Review of Palaeobotany and Palynology 256 (2018) 1–12

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

A new cycad trunk from the Palaeocene in the Neuquén Basin, Patagonia (Argentina)

L.C.A. Martínez [a,c,*], E.G. Ottone [b], A.E. Artabe [c]

[a] Instituto de Botánica Darwinion (CONICET-ANCEFN), Labarden 200, San Isidro B1642HYD, Buenos Aires, Argentina
[b] Instituto de Estudios Andinos Don Pablo Groeber-CONICET, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón n° 2, Ciudad Universitaria, C1428EHA Buenos Aires, Argentina
[c] Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, La Plata B1900FWA, Argentina

ARTICLE INFO

Article history:
Received 15 December 2016
Received in revised form 9 May 2018
Accepted 19 May 2018
Available online 22 May 2018

Keywords:
Cycadales
South America
Anatomy
Systematics
Danian
Cenozoic

ABSTRACT

To date only two genera of cycad stems have been described from Cenozoic strata (*Bororoa* and *Menucoa*). We describe a new species of *Wintucycas*, *Wintucycas beatrizae* sp. nov. (Encephalartoideae), from the basal Palaeogene of Patagonia. The new species is based on anatomically preserved mature cycadalean stems which have been recovered from the Pichaihue Limestones (Neuquén Basin, Patagonia, Argentina). The new species is characterized by the presence of a columnar stem with an armor of persistent leaf bases, vascular bundles displaying an omega pattern, the absence of cataphylls, a wide pith with medullary vascular bundles, mucilage canals and idioblasts, a polyxylic vascular cylinder, inverted xylem, and manoxylic wood. The presence of *W. beatrizae* sp. nov. in the Pichaihue Limestones suggests warm climate conditions during the early Palaeogene in the Neuquén Basin, and also extends the range of this genus of Cycadales (Encephalartoideae) into the Cenozoic.

1. Introduction

The extant cycads are surviving representatives of once diverse or abundant group of Mesozoic plants. In this sense, the Cycadales are living fossils and the most antique and primitive of living seed-bearing plants, with an origin in the Permian (Mamay, 1969; Zhu and Du, 1981; Du and Zhu, 1982; Gao and Thomas, 1989).

The cycads are a monophyletic group, according to both morphological and molecular studies (Stevenson, 1990, 1992; Chase et al., 1993; Soltis et al., 2002). Some of the anatomical characters considered as synapomorphies are girdling leaf traces, coralloid roots, cycasins, an omega pattern of vascular bundles in the petiole base and primary-thickening meristem derivatives produced centrifugally (Stevenson, 1990, 1992; Soltis et al., 2002). Nevertheless, relationships among the living taxa of cycads raise many questions and, at present, the molecular data are still not consistent with the morphological data (Hill et al., 2003; Zgurski et al., 2008). This situation becomes more complex when fossil taxa are included (Hermsen et al., 2006; Cúneo et al., 2010; Martínez et al., 2012). On the other hand, some relationships are well supported in those analyses: *Cycas* L. as a sister group of all other cycads, *Ceratozamia*–*Microcycas*–*Zamia* clade, and an *Encephalartos*–*Lepidozamia*–*Macrozamia* clade (Hermsen et al., 2006; Cúneo et al., 2010; Martínez et al., 2012).

The clade that groups *Encephalartos* Lehmann, *Lepidozamia* Regel and *Macrozamia* Miquel, also includes most of the fossil taxa Patagonia (*Menucoa* Petriella, *Neochamberlainia* Artabe, Zamuner et Stevenson, *Worsdellia* Artabe, Zamuner et Stevenson, *Wintucycas* Martínez, Artabe et Bodnar, and *Zamuneria* Martínez, Iglesias et Artabe) (Martínez et al., 2012, 2017).

In this paper, we describe a new species of *Wintucycas* from the basal Palaeogene of the Neuquén Basin. This new record expands the past diversity of Encephalarteae in the South American. Furthermore, the occurrence of *Wintucycas* in the Pichaihue Limestones provides additional information on the climate and the palaeoecology at the time of deposition of this unit.

