



Permineralized conifer-like leaves from the Jurassic of Patagonia (Argentina) and its paleoenvironmental implications

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Abstract: Anatomically preserved conifer-like leaves from the Middle Jurassic La Matilde Formation at the Barda Blanca locality in the Gran Bajo de San Julián area, southern Patagonia are described here. Leaves are assigned to conifers based on the following foliar features: thick-walled epidermal cells, a sclerenchymatic hypodermis, resin canals and transfusion tracheids associated with the vascular bundle. General mesophyll anatomy and inferred foliar morphology suggest a similarity to large, broad, linear-lanceolate, multi-veined conifer-like leaves. The general foliar habit indicates an affinity with the large, multi-veined leaves of the Araucariaceae; especially with those exhibited by the species of the *Araucaria* sections, *Araucaria* and *Bunya*. Anatomically, the permineralized leaves exhibit xeromorphic foliar features, including thick-walled epidermal cells, an isobilateral mesophyll with well-developed palisade cells and mechanical tissue. The general leaf anatomy shown by the Patagonian specimens along with sedimentological data may suggest that during the deposition of the La Matilde Formation at the Barda Blanca locality, the parent plant was well adapted to the environmental conditions, which probably consisted of a high light intensity with an adequate quantity of water in the soil, which increased the maximum leaf conductance of CO₂.

Key words: conifers, Jurassic, La Matilde Formation, leaves, Patagonia, permineralized.

INTRODUCTION

The Jurassic sediments of southern Patagonia yield plenty of petrified plant fossils that comprise well-preserved filicean stems, gymnosperm woods and

reproductive conifer structures. Of note is the world renowned petrified forest of the Middle Jurassic La Matilde Formation at the Monumento Natural Bosques Petrificados locality, which has become famous for its high amount and enormous *in situ* trunks as well as fallen logs, which have been assigned to *Agathoxylon matildense* (Zamuner and Falaschi 2005). Furthermore, the finding of numerous large logs that show branches of all order

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allowed Falaschi et al. (2011) to suggest that these Araucariaceae trees were composed of a main, orthotropic stem bearing up to seven plagiotropic branches in pseudowhorls. In addition, the outer bark anatomy of some of these trees has revealed a conspicuously banded periderm structure (Singer and Archangelsky 1958, Hibbett et al. 1997).

The outcrops of the La Matilde Formation at the Gran Bajo de San Julián area contain a rich and diverse petrified plant assemblage that includes stems of *Millerocaulis* and *Osmundacaulis* of the Osmundales (Herbst 2001, 2003) and trunks of *Ginkgomyeloxylon* of the Ginkgoales (Gnaedinger 2012) and of several conifers. Within this last group, the Podocarpaceae is well-represented by *Podocarpoxylon*, *Circoporoxylon* and *Circoporopitys* (Gnaedinger 2007a), whereas the Araucariaceae are represented by several species of *Agathoxylon* (Kloster and Gnaedinger 2018), the Cupressaceae by *Protelicoxylon* and *Herbstiloxylon* (Gnaedinger 2007b), and the Taxaceae by *Prototaxoxylon* (Gnaedinger and Herbst 2006).

Records of petrified fertile structures found in the La Matilde Formation at the Monumento Natural Bosques Petrificados locality are restricted to conifers. Of them, *Masculostrobus altoensis* is a pollen cone with helically arranged microsporophylls that show, due to poor preservation, an unknown arrangement and number of microsporangia, making the assignment to a conifer family difficult (Menéndez 1960). Among seed cones, those of *Pararaucaria patagonica*, previously described by Calder (1953) and Stockey (1977), were anatomically reinvestigated by Escapa et al. (2012). These authors found a seed-enclosing pocket of ovuliferous scale tissue and a trilobed ovuliferous scale and thus included the cones within the Cheirolepidiaceae. However, the best preserved and exquisitely petrified seed cones belong to *Araucaria mirabilis*, which are assigned to the Section *Bunya* of *Araucaria*. These include first-year cones that show several development

stages and mature cones with embryos (Spegazzini 1924, Stockey 1978).

Additionally, several other remains have been reported in the petrified forest, including the common Dematiaceae saprophyte fungus, *Paleopericonia frietzschei*, which are found in some of the *Araucaria mirabilis* cones (Ibáñez and Zamuner 1996), abundant araucarian-like woody seedlings, and what are believed to be aerial lignotubers borne in the axils of leaves (Taylor et al. 2009).

Despite the abundant and diverse petrified plant fossils found in the sediments of the La Matilde Formation, remains of leafy branches are limited to *Araucarites sanctaecrucis*. These fossils are based on petrified woody branches with spirally rhomboidal, imbricate and appressed leaves, which do not show any preserved internal tissues (Spegazzini 1924, Calder 1953).

The occurrence of Mesozoic permineralized leaves in Patagonia is very rare. These include the unusual hot spring chert deposits from the La Matilde Formation and the Middle-Late Jurassic Chon Aike Formation, where permineralized scale leaves with preserved foliar tissues, belonging to araucarian-type and cycadophyte leaves, have been recorded, although they have not been fully described (Channing et al. 2007, García Massini et al. 2016).

The only other record includes permineralized conifer-like leaves with anatomically preserved tissues, which are herein described from the La Matilde Formation in the area of Gran Bajo de San Julián in southern Patagonia. The general mesophyll anatomy and the inferred foliar morphology suggest a similarity to large, broad, linear-lanceolate, multi-veined conifer-like leaves. Although it is difficult to assign these leaves to any conifer family, the general foliar habit indicates a certain affinity to the leaves of the Araucariaceae, especially to those exhibited by the species of the *Araucaria* sections, *Araucaria* and *Bunya*.

MATERIALS AND METHODS

The leaves studied here are preserved in blocks of permineralized coal balls collected by one of the authors (SG) in 1998 from the La Matilde Formation at the Barda Blanca locality (Estancia Meseta Chica) in the Gran Bajo de San Julián area, Santa Cruz Province, Argentina (Fig. 1). The La Matilde Formation and the Chon-Aike Formation are included in the Bahía Laura Group, a well-known volcanoclastic rock complex that is widely distributed in the province of Santa Cruz (De Barrio et al. 1999). According to Panza and Irigoyen (1995) the base of the Bahía Laura Group is either the Roca Blanca Formation (Lower Jurassic) or the Bajo Pobre Formation (probably Aalenian-Bajocian), whereas the top constitutes the “brown clays series” (San Julián Formation), which have been assigned to the Tertiary due to its content of angiosperm leaves (De Giusto 1955, Bertels 1977, De Giusto et al. 1980). Although the age of the Bahía Laura Group is still controversial, some authors have used radiometric dating from the La Matilde and Chon-

Aike Formations to provide an age of between 157 and 162 Ma ± 5-10 Ma; indicating the Bathonian-Callovian interval (Spalletti et al.1982, De Barrio 1993, Echeveste et al. 2001).

The La Matilde Formation in the Gran Bajo de San Julián area comprises approximately 70-80 m of tuffs, including sandy tuffites, lithic tuffs (tufolites) and chonites with varied coloration, which are generally in tabular strata with very subordinate amounts of fine conglomerates. Carbonaceous pelitic levels, up to true coals, are generally located near the base of the sequence and crop out in particular at the Barda Blanca locality, where the leaves described herein were found. In these levels, abundant wood and some other fossils such as conchostracans, pelecypods, insects and anurans have also been recorded (Stipanovic and Reig 1957, Gallego 1994, Morton and Herbst 2001, Báez and Nicoli 2004, Gnaedinger 2007a).

