to Araucaria**— The leafy branches of the two fossil species can be assigned to *Araucaria* on the combined basis of their crowded, spiral (helical) leaf phyllotaxy (Figs. 3, 4), scale to needle-like morphology with broad attachment to the branch (lacking a petiole; Fig. 5A-D), and amphistomy (Fig. 6A-D; de Laubenfels, 1953). Leaves of *Agathis*, and fossil *Agathis zamunerae* from the same localities are, in contrast, in well-separated pairs (sub)opposite along the branch, broad and oval or elliptic with a narrow false petiole, and hypostomatic (de Laubenfels, 1953). *Agathis* leafy branches also differ from *Araucaria* because they have distinct terminal buds with overlapping scales (as seen in *Agathis zamunerae*), whereas *Araucaria* have only a cluster of smaller leaves at the branch apex (Fig. 5F, I; de Laubenfels, 1988). The leaves of the fossils described here also differ significantly from *Wollemia*, which has trimorphic, usually four-ranked, obtuse to rounded leaves that are opposite to subopposite and twisted with no petiole (decurrent; Jones et al., 1995; Farjon, 2010).

The fossil ovuliferous complexes are typical of *Araucaria*, with a single inverted seed embedded in central tissues (Figs. 7, 8) and a scale that is partially fused with the
bract, shown by the presence of a ligule (extant: Figs. 2J, K; fossils: Fig. 8A-E; Wilde and Eames, 1952; de Laubenfels, 1972, 1988; Stockey, 1994; Farjon, 2010). The presence of broad, symmetrical bracts that are inferred to be thinned laterally into wing-like extensions, with a narrow, spinose projection from the apex above a thickened apical margin (Fig. 2J), is a characteristic of *Araucaria* directly observed in the fossils (Fig. 7-8; de Laubenfels, 1988). In contrast, *Agathis* and *Wollemia* have ovuliferous scales that are completely fused with the bract, thus lacking a ligule (Jones et al., 1995). Seeds of *Wollemia* and *Agathis*, including *Agathis zamunerae*, are dehiscent, and the ovuliferous complexes are completely lignified, lack a projecting apical spine, and have characteristic basal embayments (Wilf et al., 2014).

The pollen cones of both fossil species (Figs. 9, 10) are typical of those from extant *Araucaria* (Fig. 2E) based on the morphology of the basal bracts, which occur in dense clusters overlapping the cone body and are triangular to lanceolate with sharp apices (broad at the base and flattened; de Laubenfels, 1988). The basal bracts on pollen cones of *Agathis* (including *A. zamunerae*) diverge below the cone body and are distinctly short, rounded, and ovate, occurring in pairs of only three bracts (Farjon, 2010; Wilf et al., 2014). Microsporophyll apices of *Agathis* are rounded; however, the fossils described here, like living *Araucaria*, have pointed, acute apices (Fig. 10E; Wilf et al., 2014). *Wollemia* differs from the fossils described here in having basal bracts that are broadly triangular to semicircular (Jones et al., 1995) that do not subtend the fallen cones and microsporophyll apices that are rounded and clavate (Chambers et al., 1998).

The leafy branches, ovuliferous complexes, and pollen cones of both fossil species have diagnostic characters of *Araucaria*. Because the fossils described here fit the
descriptions for living *Araucaria*, and there is no extinct genus that is similar to the fossils, there is no need to assign them to an extinct genus. For example, *A. pichileufensis* and *A.* new species both differ from the extinct genus *Araucarioides*, which has multi-veined leaves that are flattened and strap-like with obliquely oriented stomata (Bigwood and Hill, 1985; Pole, 2008).

*Assignment to Section Eutacta*— The fossil leafy branches are similar to those of extant Sect. *Eutacta* (Fig. 2A-C, F-H). Both fossil species present foliar dimorphism, and in the extant species of *Araucaria*, only Sect. *Eutacta* and Sect. *Intermedia* have foliage that is differentiated into juvenile and adult states (de Laubenfels, 1988; Farjon, 2010). The adult leaf type in Sect. *Intermedia* is multi-veined, large, flat, and spreading, which is not similar to the morphology of either fossil species. The adult leaves in extant Sect. *Eutacta* have small, univeined leaves (Fig. 2C, H; Wilde and Eames, 1952; de Laubenfels, 1972; Farjon, 2010) that are consistent with the small, scale-like, imbricate, univeined, and adpressed leaves present in both fossil species (Fig. 3F-J; 4E-F; 5B, D). Typically, the stomata in mature leaves of Sect. *Eutacta* are oriented obliquely or perpendicularly to the long axis of the leaf (Stockey and Ko, 1986). The fossil stomata seen on *A.* new species are perpendicular (Fig. 6G), so they are similar to *Eutacta*. However, the small number of fossil stomata observed from *A. pichileufensis* were mostly oriented parallel to the long leaf axis (Fig. 6E), which is the only character of *A. pichileufensis* that is shared with the other three extant sections of *Araucaria* (Stockey and Ko, 1986).

The fossil ovuliferous complexes of both species retain a single seed that is embedded in the scale tissues based on the coalifications seen in the fossils (Fig. 7, 8).
The central scale portion, including the seed and apophysis region, is often darker in color compared to the lateral bract wings, suggesting that the wings were thinner than the central body, which is characteristic of Sect. *Eutacta*. Sometimes, only the central body is preserved, and the ovuliferous complex appears to be lacking wings entirely (Fig. 8G) or is narrower than the majority of complete specimens (Fig. 8A). The incomplete preservation of the wings is probably taphonomic or due to breakage before preservation that was commonly observed in herbarium specimens (Fig. 2J) and leaf litter in extant *Araucaria* Sect. *Eutacta* in living collections at the Montgomery Botanical Center and Huntington Botanical Gardens. Some fossil ovuliferous complex specimens have longitudinally striated seeds that may show internal seed structure (Fig. 8K). *A. pichileufensis* seeds have resin ducts (Fig. 8K); when viewed with epifluorescence, the striations on one specimen glowed (Fig. 8H), showing amber casts of resin ducts. The ovuliferous complex fossils are very different from extant *Araucaria bidwilli* (Sect. *Bunya*) which are large, completely woody, and have round, dehiscent seeds. They are also very different from extant Sect. *Araucaria*, which has ovuliferous complexes that are large and nut-like, completely lacking any lateral wings. They differ from extant Sect. *Intermedia* because the fossils are much smaller than ovuliferous complexes of *Araucaria hunsteinii*.

The terminal attachment of pollen cones seen in *Araucaria pichileufensis* (Fig. 9A) is, within *Araucaria*, exclusively a character of extant Section *Eutacta* (Fig. 2C). All three other sections have axillary pollen cones (de Laubenfels, 1988; Farjon, 2010).

*Whole plant hypothesis* — For the *Araucaria* fossils at Río Pichileufú and Laguna del Hunco, we hypothesize that the leafy branch, ovuliferous complex, and pollen cone
organs originated from a single species of plant at each locality, respectively. All the *Araucaria* plant organs described here are found together in the same fossil horizons at their respective sites, and they are clearly distinguishable from the associated *Agathis zamunerae* fossils in each organ category (as described here and by Wilf et al., 2014). Variation among each of the organs is within range for a single species; thus, there is no evidence of more than one *Araucaria* species being present at either locality. The pollen cone organically attached to a leafy branch at Río Pichileufú confirms the hypothesis that the dispersed pollen cones with triangular basal bracts found in the same fossil horizons as the isolated leafy branches at Río Pichileufú are also part of the *Araucaria pichileufensis* plant. Another line of evidence for the association of isolated pollen cones and the leafy branch segments is the observation of parallel stomatal orientation on a basal bract of a pollen cone from a Río Pichileufú (Fig. 10D), which is equivalent to the orientation of stomata on the leaves of *A. pichileufensis* (Fig. 6E). Cuticle seen on ovuliferous complexes from Laguna del Hunco had perpendicular stomatal orientations (Fig. 8J) that were also equivalent to those of leaves at that locality (Fig. 6G).

**Differentiation of two fossil species—** *A. pichileufensis* (Río Pichileufú) and *A. new species* (Laguna del Hunco) are differentiated based on size and morphological differences in the reproductive organs as well as subtle differences among their leaf forms (measurements summarized in Table 2) and stomatal orientation.

In *Araucaria pichileufensis*, the dimorphic leaf forms are (1) subulate and spreading; and (2) lanceolate and adpressed. In *A. new species*, the dimorphic forms are (1) acicular and falcate, and (2) ovate and imbricate. Stomata are oriented differently between the two species. *A. pichileufensis* has parallel orientation of stomata relative to
the leaf axis \( n = 3 \); Fig. 6E), and \( A. \) new species has perpendicular stomata \( n = 7 \); Fig. 6G).