2. Geological setting

The Andean system records the development of a series of forearc and retroarc basins along the western margin of Gondwana. One of these, the retroarc Neuquén Basin, extends from 35–39°S to 69–70°W in west-central Argentina (Ramos, 1999). The Neuquén Basin is exposed in the Principal Cordillera as a narrow belt that, south of 36°S, expands towards the eastern foreland forming the large Neuquén embayment (Legarreta and Uliana, 1991, 1999). The Neuquén Basin comprises

---

* Corresponding author at: Instituto de Botánica Darwinion (CONICET-ANCEFN), Labarden 200, San Isidro B1642HYD, Buenos Aires, Argentina.

E-mail addresses: lmartinez@darwin.edu.ar, (L.C.A. Martínez), ottone@gl.fcen.uba.ar (E.G. Ottone).

https://doi.org/10.1016/j.revpalbo.2018.05.006

succession of marine and continental sedimentary rocks, more than 6000 m thick that ranges from the Late Triassic to the Palaeogene, and accumulated in a variety of conditions (Legarreta and Gulisano, 1989; Legarreta and Uliana, 1991; Howell et al., 2005).

The infill of the Basin begins with a series of pyroclastic, volcanic and epiclastic deposits referred to the Precuyano Cycle (Late Triassic–Early Jurassic) (Carbone et al., 2011). These rocks are overlain by the "mostly marine" Cuyo (Toarcian–Callovian), Lotena (Callovian–Oxfordian), and Mendoza (Kimmeridgian–early Barremian?) groups, and the Bajada del Agrio (also known as Rayoso) Group (Barremian–Albian), which represent the end of the marine Pacific transgressions into the region (Leanza and Hugo, 2005). The Upper Cretaceous comprises the continental – dinosaur rich – beds of the Neuquén Group, and the continental, volcaniclastic and marine beds of the Malargüe Group (Garrido, 2011; Rodríguez, 2011). The Malargüe Group includes a cycle of marine deposition related to the opening of the Atlantic (Weaver, 1927; Uliana and Dellapé, 1981; Barrio, 1990).

The silicified plant material studied herein was recovered ca. 55 km southwest of the Chos Malal locality, near the village of Colipilli from the Maastrichtian–Danian Pichaihue Limestones, which are in part equivalent to the Malargüe Group (Aguirre-Urreta et al., 2011) (Fig. 1). Pichaihue is a classic locality of the Neuquén Basin where, as early noticed by Groeber (1952), the widespread Neuquén Group is absent, and thus the Pichaihue Limestones unconformably overlie the andesites, andesitic volcanic agglomerates and tuffs of the Late Cretaceous Colipilli Group (Zamora Valcarce et al., 2006, 2007).

The Pichaihue Limestones crop-out in the vicinity of Cerro León as isolated patches on the Colipilli volcanics, and constitute probable erosional remains of a larger, continuous cap (Aguirre-Urreta et al., 2011). The main outcrop, where the fossil plants here studied have been recovered, is ca. 1 km northwest from Cerro León, an eastern flank of the Colipilli syncline (Figs. 1 and 2).

The section is composed of interbedded pyroclastic flows, tuffs, limestones and stromatolites. The base is not exposed and its lower part is characterized by proximal pyroclastic flows that include several amalgamated levels. The fossil plant horizons appear interbedded towards the top of the flow deposits. The fossil assemblage includes abundant logs of regularly preserved pycnoxylic wood, up to 1.4 m long, palms (*Palmoxylon pichaihuensis* Ottone, 2007), and rare trunks of cycads that are entombed by a mostly covered, friable, probably tuffaceous bed, which is 3–4 m thick. The trunks show random directional orientations and distributions and probably comprise an allochthonous or parautochthonous accumulation (Ottone, 2007, 2009).