Acetate peels were prepared by standard techniques after etching the cut and polished coal ball surfaces in 48% hydrofluoric acid (Galtier and Phillips 1999). Selected peels were then mounted

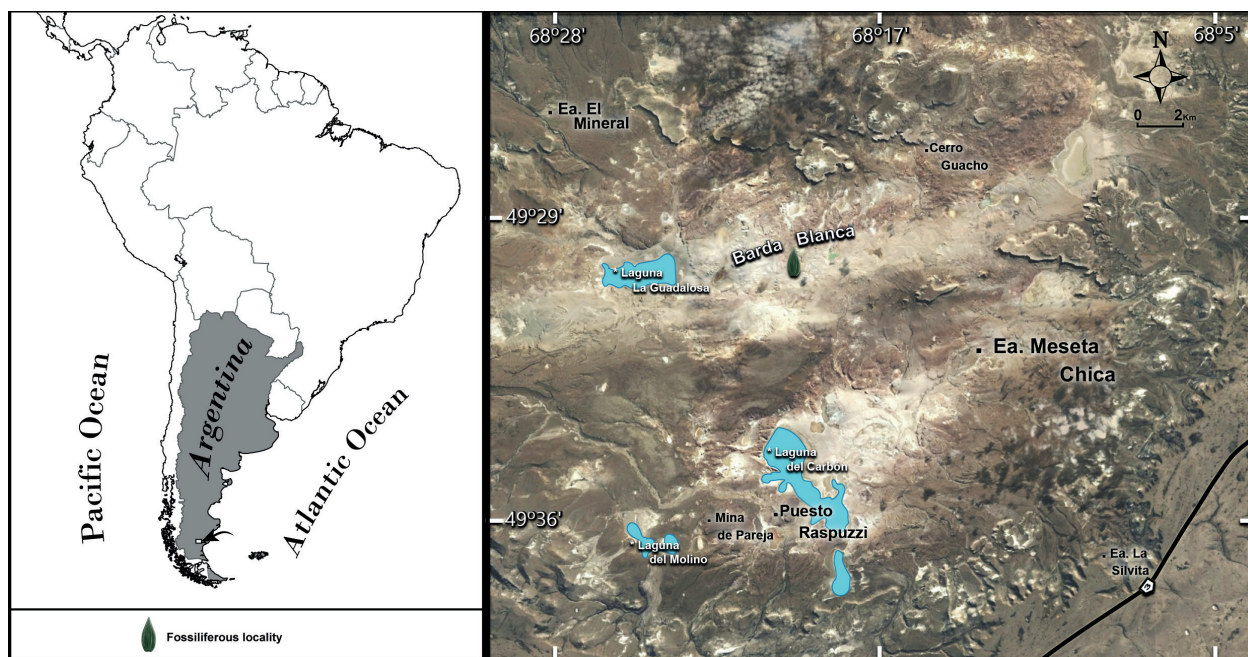


Figure 1 - Location map showing the Barda Blanca fossiliferous locality, Santa Cruz Province, Argentina.

on microscope slides for photomicrography. Comparative material for the three species of *Araucaria*, *A. angustifolia*, *A. bidwillii* and *A. araucana*, were collected from cultivated individuals growing in two distinct areas. The two former taxa were collected from the Parque Centenario garden near the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” in Buenos Aires Province, and the later taxon in Bariloche City, Río Negro Province. Leaves were fixed in formalin-acetic alcohol (FAA), dehydrated in a graded ethanol series, embedded in Paramat, sectioned at approximately 10 μm and stained in safranin-fast green (O’Brien and McCulley 1981). In addition, young stems of *A. angustifolia* were sectioned in tangential and radial views using a sledge microtome and stained in safranin. Fossil and extant materials were observed with a Leica DM2500, and micrographs were taken with a Leica DFC 280 and a Leica ICC50.

The recent systematic treatment of Christenhusz et al. (2011) for extant gymnosperms was taken into consideration. However, for fossil conifers, the study followed the supra-generic systematic treatment outlined in Taylor et al. (2009).

Specimens and microscope slides are deposited in the paleontological collections of the Universidad Nacional del Nordeste (UNNE) “Dr. Rafael Herbst” Paleobotany Section; Corrientes, Argentina under the acquisition numbers CTES-PB 14241a and CTES-PMP 3554a, respectively.

RESULTS

SYSTEMATIC PALEOBOTANY

Subclass PINIDAE Cronquist, Takhtajan and Zimmermann 1966

Order CONIFERALES *sensu* Taylor, Taylor and Kring 2009

Family *Incertae sedis*

Description. The description is based on permineralized packs of solitary conifer-like leaves, up to 15 preserved in longitudinal or oblique-paradermal sections (Fig. 2a, b). The largest is 6.3 mm long and 0.8 mm deep, and the smallest is 2.7 mm long and 0.9 mm deep (Fig. 2a, c). Two of the smallest specimens are incomplete and appear to be transversally and obliquely oriented and probably represent apical portions of leaves. These sections are somewhat semi-circular in outline and reach approximately 0.8 to 1.2 mm in diameter (Figs. 2a, 4d). Several leaf epidermal or mesophyll features are difficult to recognize due to poor preservation. However, several significant anatomical characters were accurately identified in some of the leaves. Because all of the specimens show the same anatomical details, it is assumed that they belong to the same type of conifer-like leaf. The presence of conspicuous, well-developed palisade tissue and hypodermal fiber layers indicate that the leaves are all mature.

The foliar epidermis in most of the specimens is difficult to recognize and is usually preserved in patches of paradermal views, with a few cases preserved in longitudinal section. The epidermal cells are mostly elongate, rectangular and reach 28 μm long and 15.5 μm wide, although some are quadrangular and reach 24 μm long and 20 to 24 μm wide (Fig. 3e). Anticlinal cell walls are straight, smooth and 14 μm deep, whereas periclinal walls are 8.8 μm thick (Fig. 3f). Stomatal apparatuses are difficult to identify; however, what appear to be sub-stomatal chambers can be distinguished in both adaxial and abaxial surfaces. These chambers are approximately 111.4 μm long and 113 μm wide and can be discerned as irregularly elongate empty areas between palisade parenchyma (Figs. 2c-e, 3a, c). In only one case have the remains of a guard cell in longitudinal view been recognized, which show only one entire rounded extreme because the opposite extreme is missing. The guard cell extreme has a conspicuous periclinal wall 6.4 μm thick,