Comparisons of the measurements of the ovuliferous complexes for the two species are shown in box plots in Figure 11. The broad lateral wings of \( A. \) pichileufensis contribute to the maximum width of the ovuliferous complexes, which is, on average, about five millimeters greater than the total length, resulting in the overall broad, flabellate outline. In contrast, the lateral wings of \( A. \) new species are much narrower, with a maximum width that is on average almost identical to the total length, making the overall outline more cuneate (Fig. 11A-C). When the length and width are compared with one another as a ratio, the ovuliferous complexes of \( A. \) new species have a length to width ratio that is close to one, and \( A. \) pichileufensis has ovuliferous complexes that are generally wider than they are long (Fig. 11C). The ovuliferous complexes of \( A. \) pichileufensis have maximum widths of ca. 28.7 mm positioned at ca. 48\% of the ovuliferous complex length, whereas the maximum width of the lateral wings of \( A. \) new species is ca. 18.9 mm, positioned at ca. 63\% of the total length (Fig. 11 B, D). At the convex apophysis of the ovuliferous complex, \( A. \) pichileufensis is more triangular, and \( A. \) new species is more rounded. \( A. \) pichileufensis has broader base widths than \( A. \) new species (ca. 9.5 mm in \( A. \) pichileufensis vs. ca. 6.5 mm in \( A. \) new species), but the ratio of the maximum width to the base width for both species is about the same. Ligule size also differs between the two fossil species. Ovuliferous complexes of \( A. \) pichileufensis have longer triangular ligules (Fig. 8A, C), and \( A. \) new species have short, broad triangular ligules (Fig. 8B, D).
Based on the single complete specimen for each species, pollen cones of A. new species are longer than pollen cones of A. pichileufensis. The A. new species pollen cones are also on average wider and have slightly larger microsporophylls.

*Comparison with other fossils*— Some Mesozoic fossils based solely on ovuliferous complexes could belong to Section *Eutacta* (see Introduction). The two Mesozoic fossils with possible affinity to *Eutacta* that include multi-organ preservation are different from the fossils from Laguna del Hunco and Río Pichileufú. *Brachyphyllum mamillare* and associated *Araucarites phillipsii* from the Jurassic of Yorkshire (Kendall, 1949; Harris, 1979) have short leaves (only reaching lengths of 1.5–4 mm), small ovuliferous complexes (15 mm by 13 mm), and small pollen cones (only 12 mm long and 6 mm wide). Associated *Brachyphyllum feistmantelii* and *Araucarites chilensis* from the Jurassic-Cretaceous boundary interval in Argentina (Baldoni, 1979) also have small ovuliferous complexes (10 mm long and 8 mm wide) and pollen cones (12–13 mm long and 6–9 mm wide).

Table 2 outlines the Cenozoic occurrences and measurements of fossils assigned to Sect. *Eutacta* from the *Araucaria* fossil record. *A. pichileufensis* and A. new species are compared with the Sect. *Eutacta* fossils from Table 2 that are closest in time (from the Eocene or Oligocene; there are no Paleogene examples) to the Laguna del Hunco and Río Pichileufú floras.

Slightly older than the *Araucaria* new species from Laguna del Hunco and also from the La Huitrera Formation, early Eocene *Araucaria* cf. *A. pichileufensis* was reported from Pampa de Jones, Neuquén, Argentina (Wilf et al., 2010). The single illustrated ovuliferous complex specimen is much more similar to A. new species than to
A. pichileufensis. Although partially preserved, the Pampa de Jones specimen has a small maximum width (at least 15 mm) and cuneate shape like A. new species, with narrow lateral extensions on either side of the seed. A ligule is preserved on the Pampa de Jones specimen that is similar to those observed at Laguna del Hunco but with a shorter length. The Pampa de Jones ovuliferous complex probably belongs to A. new species.

_Araucaria fildesensis_ from the early-middle Eocene Fossil Hill Formation of King George Island, Antarctica is based on a single ovuliferous complex (Shi et al., 2018). It differs from the ovuliferous complexes of _A. pichileufensis_ in size because it is much narrower in overall width. Although the measurements of _A. fildesensis_ are within the range of length and width of A. new species, the measurements for the maximum width of A. new species include obvious lateral extensions that are differentiated from the central body of the ovuliferous complex. The ovuliferous complex of _A. fildesensis_ is kite-shaped, rather than flabellate (fan-shaped), and, compared to the ovuliferous complexes of _A. pichileufensis_ and A. new species, the Antarctic fossil appears to lack any thin lateral extensions on either side of the seed. Although the margins of the ovuliferous complex appear fairly straight, it is likely that the wings were either broken off before preservation or incompletely preserved in the single known specimen due to the variability seen in the living material of Sec. _Eutacta_ (i.e., Fig. 2J). The narrowly obovate seed of _A. fildesensis_ also differs from both _A. pichileufensis_ and A. new species, with a seed width of only 4.5 mm compared with maximum seed widths of _A. pichileufensis_ at ca. 7.3 mm and A. new species at ca. 8.8 mm. Shi et al. (2018) separately described associated leafy shoots from the Fossil Hill locality assigned to Sect. _Eutacta_ as _Araucaria_ sp. Based on the awl-shaped leaves, Shi et al. (2018) assumed that these leafy
shoots were juvenile forms. The Antarctic leaf specimens differ significantly from the leaves of *A. pichileufensis* and *A.* new species. The angle of insertion of the Antarctic leaves, at 45–70°, results in leaves that are at times close to perpendicular to the branch and only slightly incurving. The leaves of *A.* new species are more incurving than the Antarctic leaves and are inserted at angles of ca. 29°. Leaves of Antarctic *Araucaria* sp. are also much more widely spaced on the branches than the Patagonian leaves, allowing for a clear view of the branch that is rarely seen on any specimen from Río Pichileufú or Laguna del Hunco. The Antarctic leaves are much longer and narrower compared with the fossils described here and are uniformly acicular rather than lanceolate. Shi et al. (2018) inferred that mature leafy shoots of *Araucaria* sp. from the Fossil Hill locality represent the same taxon that Zhou and Li (1994) described earlier, which have imbricate, keeled and lanceolate to ovate foliage (Zhou and Li, 1994). The *Araucaria* sp. leaves of Zhou and Li (1994) and Shi et al. (2018) differ from *A. pichileufensis* and *A.* new species because the Antarctic leaves are significantly wider and broader toward the leaf apex.

Early Eocene *Araucaria readiae* from Regatta Point, Tasmania is based on a single leafy branch specimen (Hill and Bigwood, 1987). *A. readiae* differs from either species described here because the leaves are wider and have an oblique orientation of stomata.

*Araucarites ruei* from the “Eogene” of the Kerguelen Archipelago is based on dimorphic foliage and ovuliferous complexes (Seward and Conway, 1934). The larger foliage form of *Araucarites ruei* has broad, triangular, imbricate leaves with obtuse apices that differ from *A. pichileufensis* and *A.* new species. The smaller leaf form of
Araucarites ruei also differs from the Patagonian fossils in having wide angles of insertion and leaves spaced out along the branch, which is more similar to the foliage of A. fildesensis. Varying widths of ovuliferous complexes are preserved for Araucarites ruei, showing differential preservation of the lateral wings. The rounded apophysis region of Araucarites ruei and the width of the ovuliferous complexes are more similar to the apophysis and width of A. new species than A. pichileufensis.

Late Eocene- early Oligocene Araucarites alatisquamosus from the Loreto Formation, Río de las Minas, Chile is based on ovuliferous complexes (Ohsawa et al., 2016). Araucarites alatisquamosus differs from either fossil species described here from Argentina because the ovuliferous complexes are significantly larger (at least 12 mm longer than A. pichileufensis and at least 19 mm longer than A. new species). The ovuliferous complexes and seeds of Araucarites alatisquamosus are larger than any other Cenozoic fossil attributed to Sec. Eutacta. Leaves from Río de las Minas are assigned to Araucaria nathorstii Dusén (Sect. Araucaria), and an unnamed smaller leaf type is morphologically similar to Sect. Eutacta, including oblique or perpendicular stomatal orientation. The Araucaria sp. leaf type from Chile has an obtuse apex that is unlike the fossil leaves from either Laguna del Hunco or Río Pichileufú.

Comparison with living Araucaria— Figure 12 compares measurements of organs of both Patagonian fossil species with those of all extant species of Araucaria from Farjon (2010) and Mill et al. (2017). Both A. pichileufensis and A. new species consistently overlap or are within the size ranges of species from extant Sect. Eutacta for adult foliage (Fig. 12A; includes abaxial measurements of the adpressed/imbricate fossil leaf forms), ovuliferous complexes (Fig. 12B), and pollen cones (Fig. 12C; single
complete fossil specimen for each locality shown as a star). Compared with one another, A. new species has wider and slightly shorter leaves than *A. pichilefuensis*. *Araucaria pichileufensis* has larger ovuliferous complexes but smaller pollen cones compared with A. new species. Although both Patagonian fossils have small reproductive organs, A. new species has some of the smallest ovuliferous complexes compared with the living species of *Eutacta*. In general, extant *Araucaria* are known to have larger male and female cones than those in the fossil record (Gleiser et al., 2019), and the fossil species described here fit that pattern (Fig. 12B, C).