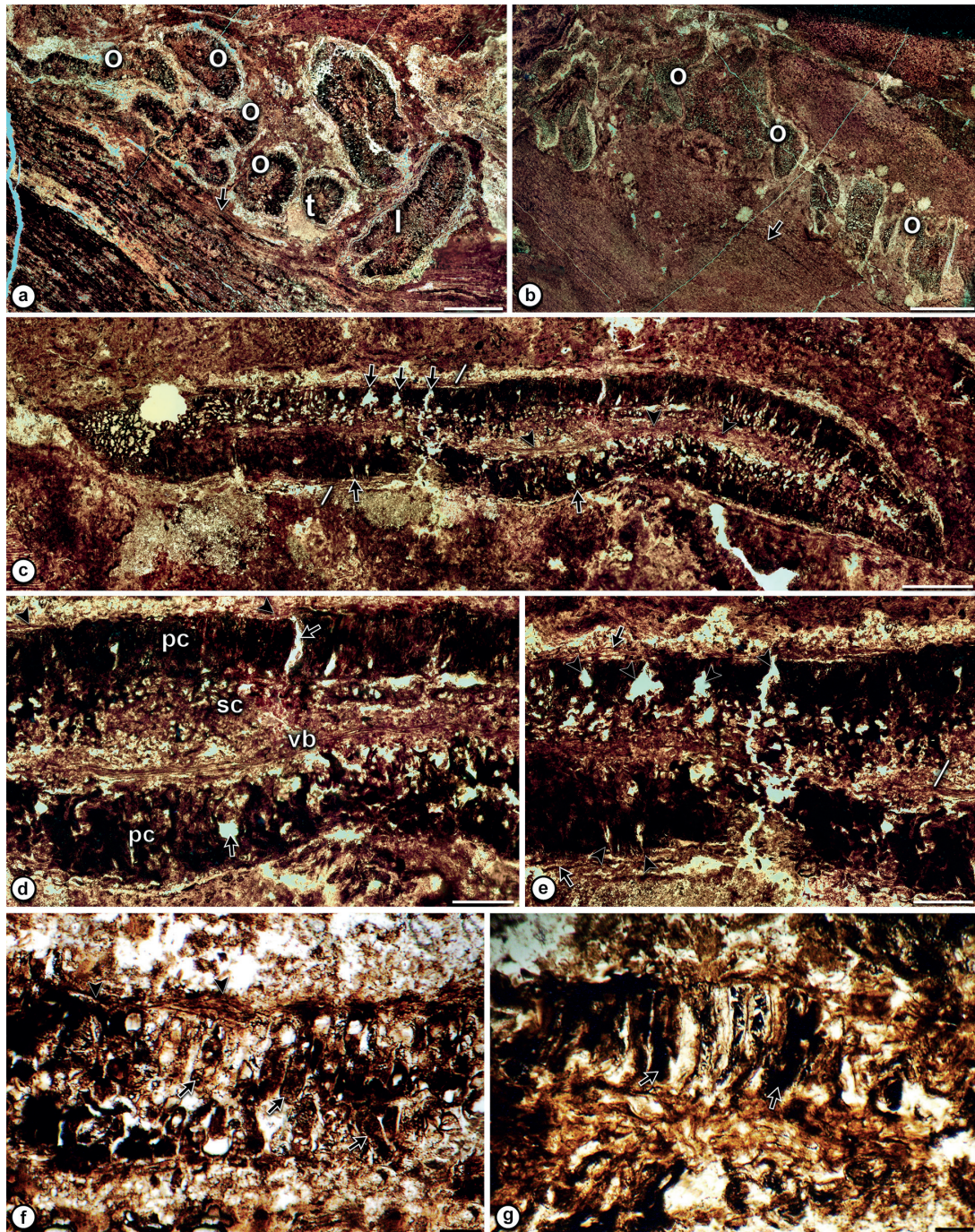


Figure 2 - Permineralized conifer-like leaves. (a-b) Packs of solitary leaves preserved in longitudinal (l), transverse (t) and oblique sections (o). Note associated conifer-like stems (arrows); in tangential section in A, in radial section in B. Bar scales A = 1 mm; B = 2 mm. (c-g) Leaf in longitudinal section. (c) Leaf showing isobilateral mesophyll, stomata in both surfaces (arrows), vascular bundle (arrow heads) and layers of hypodermal fiber (bars). On the left the section turns rather oblique. Bar scale = 500 μ m. (d) Leaf showing densely packed palisade parenchyma cells (pc), damaged spongy parenchyma cells (sc), vascular bundle (vb), layers of hypodermal fiber (arrow heads) and sub-stomatal chambers (arrows). Bar scale = 200 μ m. (e) Leaf showing discontinuous layers of hypodermal fiber (arrows) and sub-stomatal chambers (arrow heads). Note collapsed vascular bundle (Bar). Bar scale = 200 μ m. (f-g) Detail of palisade parenchyma. Note dark contents (arrows). Bar scales = 50 μ m. (f) Two cells thick. Arrow head indicates probably preserved fiber layers. g. One cell thick.

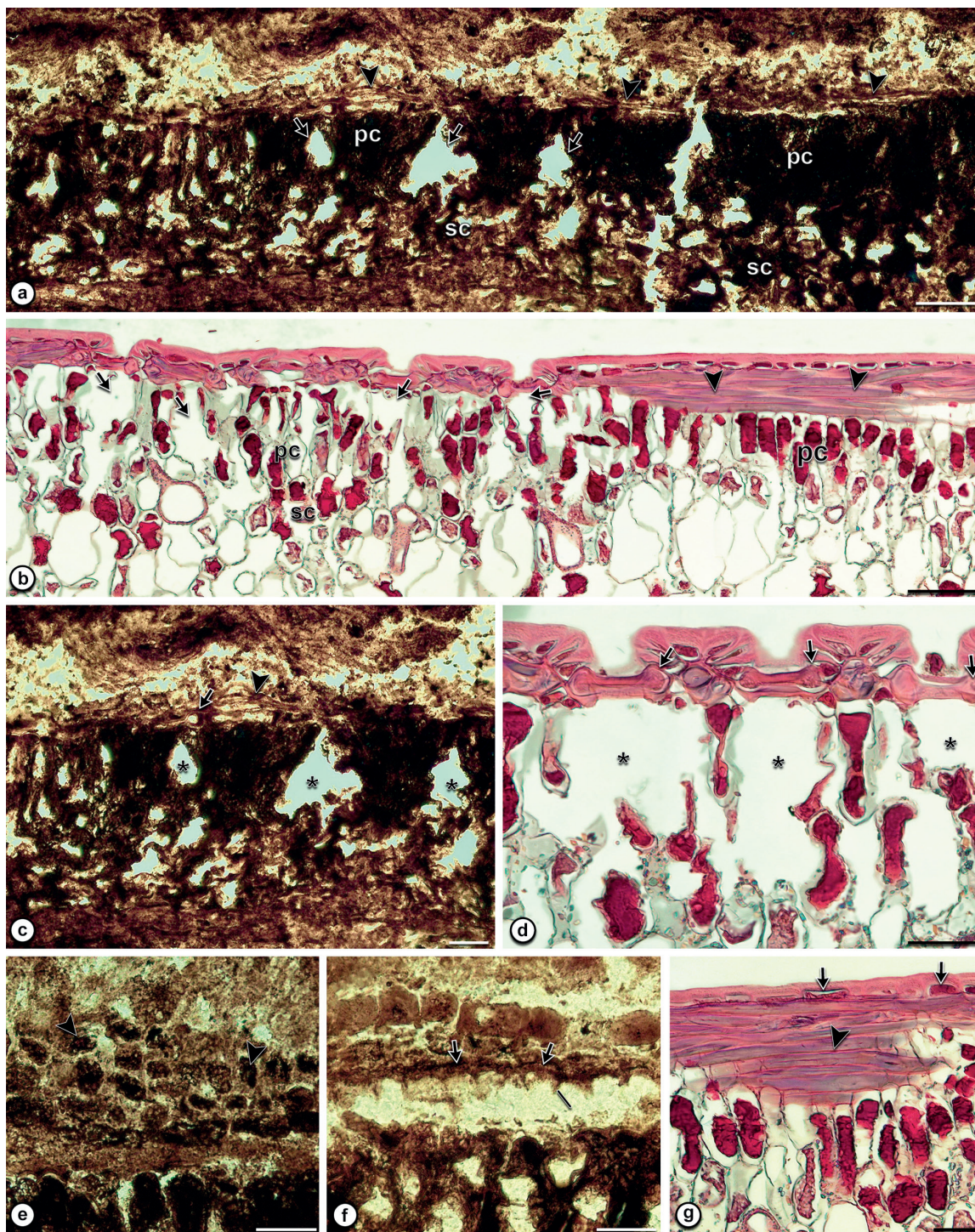


Figure 3 - Permineralized conifer-like leaf and comparative leaf of extant *Araucaria araucana*. (a-g). Longitudinal section. (a, c, e, f) Fossil leaf. (b, d, g) Extant leaf. (a-b) Leaves showing palisade parenchyma cells (pc), spongy parenchyma cells (sc), sub-stomatal chambers (arrows) and layers of hypodermal fibers (arrow heads) Bar scale = 100 μ m. (c-d) Details of stomata (arrows) and sub-stomatal chambers (asterisks). Arrow head indicates layers of hypodermal cell. Bar scale = 50 μ m. (e-g) Details of epidermal cells. Bar scales = 50 μ m. (e) Epidermal cells preserved in patches in paradermal view (arrow heads). (f-g) Epidermal cells in longitudinal view (arrows). Note anticlinal walls (bar) and layers of hypodermal fibers (arrow head).

the middle part of which is thin, reaching $3\ \mu\text{m}$ thick (Fig. 3c). Contiguous to the epidermis, three to four hypodermal fiber layers are preserved in longitudinal view with an incomplete length of $214\ \mu\text{m}$ long and $13\ \mu\text{m}$ wide (Fig. 2c-f). In transversal view, section fibers are $22\ \mu\text{m}$ in diameter. It appears that the second, third and fourth layers are discontinuous. In most cases due to preservation, the hypodermal cell layers appear detached from the epidermal cells (Fig. 3f).

The mesophyll is isobilateral with adaxial and abaxial palisade layers organized into one to two parenchymal cell thicknesses (Fig. 2c, f, g). These cells are elongate rectangular, $102\ \mu\text{m}$ long and $25\ \mu\text{m}$ wide, with blunt ends and appear densely packed, especially along the abaxial side where the individual cells are difficult to recognize. Most of the palisade cells are full of a dark material that can probably be attributed to resins. In between are spongy parenchymal cells that are somewhat isodiametric in shape and up to $54\ \mu\text{m}$ in diameter. However, in most cases, the parenchymal cells are damaged, which has resulted in irregular shaped elements that are difficult to distinguish individually (Figs. 2d, 3a, 4a, g, h). Although resin canals are poorly preserved, they have been observed in a few longitudinally sectioned leaves within the spongy mesophyll (Fig. 4g, h). Resin canals are distinguished as incomplete longitudinal lacunae up to $70\ \mu\text{m}$ wide, whereas epithelial cells are preserved in patches. Each of these cells is rectangular-elongate, reaching $26.5\ \mu\text{m}$ long and $7.3\ \mu\text{m}$ wide (Fig. 4h).

A vascular bundle in longitudinal view is recognized in the mesophyll of the largest leaf, showing a somewhat rectilinear trajectory (Figs. 2c, 4a). The bundle appears collateral with the xylem composed of tight files of up to 9 tracheids approximately $3.8\ \mu\text{m}$ wide, each showing helical wall thickenings (Fig. 4a). Contiguous to the most adaxially placed tracheids, patches of several transfusion tracheids are recognized. They are

almost quadrangular in shape, are approximately $29.7\ \mu\text{m}$ long and $25\ \mu\text{m}$ wide and have poorly preserved areolate pits; in any case, characteristic reticulate wall thickening has been identified (Fig. 4b). Phloem cells have not been recognized due to poor preservation. Two damaged vascular bundles, $26\ \mu\text{m}$ in diameter in transverse view, are observed in apical sections of leaves that are transversally and obliquely oriented (Fig. 4d). Within the bundle, only xylem tracheids are recognized, as all other individual vascular cells are too difficult to discern (Fig. 4d). Xylem tracheids appear in two groups of very small quadrangular cells that have thick walls and empty lumens and look quite distinct from the surrounding foliar tissues (Fig. 4d). Of note in these apical sections is a well-developed palisade mesophyll, as the epidermal cells and hypodermal fibers exhibit poor preservation (Fig. 4d).

Some of the leaves were found in close association with young conifer-like stems that have been preserved in longitudinal-tangential and longitudinal-radial views (Fig. 2a-b). Their lengths and widths are incomplete and reach up to $20\ \text{mm}$ long and to $9\ \text{mm}$ wide. In radial view, the rays are homocellular and composed of approximately quadrangular cells $21\ \mu\text{m}$ long and $11\ \mu\text{m}$ wide (Fig. 5a). Tangential ray walls appear straight. The latter and the horizontal walls are unpitted. The arrangement of the pits on tracheid radial walls is uniseriate. Pits are contiguous with neighboring pits, are circular in outline reaching $9.4\ \mu\text{m}$ in diameter and have circular inner aperture $2.5\ \mu\text{m}$ in diameter. Cross-fields possess five contiguous alternate bordered pits; however, the exact number is difficult to determine due to poor preservation (Fig. 5c). In tangential view, the rays are exclusively uniseriate and range from 1-6 cells, with the most common being 1-2 cells high. The transverse and tangential walls of the parenchymal cells are smooth. These cells are barrel-shaped, reaching $19\ \mu\text{m}$ high and $10\ \mu\text{m}$ wide. No pits are observed in tracheid tangential walls (Fig. 5e).