Both *A. pichileufensis* and A. new species are on the small end of leaf size for living Sect. *Eutacta* (Fig 12A; consistent with findings by Merkhofer et al., 2015). *A. pichileufensis* has leaves similar in size to *A. humboldtensis* J.T. Buchholz, A. *heterophylla*, and *A. columnaris* (Farjon, 2010). Average leaf size of A. new species is closest to the ranges of *A. scopulorum* de Laub. (Farjon, 2010). However, it is important to note that in extant specimens, a single leaf can be extracted from a branch and measured in its entirety. However, the widest point of an individual fossil leaf is probably obscured by overlapping adjacent leaves along the branch. The same is true for the length of leaves, which is also underestimated due to overlapping on the branch. In shape, the lanceolate adpressed foliage of *A. pichileufensis* is comparable with the adult leaves of *A. cunninghamii*, *A. heterophylla*, or *A. subulata*. The ovate imbricate form of A. new species is similar in shape to the adult foliage of *A. columnaris* and *A. humboldtensis*.

The ovuliferous complexes of *A. pichileufensis* are most similar to *A. cunninghamii*, both in size and in the flabellate shape. The ovuliferous complexes of *A.
new species are significantly smaller than ovuliferous complexes of any living Sect. *Eutacta* but are on average closest in size to *A. rulei* F. Muell. (Fig. 12B).

For each fossil species, there is one complete pollen cone specimen. The small sample size limits comparisons because, in the living species, the pollen cones can vary in length considerably. The *A. pichileufensis* specimen is similar in length to those from *A. columnaris*; however, the fossil pollen cones differ greatly in width and microsporophyll size and shape. Pollen cones of *A. columnaris* are at least 10 mm wider than *A. pichileufensis* and have much larger microsporophylls that are oblong, triangular, and spreading (Farjon, 2010). The width of the *A. pichileufensis* pollen cones is most similar to *A. cunninghamii*, which has the narrowest cones. *A. cunninghamii* cones have peltate, rhombic to rounded microsporophyll laminae and thin, long basal bracts that are both similar to those of the *A. pichileufensis* specimens.

Similarly, *A. new species* pollen cones also have smaller widths similar to *A. cunninghamii* or *A. scopulorum* de Laub., but the pollen cone lengths are within the ranges of *A. laubenfelsii* Corbasson, or *A. nemorosa* de Laub. (Farjon, 2010). However, the imbricate microsporophylls of *A. laubenfelsii* are triangular, much larger than *A. new species*, and have obtuse apices; *A. nemorosa* also has much larger microsporophylls than *A. new species*, with ovate lamina with denticulate margins (Farjon, 2010). *A. scopulorum* has ovate-triangular lamina that can appear rhombic and resemble the Laguna del Hunco cones, but the basal bracts of *A. scopulorum* are much shorter and wider than those of *A. new species* and highly incurved at the apices. The fossilized basal bracts on the Laguna del Hunco specimens are much slenderer than basal bracts of *A. scopulorum*, appearing to taper distally rather than having an incurved apex. Like *A.
*pichileufensis*, the triangular basal bracts of *A.* new species are much more similar to those of *A. cunninghamii.*
RESULTS OF PHYLOGENETIC ANALYSIS

Figure 13 shows the results of the total evidence phylogeny at the family level, with relationships of Araucariaceae to the outgroups illustrated. Figure 14 shows the expanded strict consensus tree of Araucariaceae. The overall topology, including the Agathioid clade resolving as sister to Araucaria, the stem Agathioid position of the Early Cretaceous fossils Emwadea microcarpa (Dettmann et al., 2012) and Wairarapaia milenhalli (Cantrill and Raine, 2006), and the topology of the living Agathis species (not shown here) are the same as reported Escapa et al. (2018) and Escapa and Catalano (2013). The position of the six Jurassic to late Cretaceous fossil Araucaria species on the stem of Araucaria and the topology of the sections within the crown of Araucaria are also the same as previously reported (Escapa and Catalano 2013; Escapa et al. 2013).

The fossil Araucaria pichileufensis diverges from the stem of Section Eutacta and as sister to the crown clade of Section Eutacta (Fig. 13). Consistent with previous studies (Escapa and Catalano 2013; Escapa et al. 2013), the first species of crown Sect. Eutacta to diverge is A. cunninghamii, followed by A. heterophylla, which is found as sister to the New Caledonian Eutacta clade. A. new species from Laguna del Hunco diverges within the New Caledonian clade.

The New Caledonian Eutacta species are color-coded in Figure 14, according to the classification put forward by Gaudeul et al. (2012) in their molecular phylogeny. The addition of fossils to the analysis does not disrupt the Gaudeul et al. (2012) configuration of the three phenotypic groups as clades within the New Caledonian species. Interestingly, A. new species is found among the “large-leaved” clade, although the
fossils from Laguna del Hunco have some of the smallest leaves compared with any of the extant species (Fig. 12A).
DISCUSSION

**Phylogenetic relationships** — Including the fossils did not disrupt the topology of *Araucaria*, including the relationships within Sect. *Eutacta* and the New Caledonian clade, found by the molecular-only analysis. The position of *A. pichileufensis* on the stem of *Eutacta* (Fig. 14) could be supported by the parallel orientation of its stomata (Figs. 6A, E, F; 10D), which is one of the few scored discrete characters that differs among the two Eocene fossil species and appears to be plesiomorphic in *Araucaria*. The stomatal orientation distinguishes it from living Sect. *Eutacta* species, which only have oblique or perpendicular stomata; parallel stomata are seen in extant Sect. *Araucaria*, Sect. *Bunya*, and Sect. *Intermedia* (Stockey and Ko, 1986). The terminal attachment of pollen cones (in *Araucaria*, a derived character state for Sect. *Eutacta*) and observed nonsaccate pollen (a shared character for all Araucariaceae) are scored for *A. pichileufensis*, but these characters are missing for *A. new species*. The preservational absence of these two characters for *A. new species* appears not to influence its phylogenetic position, which is well within the *Eutacta* clade (Fig. 14).

Among the continuous characters, the most noticeable difference among the two fossil species was in the pollen cone length (greater in *A. new species*; limited by a single measurement for both species) and the seed length (slightly larger in *A. pichileufensis*, although there is overlap in seed size among both species). In extant conifers, pollen and seed cone size increases with branch diameter (Leslie et al., 2014), and the increase in the ovuliferous complex and seed size could be related to increased protective tissues or adaptations for dispersal (Leslie, 2011), but these hypotheses are not directly testable in
the fossil record. The distance of A. new species from A. pichileufensis on the tree is probably driven by either the stomatal orientation or the continuous characters.

**Paleoecological and biogeographic implications** — Presence of *Araucaria* Sect. *Eutacta* in the Eocene Laguna del Hunco and Río Pichileufú floras fits with the documented fossil assemblages from those localities; many of the fossil species present are similar to the living conifer and angiosperm associations of present-day subtropical and tropical montane rainforests in Australasia and southeast Asia (Wilf, 2012; Wilf et al., 2013, 2019). New Guinea is one of the closest modern analogs for Laguna del Hunco and Río Pichileufú forests with the maximum number of shared genera (Wilf et al., 2019). In the diverse lower-montane forests of New Guinea, living *Araucaria* (Sect. *Eutacta*), *Agathis*, *Dacrycarpus*, *Papuacedrus*, *Castanopsis*, *Eucalyptus*, *Gymnostoma*, and many other genera from one or both of the two Eocene Patagonian floras are found together (Brass, 1941; Soepadmo, 1972; Johns, 1989; Enright, 1995; Takeuchi, 1999; Ladiges et al., 2003). The *A. cunninghamii* (Sect. *Eutacta*) in New Guinea are found in lower to upper montane forests from (90–)500–1900(–2800) m in elevation, emerging from a 30-meter canopy at heights of ca. 50-60 meters (Enright, 1995; Farjon, 2010). Recording stations at about the same altitudes as the *A. cunninghamii* stands in New Guinea report average annual rainfalls of about 1400–5700 mm (Gray, 1973) and mean annual temperatures of 19.0–24.3°C (McAlpine et al., 1975). The New Guinea modern analog gives us an idea for what the fossil environment, namely the temperature and rainfall, may have been like at Laguna del Hunco, with Sect. *Eutacta* alongside many of the same taxa that live there today.
Previous analyses of Eocene southern Argentine vegetation noted vegetative turnover and ecosystem change that began during the middle Eocene, which is the age of the Río Pichileufú flora (Barreda and Palazzesi, 2007; Dunn et al., 2015; Zucol et al., 2018). Patagonian palynological assemblages show a gradual transition away from the Paleocene and early Eocene rainforests; by the Early Eocene more arid-adapted taxa appeared, and from the middle Eocene to early Oligocene there was a trend from megothermal rainforest to micro and mesothermal forests, including the eventual dominance of *Nothofagus* (Melendi et al., 2003; Barreda and Palazzesi, 2007; Palazzesi and Barreda, 2007). Although *Nothofagus* macrofossils are absent from Río Pichileufú, low abundances of *Nothofagus fusca*-type pollen are recovered from the locality (personal comm. from W. Volkheimer in Wilf et al., 2005). Pollen data has not been published for Laguna del Hunco for comparison. Patagonian phytoliths indicate a shift from dense forests to open, grassland habitats after the middle Eocene (Dunn et al., 2015; Zucol et al., 2018). Thus, the Río Pichileufú flora may be recording one of the final New Guinea-type rainforest environments in Patagonia.