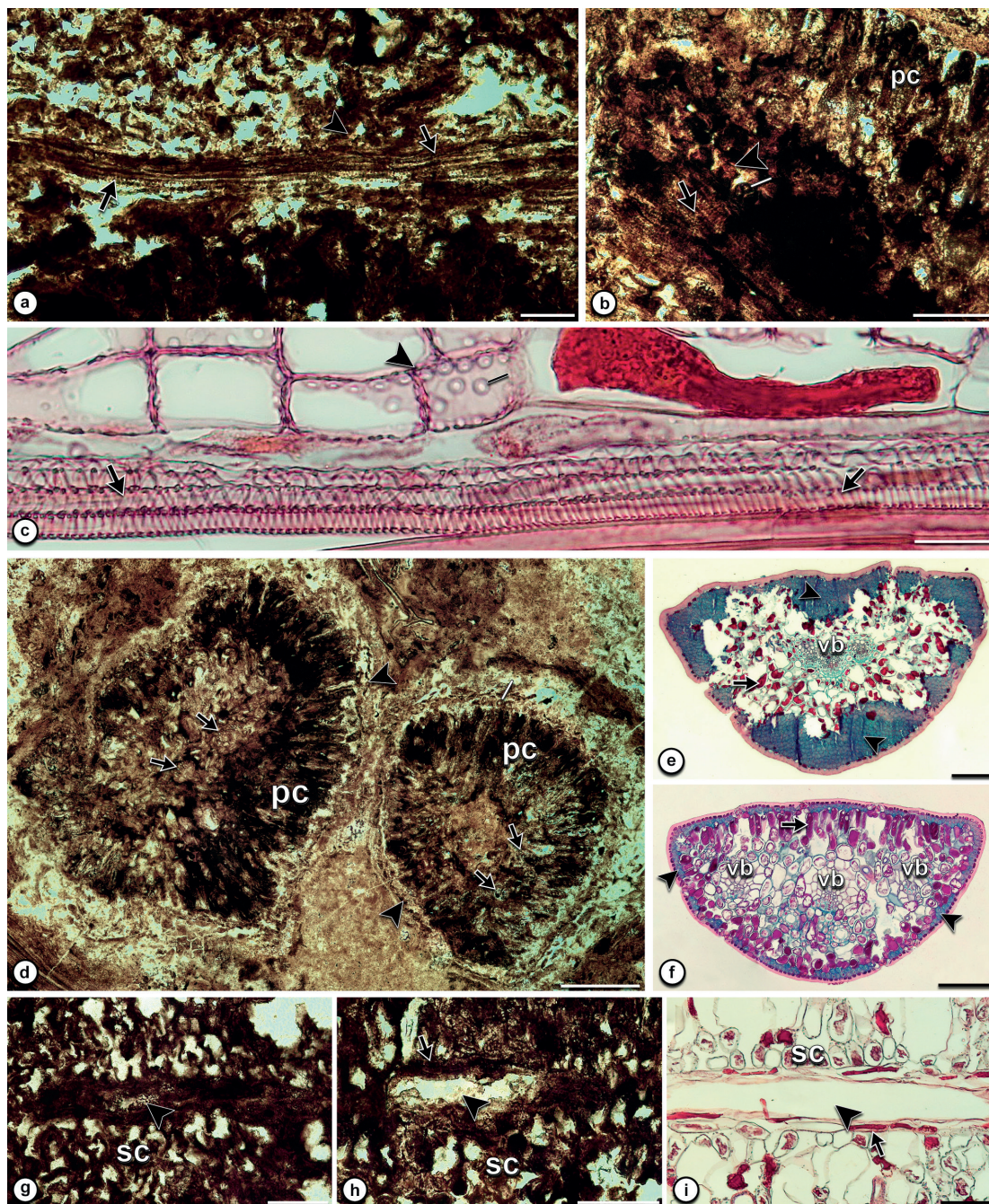


Figure 4 - Permineralized conifer-like leaf and comparative leaf of extant *Araucaria*. (a, b, d, g, h, f) Fossil leaf. (c, e, f, i) Extant leaf. (e) *A. araucana*. (f, i) *A. bidwillii*. (a-c) Details of vascular bundle in longitudinal view showing tracheids with helical wall thickenings (arrows), transfusion tracheids (arrow heads) and pits (bars). Note palisade parenchyma cells (pc). (a-b) Transfusion tracheids poorly preserved in patches. Bar scales: a = 50 μ m, b = 100 μ m, c = 25 μ m. (d-f) Apical part of leaves. (d) Oblique-transverse section. Arrows show two vascular bundles poorly preserved and arrows head probable hypodermal fibers. Note few hypodermal fibers in transverse section (bar) and palisade parenchyma cells (pc). Bar scale = 250 μ m. (e-f) Transverse section. Note three vascular bundles (vb), one incipient. Arrows indicate palisade parenchyma cells and arrow heads hypodermal fibers. Bar scales = 200 μ m. (g-i) Resin canal in longitudinal view (arrow heads). Arrows show epithelial cells. Note spongy parenchyma cells (sc). Bar scales = 100 μ m.

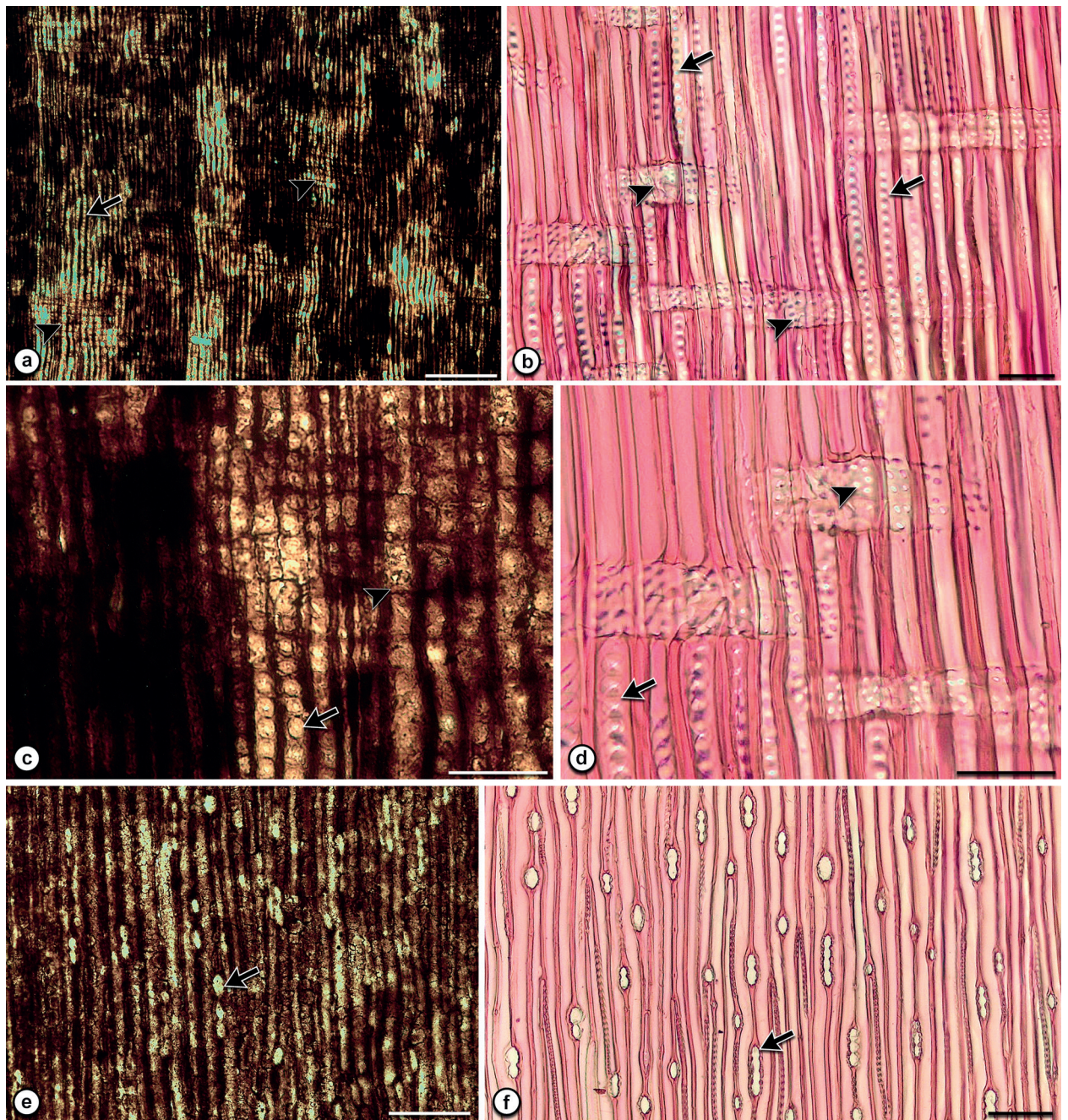


Figure 5 - Permineralized conifer-like stem and comparative stem of extant *Araucaria angustifolia*. (a, c, e) Fossil stem. (b, d, f) Extant stem. (a-d) Radial section. Tracheids with uniseriate contiguous pits (arrows) and cross-fields with numerous contiguous alternate pits (arrow heads). Bar scales: a = 200 μm , b-d = 50 μm . e, f. Tangential section. Note uniseriate rays (arrows). Bar scales = 100 μm .

DISCUSSION

BOTANICAL AFFINITY AND GENERAL REMARKS

The permineralized foliar structures described herein correspond to sterile foliage that shows general anatomical features characterizing most conifer-like leaves. This has been revealed by the presence of an epidermis with thick-walled cells, a hypodermis composed of several (3-4) fiber layers, resin canals and transfusion tracheids associated with the vascular bundle (Chamberlain 1935, Evert 2006).

Taking into consideration other organs of foliar origin, such as cataphylls and bracts, it appears that they show quite distinct anatomical features to those observed in the fossils from the La Matilde Formation. In no case does the Patagonian foliage exhibit a mesophyll of undifferentiated parenchymal cells with few sclerenchymal cells and a poorly developed xylem that characterizes the cataphylls or bud scales of most conifers (Romberger 1963), such as Pinaceae (Sacher 1955) or Podocarpaceae (Del Fueyo 1988), among others. In addition, the specimens' leaf anatomy from the La Matilde Formation does not even show any tissue comparable to those observed in coniferous bracts, where the ground tissue is notably undifferentiated. It is mainly parenchymatous with scattered sclereids such as in the bracts of the Cretaceous *Araucaria nipponensis* from Japan and Russia (Stockey et al. 1994) or it is merely sclerotic similar to the bracts of the Jurassic *Araucaria mirabilis* from Patagonia (Stockey 1978). In other cases, the bract ground tissue is only composed of few parenchymal cells that are full of a dark material, similar to the Jurassic Cheirolepidiaceae *Pararaucaria* from Patagonia (Escapa et al. 2012, 2013). Furthermore, bracts in extant conifers follow a similar anatomical organization, as most cases essentially formed from parenchymal cells filled with resin-like or tannin-like material and sclereids, as observed in *Abies grandis* of the Pinaceae and in several taxa of the

Cupressaceae (Singh and Owens 1982, Takaso and Tomlinson 1989, Farjon 2005), among others.