Given the documented environmental and paleogeographic changes that begin at the middle Eocene, and the drought tolerances of extant *Araucaria* Sect. *Eutacta*, it is possible that turnover in the *Araucaria* species between Laguna del Hunco and Río Pichileufú, when considered as a newly recognized component of other floral changes discussed earlier, could be a signal of a biotic response to cooling and drying. The depositional environment is similar and stable between Laguna del Hunco and Río Pichileufú (Aragón and Romero, 1984; Wilf et al. 2005). During the early Eocene, the interchange of *Araucaria* Sect. *Eutacta* through South America and Antarctica was
possible. However, during the early middle Eocene, *Araucaria* Sect. *Eutacta* was probably cut off from Antarctica to the south as the Drake Passage deepened and widened (Lawver et al., 2011) and restrained by dry, semiarid conditions to the north (Melchor et al., 2002; Ziegler et al., 2003).

*Araucaria* Section *Eutacta* eventually went extinct in South America. Some of the last fossils thought to be related to Sect. *Eutacta* in South America are the Eocene-early Oligocene ovuliferous complex *Araucarites alatisquamosus* and associated *Eutacta*-like foliage from the southern tip of Chile (Ohsawa et al., 2016), and the *Araucaria* sp. 2 foliage from the Miocene of west-central Chile, from a higher latitude than the Río Pichileufú and Laguna del Hunco floras (Troncoso and Romero, 1993).
CONCLUSIONS

The confirmed presence of *Araucaria* Sect. *Eutacta* in early Eocene Patagonia just before and during the isolation of South America adds to the Gondwanan legacy of the Laguna del Hunco and Río Pichileufú floras. For the first time, *Araucaria* fossils from Laguna del Hunco were found to be distinct from the fossil species *A. pichileufensis* from the Río Pichileufú locality, which is 4.5 million years younger and from the same formation. This is the first detection of turnover among the conifers at the two localities (excluding the extremely rare *Huncocladus laubenhelsi* from Laguna del Hunco), adding to the emerging evidence of floral turnover in Patagonia that appears to be related to environmental change following the Early Eocene Climatic Optimum and Antarctic separation.

*Araucaria* new species and *Araucaria pichileufensis* are two of the most complete representations of Section *Eutacta* known in the fossil record, with large sample sizes and multi-organ preservation. The new taxonomic treatment and combined evidence phylogenetic analysis of the *Araucaria* fossil species from Río Pichileufú and Laguna del Hunco both support placement in Section *Eutacta*. *Araucaria* new species was found within the crown of *Eutacta*, while *A. pichileufensis* was found in the stem of *Eutacta*. *Araucaria* new species resolves among the extant New Caledonian species, indicating that Sect. *Eutacta*, and perhaps the New Caledonian clade, is a remnant of the Gondwanan flora.

The fossils from Laguna del Hunco described here provide evidence that Australasian Sect. *Eutacta* was present in Patagonia 52.2 million years ago, before Gondwanan separation, and evolved at least ca. 30 million years before some current
molecular age estimates of the *Eutacta* lineage indicated. The 47.7 Ma *A. pichileufensis* fossils from Río Pichileufú show that after the initial isolation of South America, Sect. *Eutacta* survived in Patagonia and was thriving, despite the climate changes and geographic restrictions that occurred after the Early Eocene Climatic Optimum.
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FIGURE CAPTIONS

**Figure 1:** Eocene fossil localities Río Pichileufú (RP) and Laguna del Hunco (LH) on a paleo-reconstruction of Patagonia and tip of the Antarctic Peninsula. Modern coastlines are outlined in black. From a paleoglobe for the early Eocene (Ypresian), 56 million years ago, by C. R. Scotese, PALEOMAP Project.

**Figure 2:** Extant material of *Araucaria* Section *Eutacta* species for comparison with fossil material. A. *A. cunninghamii* juvenile leafy branch, showing linear leaves with pointed apices. MBC, Coral Gables, Florida, PAC 107296. B. *A. cunninghamii* leafy branch, intermediate form between juvenile and mature, showing continuous variation in leaf size and shape along a single branch. Leaves are more incurved apically than juvenile leaves, but not as wide as mature leaves. MBC, PAC 107296. C. *A. cunninghamii* mature foliage, showing terminal attachment of male cones and characteristic leaf apex (a) consisting of a cluster of small, incompletely formed leaves. Mature leaves are much wider, more imbricate, and more incurved than the intermediate foliage. Pollen cones show the helical arrangement of microsporophylls and a cross section of the cones, showing thin stalks (see inset). Morobe Province, Papua New Guinea, A, Coll. J. Havel 7549. D. Photo of dense leafy branch litter under *A. luxurians* tree at MBC. E. *A. cunninghamii* pollen cones showing helical arrangement of microsporophylls with pointed laminae apices, size variation in the cone body, curved shape, and sharp-pointed, elongate, triangular subtending basal bracts retained on the cone along the cone body after being shed from leafy branches. Queensland, Australia, A, Coll. F. H. Weatherhead, s.n. F. *A. cunninghamii*, detail of juvenile leaf form, showing broad attachment at the base and keeling on both leaf surfaces, and a sharp apex. MBC,
PAC 107296. **G. A. cunninghamii**, detail of intermediate leaf form, showing same
tetragonal base, with leaves thickened, incurved, and tapering toward the pointed apex.
MBC, PAC 107296. **H. A. cunninghamii**, detail of mature leaf form, showing wider
leaves compared to the intermediate leaf form that are more strongly incurved toward the
branch and overlapping one another. MBC, PAC 107296. **I. A. cunninghamii**, cross
section of seed cone showing overlapping, helical arrangement of individual ovuliferous
complexes and their projecting spiny apices. Queensland, Australia, A, Coll. F. H.
Weatherhead, s.n. **J. A. cunninghamii**, individual ovuliferous complexes (OC) from a
shattered cone. The central bodies of the OCs have a single central embedded seed (s),
triangular ligule (lig) above the seed, and apophysis (aph), which is the lignified,
thickened apex of the OC central body. A curved spine (sp) projects distally from the
apophysis. The apophysis is similar in shape on each of OC shown, but the thin, papery
lateral wings on either side of the central body vary in size and shape due breakage of the
wings along pleats parallel to the margin or different original position in the cone. Papua
Province, Western New Guinea, L.J. Brass and C. Verateagh 11175. **K. A. cunninghamii**,
detail of the triangular ligule (lig) on ovuliferous complex, projecting above the seed apex
and into the apophysis (aph) region. The spine (sp) is curved toward the ligule. MBC,
PAC 107296.

**Figure 3:** Selected foliage of *Araucaria pichileufensis* Berry from Río Pichileufú. **A.**
Previously unfigured syntype from the Berry 1938 type collection showing the subulate
spreading leaf form. USNM 545222. **B.** Previously unfigured syntype from the Berry
1938 collection showing continuous variation between more adpressed leaves at base of
the branch segment and subulate spreading leaves above. USNM 545210. **C. Specimen**
showing continuous variation between more spreading, longer leaves at the base of the branch segment and shorter more adpressed leaves toward the branch apex. BAR 5581. **D.** Specimen showing keeled leaves spreading from the branch, then curving around the branch toward the apex. BAR 5608. **E.** showing leaf scars toward the base and subulate spreading foliage. BAR 5576b. **F.** Showing continuous variation in a leafy branch with lanceolate adpressed foliage, where some sections of the branch are less adpressed. BAR 5592a. **G.** Syntype from the Berry 1938 collection showing the lanceolate adpressed leaf form. USNM 40383a. **H.** Syntype from the Berry 1938 collection, showing addressed foliage with a secondary episode of growth near the apex. USNM 40383d. **I.** Specimen showing the lanceolate adpressed leaf form. BAR 5602. **J.** Specimen showing the most adpressed and imbricate leafy branch recovered from Río Pichileufú. BAR 5347.

**Figure 4:** Selected foliage of *A.* new species from Laguna del Hunco. **A.** Specimen of a leafy shoot with acicular falcate form and with central axis of the branch visible. MPEF-Pb 10593. **B.** Specimen preserving leafy shoot of acicular form with an episode of secondary growth near apex. MPEF-Pb 10594. **C.** Leafy shoot with acicular falcate foliage that exhibits irregular leaf spacing. MPEF-Pb 10597. **D.** Specimen with acicular falcate form. MPEF-Pb 10596. **E.** Leafy shoot of the ovate imbricate foliage form, where leaves are shorter and wider than the acicular falcate form. An episode of secondary growth is seen emerging from the basal portion of the preserved shoot segment. MPEF-Pb 10585. **F.** Specimen of the imbricate ovate leaf form showing both full adaxial leaves and leaf scars. MPEF-Pb 10603b. **G.** Specimen showing central axis of the branch and short, broad, incurring leaves in lateral view. MPEF-Pb 10580. **H.** Specimen of the ovate imbricate leaf form showing an episode of growth and a branching point at the apex of
the leafy branch segment. MPEF-Pb 10605. I. Specimen preserving the ovate imbricate form, showing the adaxial surface of the leaves along the branch. MPEF-Pb 10602. J. Specimen of the ovate imbricate foliage form with at least four branchlets emerging from the apex. MPEF-Pb 10613.