Within Coniferales, leaves are usually needle-like with a middle vein or two bundles, such as those present in Pinaceae and in the remarkable Sciadopityaceae, which have two needles fused together along the posterior margin, or scale-like and single-veined as in Cupressaceae and in some Cheirolepidiaceae, Podocarpaceae and Araucariaceae. However, many other conifers have linear-lanceolate, small (most belonging to Taxaceae) or large (Palissyaceae, *Cephalotaxus*, and some Podocarpaceae) leaves with one vascular bundle, whereas other conifers have large, broad, multi-veined leaves similar to those observed in most Araucariaceae and in *Nageia* of the Podocarpaceae (De Laubenfelds 1953, Krüssmann 1985, Farjon 2008, Ghimire et al. 2014).

According to this, and despite the fact that the general morphology of the Patagonian leaves is difficult to discern, it is possible to infer it, at least partially, by considering the size and shape of the blade sections and the arrangement of the several foliar tissues (Fig. 6a, b, f, h). Because the largest longitudinal foliar section is 6.3 mm long, 0.8 mm thick and shows a well-developed mesophyll (Fig. 6h), it is suggested that the Patagonian leaves would have been of large size and with a kind of broad shape rather than of small size and slender form. Although the overall foliar length cannot be determined, such a long and large longitudinal section with almost straight parallel foliar surfaces is indicative of somewhat linear-lanceolate rather than scale-like or needle-like leaves. Because this longitudinal section is almost oblong in outline and, considering that neither an apical blade nor basal blade parts are preserved, it is suggested that the section most likely corresponds to a portion between the middle and the margin of the blade (Fig. 6h). However, it is possible that the longitudinal sections that are 2.7 mm long and 0.9 mm thick and do not show a vascular bundle but mainly

palisade and spongy tissues, would have been located close to the blade margin (Fig. 6f). Because a conspicuous vascular bundle in longitudinal view (Fig. 6h) and two damaged vascular bundles in the small cross-oblique sections (Figs. 4d, 6b) can be seen in the Patagonian leaves, it is proposed that the leaves were most likely multi-veined rather than univeined. That the Patagonian leaves described here are not considered two-veined is based primarily on the fact that there is neither a fossil nor extant conifer that is known to have large, broad leaves with only two bundles; they are always multi-veined (Chamberlain 1935, Axsmith et al. 1998). Furthermore, in the Patagonian leaves, the foliar apical portions that show a semi-circular outline (Fig. 4d) are indicative of terete leaf apices.

This evidence reveals that the foliage from the La Matilde Formation would have been perhaps composed of large, broad, multi-veined, linear-lanceolate leaves that became terete towards the apex (Fig. 6a) showing an isobilateral, well-developed mesophyll, resin canals, unistratified epidermis with stomata on both surfaces, a hypodermis composed of one to four fiber layers, collateral vascular bundles with xylem composed of helical thickening walled tracheids and adaxially contiguous transfusion tracheids.

COMPARISON AMONG CONIFER LEAVES

Because the morphological and anatomical data suggest an affinity of the La Matilde Formation foliage to conifers with large, broad and multi-veined leaves, the comparisons will be focused on fossil and extant coniferous taxa that have similar foliar characteristics and whose anatomy have been preserved or studied in detail.

Comparison with fossil broad multi-veined conifer leaves

Remains of large, broad multi-veined conifer leaves are common in the Mesozoic worldwide, among

which foliar impressions or compressions with preserved cuticle are remarkably abundant. There are Cretaceous records of the Araucariaceae with several species of *Araucaria* from Patagonia (*A. grandifolia*), Antarctica (*A. fibrosa*), New Zealand (*A. haastii*), Alabama (*A. bladenensis*) and Australia (*A. seorsum*, *A. lanceolatus*, *A. acutifolius*), as well as *Agathis victoriensis* from Australia (Bose 1975, Cantrill 1992, Césari et al. 2001, 2009, Del Fueyo and Archangelsky 2002, Stults et al. 2012), among others. Additionally, within the Podocarpaceae, the multi-veined leaves of *Podocarpus (Nageia) suifunensis* and *Podocarpus (Nageia) ryosekiensis* were described from the Lower Cretaceous of Russia and Japan, respectively (Krassilov 1974, Kimura et al. 1988). Furthermore, numerous multi-veined conifer taxa of unknown family have been found, such as *Desmiophyllum* from the Upper Triassic of China (Zhou 1983), *Heidiphyllum* from the Triassic of the Southern Hemisphere (Axsmith et al. 1998), *Podozamites* from the Late Triassic of Greenland (Harris 1935) and the Cretaceous of Australia (Cantrill 1990), Antarctica (Falcon Lang et al. 2001) and Brazil (Kunzmann et al. 2004), and *Lindlecladus* from the Cretaceous of Brazil (Kunzmann et al. 2004).

In contrast, Mesozoic permineralized multi-veined conifer leaves that show internal preservation are limited to those foliar remains described from Antarctica, Australia and Japan, which exhibit certain anatomical features not observed in the Patagonian leaves. The exceptionally preserved multi-veined leaves of *Notophyllum krauselii*, a Podocarpaceae from the Middle Triassic of Antarctica, differ markedly in that they show no hypodermal cells but do have a dorsiventral mesophyll differentiated into adaxial palisade tissue and densely packed spongy tissue, as well as accessory transfusion tissue oriented almost obliquely to the vascular bundles (Axsmith et al. 1998). Moreover, the multi-veined leaves attached to the araucarian ovulate cone axis of *Emwadea*