**Figure 5:** Fossil foliage details. A. *Araucaria pichileufensis* subulate spreading leaf type, showing the keeled abaxial profile of the leaf, and the awl-shaped, spreading foliage. BAR 5612. B. *A. pichileufensis* lanceolate adpressed leaf type, showing the abaxial face and incurving lateral profile of leaves. BAR 5576b. C. A. new species acicular falcate leaf type, showing the tightly packed, incurving, acicular, slender leaves. MPEF-Pb 10593. D. A. new species ovate imbricate leaf type, showing the broad, ovate abaxial face and incurving lateral profile of leaves. MPEF-Pb 10603a. E. *Araucaria pichileufensis* leaf scars, showing the shape of the broad attachment of the leaves where the leaf has completely broken off. BAR 5579a. F. *Araucaria pichileufensis* leafy branch apex, showing leaves that are smaller and incompletely formed compared to the leaves lower on the leafy shoot segment coming together into a rounded apex. BAR4225. G. A. new species, leafy branch of the ovate imbricate type showing a branching point toward the base of the specimen and a growth episode emerging from the right branch. MPEF-Pb 10606. H. A. new species leaf scars, showing the broad attachment of the leaves where the leaf has broken off. MPEF-Pb 10615. I. A. new species leafy branch apex, showing smaller leaves compared to those lower on the branch segment forming a cluster at the apex. MPEF-Pb 10589.

**Figure 6:** In situ fossil leaf cuticle. A. *Araucaria pichileufensis*, profile of leaves under epifluorescence. A darker ridge (m) is the leaf margin, showing the separation of the
abaxial (ab) and adaxial (ad) surfaces of the leaf. Parallel stomatal impressions are mainly disposed on the abaxial side of the leaf, but a few are also seen on the adaxial side (Also Fig. 6E-F). BAR5576a. B. A. new species, profile of leaf with the margin (m) indicated. Specimen shows many rows of stomata along the curved adaxial surface that are perpendicular to the long axis of the leaf. A few perpendicular stomata are also seen in rows on the abaxial surface of the leaf (Also Fig. 6G). MPEF-Pb 10610. C. A. new species, showing row of coalified, perpendicular stomata along leaf seen in lateral view (Also Fig. 6H) .MPEF-Pb 10580. D. A. new species, stomata organized in rows on abaxial face of an ovate leaf. MPEF-Pb 10586a. E. A. *pichileufensis*, showing mostly parallel orientation of stomata, with some oblique. Long axis of the leaf is up. BAR5576a. F. *Araucaria pichileufensis*, stomata at higher magnification in a stacked image, showing parallel orientation of stomata. Subsidiary cell boundaries not evident. BAR5576a. G. A. new species, showing mostly perpendicular orientation of stomata, with some oblique. MPEF-Pb 10610. H. A. new species, coalified stomata at higher magnification, oriented mostly perpendicular, subsidiary cells not well preserved. MPEF-Pb 10580.

**Figure 7:** Selected fossil ovuliferous complexes from Río Pichileufú (left) and Laguna del Hunco (right). A. *Araucaria pichileufensis*, lectotype. Shows the triangular convex apophysis, broad lateral wings that are rounded at the distal margins, and single embedded seed. USNM 40383e. B. A. new species, specimen shows the narrow width and narrow, upright lateral extensions that are squared off at the distal lateral margins. MPEF-Pb 10515. C. A. *pichileufensis*, syntype previously unpublished from the Berry 1938 type collection showing the characteristic triangular apophysis and broad, rounded
lateral extensions. USNM 54512. **D.** A. new species, showing the rounded apophysis and narrow lateral extensions. MPEF-Pb 10537. **E.** *A. pichileufensis*, specimen showing the darker central body and thin lateral extensions that are rounded on the left side that is complete, and partly missing on the right side in this view. BAR 4352b. **F.** A. new species, showing characteristic rounded apophysis and narrow lateral extensions. MPEF-Pb 10569.

**Figure 8:** Fossil ovuliferous complex details. **A-D:** ovuliferous complex specimens from Río Pichileufú and Laguna del Hunco showing ligules (lig). **A.** *Araucaria pichileufensis*, lateral wings are incompletely preserved but the central body shows triangular shape of apophysis and large triangular ligule above the seed. BAR5580. **B.** A. new species, holotype. Ligule is short above inverted seed. MPEF-Pb 10556. **C.** *A. pichileufensis* specimen with oxidized preservation showing triangular apophysis and large triangular ligule above the seed (Also Fig. 8E). BAR5626. **D.** A. new species, showing short, broad triangular ligule above seed. MPEF-Pb 10567. **E.** *A. pichileufensis*, detail of ligule. BAR 5626. **F.** *A. pichileufensis* ovuliferous complex with raised striations on seed (Also Fig. 8H). BAR 5591. **G.** *A. pichileufensis*, showing preservation of just the central body of the ovuliferous complex on multiple planes of the rock. BAR 5598b. **H.** *A. pichileufensis*, detail of resin canals filled with amber casts shown under epifluorescence. BAR 5591. **I.** A. new species ovuliferous complex with partial preservation of lateral wings. Arrow indicates region where stomata were observed (Also Fig. 8J). MPEF-Pb 10533. **J.** Stomata on A. new species ovuliferous complex viewed under epifluorescence, showing perpendicular orientation. Apex is up. MPEF-Pb 10533. **K.** A. new species, detail of seed showing striations. MPEF-Pb 10531.
Figure 9: Fossil pollen cones from Río Pichileufú and Laguna del Hunco. A. Araucaria pichileufensis pollen cone terminally attached to a leafy branch segment. BAR 5618b. B. A. pichileufensis pollen cone showing helical microsporophylls and leaf-like triangular basal bracts. BAR 5619a. C. A. new species, incomplete pollen cone showing triangular subtending basal bracts. Inset shows peltate, pointed microsporophyll laminae and internal structure of cone with microsporophyll stalks. MPEF-Pb 10618. D. A. new species, pollen cone showing pointed, rhombic laminae and long, pointed basal bracts. MPEF-Pb 10617.

Figure 10: Fossil pollen cone details. A-E: BAR 5582. A. Araucaria pichileufensis cone showing internal part of cone body (C, D) and lanceolate basal bracts (D). B. A. pichileufensis fossil pollen visible in clumps along microsporophyll stalks. BAR 5582a. C. Individual A. pichileufensis pollen grain showing nonsaccate, inaperturate, globose-subglobose pollen morphology. D. A. pichileufensis cone basal bract under epifluorescence, showing mostly parallel orientation of stomata. E. A. pichileufensis cone that is counterpart to that shown in 10A, showing cone apex and peltate microsporophylls. F. A. pichileufensis, detail of overlapping lanceolate basal bracts with pointed apices that emerge directly at the base of the cone. BAR 5619b. G. A. new species, detail of lanceolate basal bracts with pointed apices emerging at the base and overlapping the cone body. MPEF-Pb 10618. H. A. new species, detail of basal bracts, showing the attachment at the base and the broad triangular bases of the lanceolate bracts. MPEF-Pb 10614.

Figure 11: Box plots showing size comparisons of fossil ovuliferous complexes (OC) between Araucaria pichileufensis (gray; from Río Pichileufú, ~47.7 Ma) and Araucaria
new species (white; from Laguna del Hunco, ~52.2 Ma). Median (bold line) and mean (+) shown. Box limits indicate the 25th and 75th percentiles as determined by R software; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles. Outliers are represented by dots. Results of the two sample t-test are given, including the t-statistic and the p-value. **A.** OC total length, in millimeters. *A. pichileufensis* has OCs that are ca. five millimeters longer than *A. new species*. **B.** OC maximum width, in millimeters. *A. pichileufensis* has OC that are on average about ten millimeters wider than *A. new species*. **C.** OC ratio of the total length to the maximum width. **D.** OC position of maximum width shown as the percentage of the OC total length. *A. pichileufensis* has an average maximum width of the OC at about half of the total length of the OC, while *A. new species* has the maximum width positioned higher than *A. pichileufensis*, at about 60% of the total length of the OC.

**Figure 12:** Size comparisons of fossil taxa *Araucaria pichileufensis* and *A. new species* with extant *Araucaria* species. Measurements for extant species are from Farjon (2010) and Mill et al. (2017). **A.** Foliage length and width plot showing both fossil taxa overlapping one another and species with some of the smallest sized leaves from Sect. *Eutacta*. **B.** Ovuliferous complex length and width plot showing both fossils in the smallest range of all living Sect. *Eutacta* and *A. new species* being the smallest of all and occupying a larger range than *A. pichileufensis*. **C.** Pollen cone length and width plot showing the single complete fossil specimens from each locality plotted as a star. Fossil pollen cone specimens are just on the edge of measurements in living Sect. *Eutacta*, with the cone from *A. new species* overlapping in the range of Sect. *Bunya* as well.
**Figure 13:** Summary of phylogenetic relationship of Araucariaceae to the outgroup conifer families produced in the total evidence phylogenetic analysis (including morphology, DNA, and fossils).

**Figure 14:** Expanded total evidence phylogeny of Araucariaceae, with *Agathis* condensed. Strict consensus of the most parsimonious tree is shown. Fossil taxa are indicated with an asterisk. The stem (S) and crown (C) nodes for *Araucaria* and the Agathiod clade are indicated. The stem (s) and crown (c) of Section *Eutacta* are distinguished. The extant species from New Caledonia are color-coded according to the systematic treatment of Gaudeul et al. (2012): “large-leaved” species = red; “small-leaved” species with an interior distribution = light blue; “small-leaved” species with a coastal distribution = dark blue. *Araucaria humboltensis* is considered as a “small leaved” interior distributed species after the treatment of Escapa and Catalano (2013).
Figure 1: Eocene fossil localities Río Pichileufú (RP) and Laguna del Hunco (LH) on a paleoreconstruction of Patagonia and tip of the Antarctic Peninsula. Modern coastlines are outlined in black. From a paleoglobe for the early Eocene (Ypresian), 56 million years ago, by C. R. Scotese, PALEOMAP Project.
Figure 2: Extant material of *Araucaria* Section *Eutacta* species for comparison with fossil material. **A.** *A. cunninghamii* juvenile leafy branch, showing linear leaves with pointed apices. MBC, Coral Gables, Florida, PAC 107296. **B.** *A. cunninghamii* leafy branch, intermediate form between juvenile and mature, showing continuous variation in leaf size and shape along a single branch. Leaves are more incurved apically than juvenile leaves, but not as wide as mature leaves. MBC, PAC 107296. **C.** *A. cunninghamii* mature foliage, showing terminal attachment of male cones and characteristic leaf apex (a) consisting of a cluster of small, incompletely formed leaves. Mature leaves are much wider, more imbricate, and more incurved than the intermediate foliage. Pollen cones show the helical arrangement of microsporophylls and a cross section of the cones, showing thin stalks (see inset). Morobe Province, Papua New Guinea, A, Coll. J. Havel 7549. **D.** Photo of dense leafy branch litter under *A. luxurians* tree at MBC. **E.** *A. cunninghamii* pollen cones showing helical arrangement of microsporophylls with pointed laminae apices, size variation in the cone body, curved shape, and sharp-pointed, elongate, triangular subtending basal bracts retained on the cone along the cone body after being shed from leafy branches. Queensland, Australia, A, Coll. F. H. Weatherhead, s.n. **F.** *A. cunninghamii*, detail of juvenile leaf form, showing broad attachment at the base and keeling on both leaf surfaces, and a sharp apex. MBC, PAC 107296. **G.** *A. cunninghamii*, detail of intermediate leaf form, showing same tetragonal base, with leaves thickened, incurved, and tapering toward the pointed apex. MBC, PAC 107296. **H.** *A. cunninghamii*, detail of mature leaf form, showing wider leaves compared to the intermediate leaf form that are more strongly incurved toward the branch and overlapping one another. MBC, PAC 107296. **I.** *A. cunninghamii*, cross section of seed cone showing
overlapping, helical arrangement of individual ovuliferous complexes and their projecting spiny apices. Queensland, Australia, A, Coll. F. H. Weatherhead, s.n. J. A. cunninghamii, individual ovuliferous complexes (OC) from a shattered cone. The central bodies of the OCs have a single central embedded seed (s), triangular ligule (lig) above the seed, and apophysis (aph), which is the lignified, thickened apex of the OC central body. A curved spine (sp) projects distally from the apophysis. The apophysis is similar in shape on each of OC shown, but the thin, papery lateral wings on either side of the central body vary in size and shape due breakage of the wings along pleats parallel to the margin or different original position in the cone. Papua Province, Western New Guinea, L.J. Brass and C. Verateagh 11175. K. A. cunninghamii, detail of the triangular ligule (lig) on ovuliferous complex, projecting above the seed apex and into the apophysis (aph) region. The spine (sp) is curved toward the ligule. MBC, PAC 107296.
Figure 2: Extant material of *Araucaria Section Eutacta*
Figure 3: Selected foliage of *Araucaria pichileufensis* Berry from Río Pichileufú.  

A. Previously unfigured syntype from the Berry 1938 collection showing the subulate spreading leaf form. USNM 545222.  

B. Previously unfigured syntype from the Berry 1938 collection showing continuous variation between more adpressed leaves at the base of the branch segment and subulate spreading leaves above. USNM 545210.  

C. Specimen showing continuous variation between more spreading, longer leaves at the base of the branch segment and shorter more adpressed leaves toward the branch apex. BAR 5581.  

D. Specimen showing keeled leaves spreading from the branch, then curving around the branch toward the apex. BAR 5608.  

E. Specimen showing leaf scars toward the base and subulate spreading foliage. BAR 5576b.  

F. Showing continuous variation in a leafy branch with lanceolate adpressed foliage, where some sections of the branch are less adpressed. BAR 5592a.  

G. Syntype from the Berry 1938 collection showing the lanceolate adpressed leaf form. USNM 40383a.  

H. Syntype from the Berry 1938 collection, showing addressed foliage with a secondary episode of growth near the apex. USNM 40383d.  

I. Specimen showing the lanceolate adpressed leaf form. BAR 5602.  

J. Specimen showing the most adpressed and imbricate leafy branch recovered from Río Pichileufú. BAR 5347.
Figure 3: Selected foliage of *Araucaria pichileufensis* Berry from Río Pichileufú
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Figure 9: Fossil pollen cones from Río Pichileufú and Laguna del Hunco. A. *Araucaria pichileufensis* pollen cone terminally attached to a leafy branch segment. BAR 5618b. B. *A. pichileufensis* pollen cone showing helical microsporophylls and leaf-like triangular basal bracts. BAR 5619a. C. A. new species, incomplete pollen cone showing triangular subtending basal bracts. Inset shows peltate, pointed microsporophyll laminae and internal structure of cone with microsporophyll stalks. MPEF-Pb 10618. D. A. new species, pollen cone showing pointed, rhombic laminae and long, pointed basal bracts. MPEF-Pb 10617.
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Figure 11: Box plots showing size comparisons of fossil ovuliferous complexes (OC) between *Araucaria pichileufensis* (gray; from Río Pichileufú, ~47.7 Ma) and *Araucaria* new species (white; from Laguna del Hunco, ~52.2 Ma). Median (bold line) and mean (+) shown. Box limits indicate the 25th and 75th percentiles as determined by R software; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles. Outliers are represented by dots. Results of the two sample t-test are given, including the t-statistic and the p-value. **A.** OC total length, in millimeters. *A. pichileufensis* has OCs that are ca. five millimeters longer than *A. new species*. **B.** OC maximum width, in millimeters. *A. pichileufensis* has OC that are on average about ten millimeters wider than *A. new species*. **C.** OC ratio of the total length to the maximum width. **D.** OC position of maximum width shown as the percentage of the OC total length. *A. pichileufensis* has an average maximum width of the OC at about half of the total length of the OC, while *A. new species* has the maximum width positioned higher than *A. pichileufensis*, at about 60% of the total length of the OC.
Figure 11: Box plots showing size comparisons of fossil ovuliferous complexes

(A) Total length

(B) Max. width

(C) Total length to max. width

(D) Position of max. width

- **Araucaria pichileufensis**
- **Araucaria new species**

**Araucaria pichileufensis**

**Araucaria new species**

- $t = 8.95, p = 7.68 \times 10^{-8}$
- $t = 8.15, p = 5.45 \times 10^{-6}$
- $t = 8.15, p = 5.45 \times 10^{-8}$
- $t = 8.15, p = 5.45 \times 10^{-6}$
Figure 12: Size comparisons of fossil taxa *Araucaria pichileufensis* and *A.* new species with extant *Araucaria* species. Measurements for extant species are from Farjon (2010) and Mill et al. (2017). **A.** Foliage length and width plot (in millimeters), showing both fossil taxa overlapping one another and species with some of the smallest sized leaves from Sect. *Eutacta*. **B.** Ovuliferous complex length and width plot (in millimeters), showing both fossils in the smallest range of all living Sect. *Eutacta* and *A.* new species being the smallest of all and occupying a larger range than *A. pichileufensis*. **C.** Pollen cone length and width plot (in millimeters), showing the single complete fossil specimens from each locality plotted as a star. Fossil pollen cone specimens are just on the edge of measurements in living Sect. *Eutacta*, with the cone from *A.* new species overlapping in the range of Sect. *Bunya* as well.
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Figure 14: Expanded total evidence phylogeny of Araucariaceae
### Table I. Taxa with modern systematics work, showing presence, absence, and turnover at species level between Laguna del Hunco and Río Pichileufú.