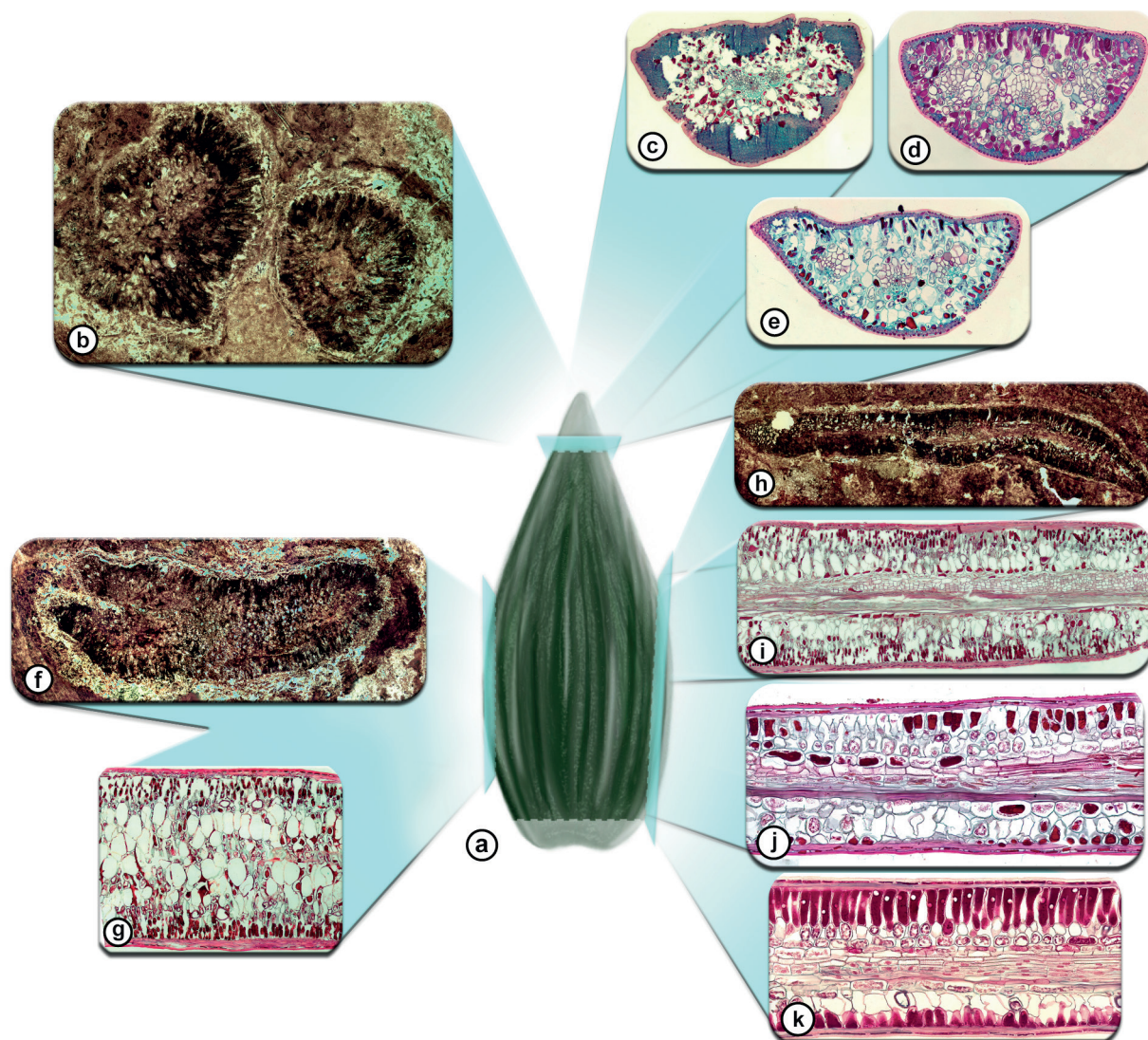


Figure 6 - Hypothetical reconstruction of the conifer-like leaves from La Matilde Formation and its comparison with extant *Araucaria* leaves. (a) Hypothesized fossil leaf showing general morphology. Large, broad linear-lanceolate and multiveined leaf. Apex and base unknown. (b, f, h) Fossil leaves. (b) Transverse-oblique view near the apex. (f, h) Longitudinal view. (f) Margin of the leaf showing no vascular bundle. (h) Most inner leaf part showing one vascular bundle. (c-e, g, i-k) Leaf of extant *Araucaria* spp. (c, g, i) *A. araucana*, (d, k) *A. bidwillii*, (e, j) *A. angustifolia*. (c-e) Transverse views. (g-k) Longitudinal views. (g) Section showing no vascular bundle. (i-k) Sections through one vascular bundle.

microcarpa from the late Albian of Australia are distinct because the stomata are confined to the adaxial epidermis, and the mesophyll is dorsiventral, poorly developed and has large mucilage cells (Dettmann et al. 2012).

Ohana and Kimura (1993) described multi-veined leaves that were quite well preserved belonging to *Brachyphyllum vulgare* from the Coniacian-Santonian of Japan, which are supposed

to be identical to the leaves found associated with the cone axis of *Araucaria vulgaris*, which are assigned to section *Yezonia* of *Araucaria* by Ohsawa et al. (1995). Leaves of the Patagonian specimens are distinguished from those of *B. vulgare* because they are hypostomatic with a dorsiventral mesophyll in which numerous and large resin channels are present below the vascular bundles.

Comparison with extant broad multi-veined conifer leaves

As noted, four extant conifers, *Nageia* of the Podocarpaceae, *Agathis*, most *Araucaria* species and *Wollemia* of the Araucariaceae, have large, broad and multi-veined leaves that share some anatomically similar characteristics but differ in others from those of the La Matilde Formation.

According to several authors, *Nageia* species are either amphistomatic or hypostomatic (Buchholz and Gray 1948, Woltz et al. 1987, Jin et al. 2010). In particular, leaves of *Nageia motleyi* and *N. wallichiana* are amphistomatic with an isobilateral mesophyll similar to that observed in the Patagonian specimens (Orr 1944, Woltz et al. 1987). The transfusion tissue in *Nageia* is reduced to a few tracheids flanking each bundle (Orr 1944), while in the Patagonian leaves they are found above the xylem. In addition, accessory transfusion tissue, which is a typical podocarpoid feature, is lacking in the Patagonian leaves similar to those of the *Nageia* species (Woltz et al 1987, Hu and Yao 1981). However, within *Nageia*, the presence of resin canals beneath each of the many vascular bundles is a distinct characteristic that it does not share with the Patagonian specimens.

Among the three araucarian taxa, leaves of the La Matilde Formation differ significantly from those of *Agathis* species in that the latter are mostly hypostomatic and the mesophyll is markedly dorsiventral in which large, branched and thick-walled sclereids are randomly arranged (Seward and Ford 1906, Kausik 1976, Stockey and Atkinson 1993).

Conversely, leaves of the monospecific *Wollemia nobilis* are amphistomatic as observed in the Patagonian specimens. However, the former are distinguished by having a dorsiventral mesophyll with singly large sclereids and enlarged mucilage cells in the spongy tissue (Chambers et al. 1998, Burrows and Bullock 1999). These

unusual mucilage cells are confined to *Wollemia* and *Araucaria* (Bamber et al. 1978, Burrows and Bullock 1999, Mastroberti and Mariath 2003, 2008). The Patagonian leaves appear to lack these mucilage cells, but this could be due to preservational factors.

Within the four recognized sections of *Araucaria* (Wilde and Eames 1952), it is considered here that those species belonging to the *Araucaria*, *Bunya* and *Intermedia* sections with large, multi-veined leaves because those of the *Eutacta* section have reduced and mostly univeined leaves. Stockey and Ko (1986) pointed out that all species of *Araucaria* are amphistomatic (Figs. 3b, d, 6i-k), which are similar to the Patagonian leaves. However, *Araucaria* differs from the latter by having large sclereids and the so-called mucilage cells in the mesophyll. Furthermore, some species of *Araucaria* have a dorsiventral mesophyll, whereas others, such as the two South American species, *A. angustifolia* and *A. araucana*, which both belong to section *Araucaria*, and *A. bidwillii* of section *Bunya*, exhibit an isobilateral mesophyll (Fig. 6i-k) similar to that of the Patagonian leaves (Seward and Ford 1906, Mastroberti and Mariath 2003). In this regard, the well-developed and densely packed adaxial and abaxial palisade cells of the Patagonian specimens are most similar to those exhibited by *A. araucana* (Figs. 3b, d, g, 6g, i) rather than those shown by *A. angustifolia* and *A. bidwillii* where they are more developed adaxially than abaxially (Fig. 6j, k).

However, the Patagonian foliar apical tissues observed in the transverse sections more closely resemble those seen in *A. angustifolia* and *A. bidwillii*, where there is a well-developed palisade mesophyll with two vascular bundles (Figs. 4f, 6d, e). In contrast, the layers of hypodermal fibers are anatomical features that the Patagonian foliar apex share with that of *A. araucana* leaves (Figs. 4e, 6c).

Because the largest Patagonian specimen is preserved in a longitudinal section along a vascular

bundle, it is not possible to confirm whether the leaves have resin canals alternating with vascular bundles, as is the case for *Agathis*, *Araucaria* (Figs. 4e, f, i, 6c-e) and *Wollemia* (Seward and Ford 1906, Bamber et al. 1978, Burrows and Bullock 1999). Moreover, this is also the reason why it is not possible to discern a precise arrangement of transfusion tissue in the Patagonian leaves. Even though the tissue in the Patagonian leaves is poorly preserved above the xylem, its arrangement partially resembles that of the three araucarian genera due to a characteristic inverted, U-shaped arc enclosing each vascular bundle (Fig. 4c) (Kausik and Bhattacharya 1977, Hu and Yao 1981, Mastroberti and Mariath 2003).

The conifer leaves from the La Matilde Formation appear to have a closer affinity to the large, broad and multi-veined leaves of the living Araucariaceae rather than those of *Nageia* of the Podocarpaceae or the permineralized ones from Antarctica, Australia and Japan. The Patagonian leaves exhibit anatomical features that more closely resemble those present in the genus *Araucaria*, such as the presence of stomata in both epidermises, an isobilateral mesophyll, densely packed palisade cells and transfusion tissue above the xylem. However, some key anatomical features are not preserved in the Patagonian specimens such as the precise position of resin canals, the presence of mucilage cells or the arrangement of transfusion tissue, which make it difficult to assign a relationship to some living species of *Araucaria*.