<table>
<thead>
<tr>
<th>Family</th>
<th>Fossil species</th>
<th>Laguna del Hunco</th>
<th>Río Pichileufú</th>
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<td><strong>FERNS</strong></td>
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<td>Osmundaceae</td>
<td><em>Todea amissa</em> M. Carvalho</td>
<td>*</td>
<td>○</td>
<td>Carvalho et al. 2013</td>
</tr>
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<td><strong>GYMNOSPERMS</strong></td>
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<td>Araucariaceae</td>
<td><em>Agathis zamunerae</em> Wilf</td>
<td>**</td>
<td>**</td>
<td>Wilf et al. 2014</td>
</tr>
<tr>
<td>Araucaria</td>
<td><em>new species</em> G. Rossetto</td>
<td>**</td>
<td>○</td>
<td>This study</td>
</tr>
<tr>
<td>Araucaria pichileufensis E.W. Berry</td>
<td>○</td>
<td></td>
<td>*</td>
<td>Berry 1938; this study</td>
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<tr>
<td>Cupressaceae</td>
<td><em>Papuacedrus prechilensis</em> (Berry) Wilf</td>
<td>*</td>
<td>*</td>
<td>Wilf et al. 2009</td>
</tr>
<tr>
<td></td>
<td>Little, Iglesias, Zamaloa, Gandolfo,</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Cúneo et Johnson</td>
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<td>Podocarpaceae</td>
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<td>*</td>
<td>Berry 1938; Florin 1940; Wilf 2012</td>
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<td>*</td>
<td>*</td>
<td>Wilf 2012</td>
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<td><em>Huncocladus laubenfelsi</em> A. Anduchow-</td>
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<td>○</td>
<td>Anduchow-Colombo et al. 2019</td>
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<td></td>
<td>Colombo, P. Wilf et I. Escapa</td>
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<td><em>Podocarpus andiniformis</em> Berry</td>
<td>*</td>
<td>*</td>
<td>Berry 1938; Wilf et al. 2005</td>
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<td>⋆</td>
<td>Wilf et al. 2017b</td>
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<tr>
<td>Ginkgoites patagonica (Berry)</td>
<td><em>Villar de Seoane Cúneo, Escapa, Wilf et Gandolfo</em></td>
<td>⋆</td>
<td>Berry 1935, 1938; Villar de Seoane et al. 2015</td>
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</tr>
<tr>
<td>Zamiaceae</td>
<td><em>Akania americana</em> Romero et Hickey and <em>Akania patagonica</em> Gandolfo, Dibbern &amp; Romero</td>
<td>⋆</td>
<td>Romero and Hickey 1976; Gandolfo et al. 1988</td>
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<td>Asteraceae</td>
<td><em>Raiguenrayun cura</em> Barreda, Katinas, Passalia et Palazzesi</td>
<td>⋇</td>
<td>Barreda et al. 2010; Barreda et al. 2012</td>
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</tr>
<tr>
<td>Atherospermataceae</td>
<td><em>Atherospermophyllum guinazui</em> (Berry) C.L. Knight</td>
<td>⋇</td>
<td>Knight and Wilf 2013</td>
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<tr>
<td>Casuarinaceae</td>
<td><em>Gymnostoma patagonicum</em> (Frenguelli) Zamaloa, G. archangelskyi Zamaloa et Romero, and</td>
<td>⋇</td>
<td>Zamaloa et al. 2006</td>
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</tr>
<tr>
<td>Family</td>
<td>Species</td>
<td>Authors</td>
<td>Notes</td>
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<td>Cunoniaceae</td>
<td><em>G. argentinum</em> Zamaloa et Gandolfo</td>
<td>**</td>
<td><strong>G. argentinum</strong> 2017</td>
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<td>Fagaceae</td>
<td><em>Castanopsis rothwellii</em> Wilf, Nixon, Gandolfo et Cúneo</td>
<td>**</td>
<td><strong>C. rothwellii</strong> 2019</td>
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<td></td>
<td>and associated foliage</td>
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<tr>
<td>Juglandaceae</td>
<td><em>Alatonucula ignis</em> Hermsen et Gandolfo</td>
<td>**</td>
<td><strong>A. ignis</strong> 2016</td>
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<td>Menispermaceae</td>
<td><em>Menispermites calderensis</em> Jud, Gandolfo, Iglesias et Wilf</td>
<td>**</td>
<td><strong>M. calderensis</strong> 2018</td>
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<td></td>
<td>and associated</td>
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<tr>
<td>Monimiaceae</td>
<td><em>Monimiophyllum callidentatum</em> C.L. Knight</td>
<td>**</td>
<td><strong>M. callidentatum</strong> 2013</td>
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<td>Myrtaceae</td>
<td><em>Eucalyptus frenguelliana</em> Gandolfo et Zamaloa</td>
<td>**</td>
<td><strong>E. frenguelliana</strong> 2011</td>
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<tr>
<td></td>
<td>and associated reproductive material</td>
<td></td>
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<tr>
<td>Proteaceae</td>
<td><em>Orites bivascularis</em> (Berry) Romero Dibbern et Gandolfo</td>
<td>**</td>
<td><strong>O. bivascularis</strong> 2007</td>
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<td>Ripogonaceae</td>
<td><em>Ripogonum americanum</em> R.J. Carp, Wilf, Conran et Cúneo</td>
<td>**</td>
<td><strong>R. americanum</strong> 2014</td>
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<th>Solanaceae</th>
<th>Physalis infinemundi Wilf</th>
<th>*</th>
<th>○</th>
<th>Wilf et al. 2017a</th>
</tr>
</thead>
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Notes: ⭐⭐⭐ = n >100; ⭐⭐ = n >40; ⭐ = n >10; ⭐ = n <10; ○ = absent; abundances are given based on amount of material cited in the literature, including Wilf et al. (2005) census data for Laguna del Hunco. Acmopyle engelhardtii is morphotype TY007 in Wilf et al. (2005).
Table II. Cenozoic fossil occurrences of *Araucaria* Section *Eutacta* and measurements.

<table>
<thead>
<tr>
<th>Species</th>
<th>Age</th>
<th>Absolute date of associated rocks (Ma)</th>
<th>Provenance</th>
<th>Citation</th>
<th>OC length (mm)</th>
<th>OC width (mm)</th>
<th>Seed length (mm)</th>
<th>Seed width (mm)</th>
<th>Leaf length (mm)</th>
<th>Leaf width (mm)</th>
<th>Pollen cone length (mm)</th>
<th>Pollen cone width (mm)</th>
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<tbody>
<tr>
<td><em>A. pichileufensis</em> Berry</td>
<td>middle Eocene</td>
<td>47.74 ± 0.05</td>
<td>Huitrera Fm, Río Negro, Argentina</td>
<td>Berry 1938; this study</td>
<td>20.5–</td>
<td>23.4–</td>
<td>11.5–</td>
<td>4.3–</td>
<td>2.9–</td>
<td>0.9–</td>
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<td>7.4</td>
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<td>26.8</td>
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<td>17.9</td>
<td>7.3</td>
<td>9.4</td>
<td>2.4</td>
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<tr>
<td><em>Araucaria</em> new species</td>
<td>early Eocene</td>
<td>52.22 ± 0.22</td>
<td>Huitrera Fm, Laguna del Hunco, Chubut, Argentina</td>
<td>this study</td>
<td>13.3–</td>
<td>13.9–</td>
<td>8.5–17</td>
<td>3.2–</td>
<td>2.4–</td>
<td>1.1–</td>
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<tr>
<td><em>A. cf. pichileufensis</em></td>
<td>early Eocene</td>
<td>54.24 ± 0.45</td>
<td>Huitrera Fm, Pampa de Jones, Neuquén, Argentina</td>
<td>Wilf et al. 2010</td>
<td>16.9</td>
<td>15</td>
<td>10.8</td>
<td>4.5</td>
<td>?</td>
<td>?</td>
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<td>Location</td>
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<td>Age (Ma)</td>
<td>Age (Ma)</td>
<td>U-Th</td>
<td>Age (Ma)</td>
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<tr>
<td><em>A. fildesensis</em> Shi, Li, Leslie et Zhou</td>
<td>early-middle</td>
<td>52 ± 1–43 ± 2</td>
<td>Fossil Hill Fm, Fildes Peninsula, King George Island, West Antarctica</td>
<td>Shi et al. 2018</td>
<td>22</td>
<td>17</td>
<td>16</td>
<td>4.8</td>
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<td>53 ± 1–43 ± 2</td>
<td>Fossil Hill Fm, Fildes Peninsula, King George Island, West Antarctica</td>
<td>Zhou and Li 1994; Shi et al. 2018</td>
<td>10–14</td>
<td>1</td>
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<tr>
<td><em>Araucarites</em> late Eocene-early</td>
<td>36.48 ± 0.47 U-Th-Pb</td>
<td>Loreto Fm, Río de las Minas, Punta Arenas, Magellan Region Chile</td>
<td>Ohsawa et al. 2016</td>
<td>32–33</td>
<td>30–34</td>
<td>18–24</td>
<td>5–5.5</td>
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<td>-</td>
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<tr>
<td><em>Araucarites</em> late Eocene-early</td>
<td>36.48 ± 0.47 U-Th-Pb</td>
<td>Loreto Fm, Río de las Minas, Punta Arenas, Magellan Region Chile</td>
<td>Ohsawa et al. 2016</td>
<td>12</td>
<td>12</td>
<td>7.6</td>
<td>1.6</td>
<td>-</td>
<td>-</td>
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<td><em>Araucarites</em> late Eocene-early</td>
<td>36.48 ± 0.47 U-Th-Pb</td>
<td>Loreto Fm, Río de las Minas, Punta Arenas, Magellan Region Chile</td>
<td>Ohsawa et al. 2016</td>
<td>12</td>
<td>12</td>
<td>7.6</td>
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<td><em>Araucaria</em> sp.</td>
<td>late Eocene - early Oligocene</td>
<td>Arenas, Magellan Region Chile</td>
<td>Ohsawa et al. 2016</td>
<td>Loreto Fm, Río de las Minas, Punta Arenas, Magellan Region Chile</td>
<td>36.48 ± 0.47 U-Th-Pb</td>
<td>11-13 6-7 ? ?</td>
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<tr>
<td><em>A. ligniticii</em> Cookson &amp; Duigan</td>
<td>Oligocene</td>
<td>Yallourn, Victoria, Australia</td>
<td>Cookson and Duigan 1951; Hill 1990</td>
<td>11-18 9-11 ? ? 3-8 1-1.5 20* 5</td>
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<tr>
<td><strong>Araucaria sp.</strong></td>
<td>Miocene</td>
<td>Kawarau Member/Nevis Oil Shale, Manuherikia Group, Bannockburn, New Zealand</td>
<td>Pole 1992</td>
<td>25–30</td>
<td>20–25</td>
<td>?</td>
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<td>4.6–7</td>
<td>0.8–</td>
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<td>25–30</td>
<td>20–25</td>
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<td>?</td>
<td>4.6–7</td>
<td>0.8–</td>
<td>35*</td>
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<td>25–30</td>
<td>20–25</td>
<td>?</td>
<td>?</td>
<td>4.6–7</td>
<td>0.8–</td>
<td>35*</td>
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| *Note:* * = incomplete cone measurement