Additionally, the anatomy of associated conifer-like stems (Fig. 5a, c, e) shows wood characters of unquestionable araucarian affinity (Philippe 1993, 1995, Philippe and Bamford 2008), such as contiguous bordered pits on the radial walls of tracheids, uniseriate rays and cross-fields with numerous, contiguous alternate bordered pits (Fig. 5b, d, f).

PALAEONVIRONMENT AT BARDA BLANCA LOCALITY

According to Mazzoni et al. (1981) and De Barrio et al. (1999) the sediments of the La Matilde Formation at Barda Blanca locality exhibit a continental sequence, characteristic of a low energy fluvial environment. These authors have also indicated that the presence of laminated pelitic deposits associated with carbonaceous levels may indicate the occurrence of several water bodies (shallow lagoons or swamps) in the flood plains, which in part exhibited marshy conditions (lentic and reducing). Simultaneous, with the La Matilde deposition, intense volcanism developed in more remote areas, whose pyroclastic products were deposited by ash and volcanic dust in the same sediment basin (Panza and Irigoyen 1995). In addition, the sedimentological data allowed Mazzoni et al. (1981) to point out that the La Matilde Formation was deposited in a humid and warm paleoclimate. These environmental conditions are supported by the diverse biota found within the La Matilde Formation sediments, including ferns (Herbst 2003), Equisetaceae (Falaschi et al. 2009), anurans (Baéz and Nicoli 2004) and gymnosperm woods with marked growth rings (Gnaedinger 2007a), among others. In general, this is in accordance with the Jurassic paleoclimate data provided by Volkheimer (1969) and Volkheimer et al. (2008) who have suggested that climatic changes for the La Matilde Formation would have occurred during its deposition, from a short period of sub-humid, then semi-arid and finally arid conditions during the Middle-Upper Jurassic.

Because plants are quite sensitive to environmental conditions, they most often respond by developing foliar anatomical features that are adapted according to whether the habitat they grow in is xeric, mesic or hydric (Pyykkö 1966, Fahn and Cutler 1992). Particularly, the permineralized leaves from the La Matilde Formation show thick-

walled epidermal cells, a well-marked palisade parenchyma on both surfaces and well-developed mechanical tissue composed of hypodermal cells one to four layers deep. Furthermore, these foliar characteristics are recognized as xeromorphic anatomical features, which are developed by plants, so-called xerophytes that inhabit either a dry climate or a dry or low-nutrient substrate (Fahn and Cutler 1992). Accordingly, leaves from the La Matilde Formation agree with the generally accepted concept that the anatomy of the conifer leaf is in most cases xeromorphic (Chamberlain 1935, Ghimire et al. 2014, among others).

The presence of thick-walled epidermal cells and hypodermal layers in the Patagonian leaves may indicate that the parent plants probably lived in a dry, sunny habitat and that the development of such features would have offered the cells protection against the effects of excessive light or against the mechanical action of the wind, as well as prevent the collapse of vital chlorenchyma. These particular foliar adaptations are also observed in extant plants that grow in xeric conditions (Pyykkö 1966, Burrows 2001). However, Fahn and Cutler (1992) have pointed out that similar characters are also exhibited in plants adapted to cold winter desiccation, such as in the conifer *Pseudotsuga menziesii*.

Pyykkö (1966) and Burrows (2001) have found that most living xeromorphic species inhabiting areas with ample light either in East Patagonia or in New South Wales, exhibit an isobilateral mesophyll distribution with well-developed palisade tissue. Additionally, Pyykkö (1966) has proven that longer palisade parenchymal cells occur in plants that grow in habitats with sufficient water availability, whereas palisade cells become shorter in comparatively drier habitats. Accordingly, leaves with marked-developed palisade tissue evaporate more water per unit area of the epidermis than those that have a less developed and less compact palisade parenchyma (Pyykkö 1966). Because the Patagonian fossil leaves

are isobilateral with well-developed palisade tissue exhibiting long and compact parenchymal cells, it may suggest that the environmental conditions of the parent plant's habitat during the deposition of the La Matilde Formation was most likely exposed to a high light intensity and an adequate quantity of water in the soil.

Burrows (2001) has found in 39 xeromorphic species from Australia a strong correlation between isobilateral mesophyll distribution and an amphistomatous condition, as was observed in the Patagonian fossil leaves. On the other hand, Parkhurst (1978) has pointed out that thick leaves are likely to be amphistomatous, and this relation has also been found in the Patagonian fossil specimens, considering that these leaves are 800 μm thick. Amphistomatous leaves are considered better adapted to increasing maximum leaf conductance of CO_2 than hypostomatous leaves (Mott et al. 1982). These authors have suggested that plants with high photosynthetic capacity have an advantage when growing in regions with high solar radiation and rapid fluctuations in available soil water. Accordingly, due to the foliar thickness and the amphistomatous conditions shown by the fossil leaves, it is suggested here that the parent plants would have been most likely adapted to an environment with high light intensity and sufficient water availability, allowing for a maximum photosynthetic CO_2 uptake.

CONCLUSIONS

The fossil material described herein represents the first anatomically preserved conifer-like leaves to be characterized from the Middle Jurassic La Matilde Formation in southern Patagonia. Leaves are assigned to conifers based on the following foliar features: thick-walled epidermal cells, a sclerenchymatic hypodermis, a mesophyll differentiated into palisade and spongy tissues, resin canals and transfusion tracheids associated with

the vascular bundle. The assignment to conifers is reinforced by the close association of the single leaves with young, conifer-like stems.

Anatomically, all of the permineralized leaves show identical foliar characters and, thus, suggest that they were all likely produced by the same parent plant. Additionally, the occurrence of well-developed palisade tissue and hypodermal fiber layers in all specimens suggest that all of the leaves were mature at the time of fossilization.

Based on the size and shape of the blade sections and the disposition of the foliar tissues exhibited by the permineralized Patagonian foliage, it is presumed that the morphology of the leaves was most likely large, broad and linear-lanceolate. Additionally, the preserved foliar anatomical features show that the leaves were amphistomatic with an isobilateral and well-developed mesophyll, possessed resin canals with rectangular-elongate epithelial cells, an unistratified epidermis, a hypodermis formed by 1 to 4 fiber layers, were multi-veined with collateral vascular bundles, and had helical thickening walled xylem tracheids and adaxially contiguous transfusion tracheids.

Although the Patagonian fossil leaves are more closely resemble conifers, it is difficult to assign them to any known family due to the poor preservation of some key foliar tissues. Among conifers with large, broad and multi-veined leaves, the foliar anatomical features of the specimens from the La Matilde Formation show a certain affinity to those of the Araucariaceae, especially those exhibited by the species of the *Araucaria* sections, *Araucaria* and *Bunya*. These features include the occurrence of stomata in both surfaces of the epidermis, an isobilateral mesophyll, densely packed palisade cells and transfusion tissue above the xylem. In the fossil leaves, it was not possible, due to the preservation, to determine the exact arrangement of transfusion tissue, the position of resin canals and the presence of mucilage cells. Therefore, the Patagonian leaves cannot be

placed in any known living species of *Araucaria*. However, the anatomical features observed in the fossil leaves are perhaps most similar to extant *A. araucana*, which is an endemic taxon of southern Patagonia.

As is the case for most conifer leaves, the Patagonian fossil specimens show xeromorphic foliar anatomical features, which include thick-walled epidermal cells and well-developed palisade and mechanical tissues. Furthermore, the occurrence in the permineralized leaves of an isobilateral mesophyll and stomata distributed along both foliar surfaces may suggest that during the deposition of the La Matilde Formation, the parent plant was well adapted to the environmental conditions, which most likely included a high light intensity and an adequate quantity of water in the soil, increasing the maximum leaf conductance of CO₂.

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AUTHOR CONTRIBUTIONS

All the authors participated equally in the design and carrying out the research and in the writing of the manuscript.

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