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<tr>
<th><strong>Araucaria sp. 2</strong></th>
<th>Miocene</th>
<th>Navidad Fm, Boca Pupuya, Matanzas, Chile</th>
<th>Troncoso and Romero</th>
<th>1993</th>
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</table>

Note: * = incomplete cone measurement
**Appendix A:** Living *Araucaria* Section *Eutacta* collections vouchered at the Pennsylvania State University Herbarium (PAC), made by Gabriella Rossetto at the Montgomery Botanical Center (MBC), Coral Gables, Florida, May 23-24, 2018.

<table>
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<tr>
<th>PAC accession number</th>
<th>Collection number</th>
<th>Species</th>
<th>Material</th>
<th>MBC plant accession number</th>
<th>Plant origins</th>
<th>Collection coordinates (at MBC; NAD 1983 UTM zone 17N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>107298</td>
<td>001</td>
<td><em>Araucaria luxurians</em> (Brongn. &amp; Gris) de Laub.</td>
<td>Juvenile and mature vegetative; female cone</td>
<td>87174*C</td>
<td>plant originally was a voucher at Adelaide Botanical Garden, Australia</td>
<td>2838066.5568, 572018.1775</td>
</tr>
<tr>
<td>107297</td>
<td>004</td>
<td><em>Araucaria columnaris</em> (G.Forst.) Hook.</td>
<td>Juvenile and mature vegetative; male cones</td>
<td>7485*A</td>
<td>plant grown from seed produced by Emil Ursini in Ft. Lauderdale- first <em>Araucaria</em> seed produced in Florida.</td>
<td>2838128.64, 572052.6459</td>
</tr>
<tr>
<td>107296</td>
<td>002</td>
<td><em>Araucaria cunninghamii</em> Aiton ex D.Don</td>
<td>Juvenile, intermediate, and mature vegetative; female cone</td>
<td>20080147*A</td>
<td>plant originally from N.Z. Botanical Research Institute Ltd., New Zealand</td>
<td>2837885.7229, 572003.6151</td>
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<tr>
<td>107295</td>
<td>003</td>
<td><em>Araucaria biramulata</em> J.Buchholz</td>
<td>Juvenile and mature vegetative; female cone</td>
<td>87177*B</td>
<td>plant originally from New Caledonia Locality: Thy. A. Watt 578 (S/86-13)</td>
<td>2838098.4808, 572029.251</td>
</tr>
</tbody>
</table>
Appendix B: List of morphological characters used in the phylogenetic analysis, from Escapa et al. (2018). Scores are in Appendices C and D.

0. Ov. cone length. Continuous character.


2. Seed length. Continuous character.


6. Microsporangia number. Continuous character


10. Ov. cone morphology: (0) spherical/globose, (1) ellipsoidal/subglobose, (2) cylindrical, (3) irregular.

11. Ov. cone spreading at maturity: (0) absent, (1) present.

12. Ov. cone at maturity: (0) mostly lignified (woody), (1) mostly coriaceous, (0) mostly fleshy.

13. Number of OC per cone: (0) 1, (1) 2–10, (2) 11–20, (3) more than 20. Ordered character.

14. OC phyllotaxis: (0) helical, (1) decussate, (2) whorled.

15. OC morphology: (0) peltate, (1) non-peltate.

16. OC spreading from the cone at maturity: (0) present, (1) absent.

17. OC proximal scallop: (0) absent, (1) present.

18. Bract/scale fusion at OC: (0) absent, (1) present.
19. Bract/scale degree of fusion: (0) totally fused, (1) relictual scale tip, (2) free scale up to 1/3 of OC length, (3) free scale more than 1/3 of OC length.

20. Bract/scale length: (0) bract longer than scale, (1) bract and scale mostly equal in length, (2) scale longer than bract.

21. OC lateral extensions: (0) absent, (1) present.

22. OC lateral extensions morphology: (0) woody, (1) thin.

23. OC vascularization at origin: (0) independent trace for bract and scale, (1) unique trace for bract and scale.

24. Bract similar to vegetative leaves: (0) absent, (1) present.

25. Number of seeds per OC: (0) 1, (1) 2-4, (2) 5-10, (3) more than 10. Ordered character.

26. Seed embedded in OS tissues: (0) absent, (1) present.

27. Ovule orientation at maturity: (0) erect, (1) recurved.

28. Seed abscission: (0) absent, (1) present.

29. Integumentary seed wings: (0) absent, (1) present.

30. Integumentary seed wing number: (0) 1, (1) 2.

31. Integumentary seed wing symmetry: (0) asymmetric, (1) symmetric.

32. Seed wings (0) continuous at the chalazal end, (1) interrupted at the chalazal end.

33. Seed position on OC: (0) adaxial, (1) terminal.

34. Epimatium: (0) absent, (1) present.

35. Pollen cone disposition: (0) axillary, (1) terminal.

36. Pollen cone aggregation: (0) absent, (1) present.

37. Pollen cone morphology: (0) spherical/globose, (1) ellipsoidal/subglobose, (2) cylindrical, (3) irregular.
38. Microsporophylls phyllotaxy: (0) decussate, (1) helical, (2) whorled.

39. Pollen sacci: (0) nonsaccate, (1) saccate.

40. Basal bracts on pollen cone: (0) absent, (1) present.

41. Pollination drop: (0) absent, (1) present.

42. Number of cotyledons: (0) 2, (1) more than 2, (2) cotyledon tube.

43. Germination: (0) epigeal, (1) cryptogeal.

44. Seedling: (0) not fleshy, (1) fleshy.

45. Phyllotaxis of mature leaves: (0) helical, (1) whorled, (2) opposite to subopposite.

46. Mature leaves in transversal section: (0) rhomboidal to tetragonal, (1) thin and broad.

47. Mature leaves apex: (0) acute, (1) obtuse.

48. Mature leaves apex curvature: (0) straight, (1) curved.

49. Mature leaves venation: (0) midrib, (1) two visible veins, (2) multiple veins, (3) without visible veins.

50. Midrib: (0) evident from external view, (0) not evident from external view.

51. Mature leaves insertion: (0) sessile, (1) reduced base, (2) petiolate.

52. Mature leaves margin: (0) entire, (1) aserrate, (2) minutely denticulate.

53. Stomata disposition on mature leaves: (0) amphistomatic, (1) hypostomatic.

54. Stomata orientation on mature leaves: (0) mostly parallel to leaf axis, (1) mostly oblique to leaf axis, (2) mostly perpendicular to leaf axis.

55. Florin rings: (0) present, (1) absent.

56. Cuticle surface: (0) relatively smooth, (1) undulating.

57. Frequent number of subsidiary cells: (0) 4–5, (1) more than 5, (2) less than 4.
58. Habit: (0) monoecious, (1) dioecious.

59. Phyllotaxy of first order branches: (0) whorled to pseudo-whorled, (1) helical, (2) irregular.

60. Branching orders: (0) 2, (1) 3, (2) 4. 61. Last order branches arrangement: (0) mostly tridimensional, (1) mostly pinnate.

62. Chromosome number (n): (0) 10, (1) 11, (2) 12, (3) 13, (4) >1

Notes: Characters are discrete and unordered unless otherwise indicated. Ov = ovuliferous, OC = ovuliferous complex.
**Appendix C:** Scores of unstandardized continuous characters (0-9 of Appendix A) for *Araucaria pichileufensis* and A. new species added to the Escapa et al. (2018) matrix.

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Notes: Two values for each continuous character indicate the minimum and maximum measurements. All measurements in millimeters.
Appendix D: Updated Escapa et al. (2018) morphological matrix of discrete characters (10-62 of Appendix A)

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Notes: Updates to the matrix are as follows: No taxa were omitted from the original matrix (Escapa et al. 2018). Only two taxa (fossils *Araucaria pichileufensis* and *Araucaria* new species from Laguna del Hunco) were added and scored into the matrix. Scores for extant *Araucaria* species were changed for character 37 (pollen cone morphology) and character 40 (basal bracts on pollen cone); these species were previously scored as unknown (?) in the original matrix. Here, those characters are scored based on data from Farjon (2010) and observations of herbarium specimens.