These levels are covered by well-stratified, whitish, tuffaceous deposits. A tuff sample placed ca. 6 m. over the plant levels yielded a U–Pb SHRIMP age of 64.3 ± 0.9. These deposits are distal pyroclastic flows and contain few ostracods, preserved as moulds. Horizon transitionally pass upward to decimetric beds of strongly silicified mudstones, wackestones, and bioclastic packstones with a few bivalves and serpulids, overlain by whitish tuffaceous deposits that contain abundant poorly preserved ostracods and bivalves. The succession finishes upwards with a calcareous interval containing well preserved stromatolites and oncolites with scarce gastropods. The stromatolites are decimetric beds with very thin lamination. The oncolites are isolated subespherical bodies up to 2.5 cm with light–dark couplets of lamina. The top levels are brecciated, indicating a later exposure of the carbonates. The total thickness of the section is about 20 m. The presence of stromatolites, oncolites, ostracods, serpulids, bivalves and gastropods, as well as silicified plant stems, suggests a shallow marine, partially brackish environment associated with non-marine deposits (Aguirre-Urreta et al., 2011).

3. Materials and methods

The material studied comprises four well-preserved silicified cycad trunks. In order to study the anatomy, thin sections were made using traditional techniques; transverse (TS), radial (RLS) and tangential (TLS) sections were made. Cell dimensions are based on at least 25

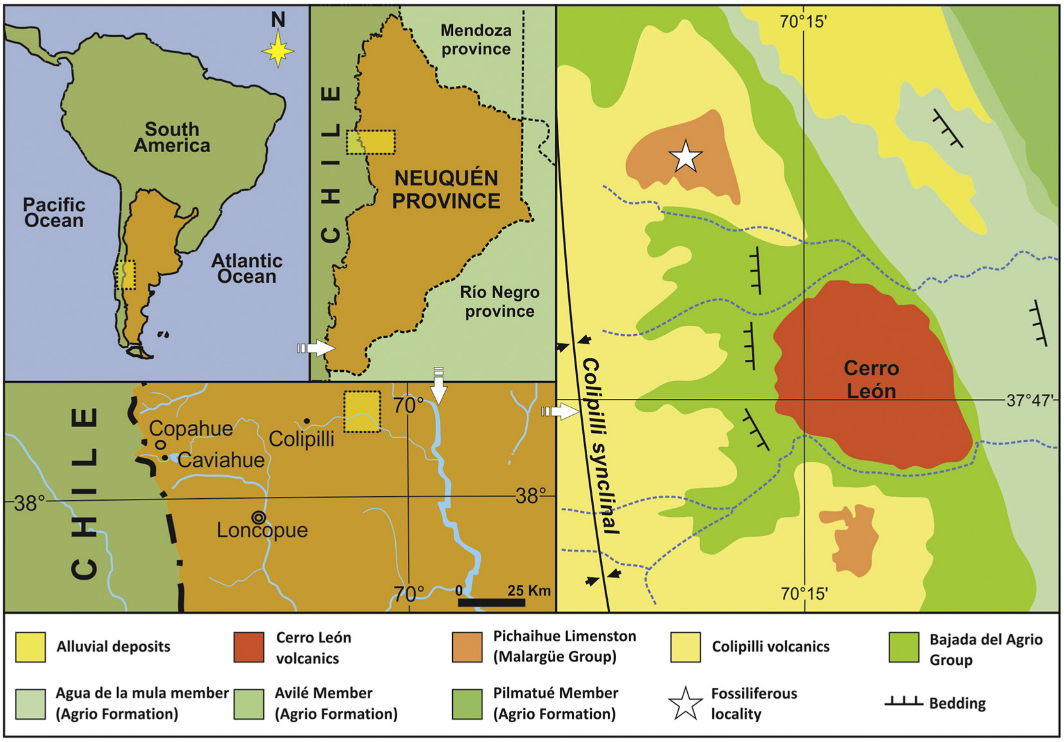

Fig. 1. Location map of Pichaihue (PI), Neuquén Province, Argentina.

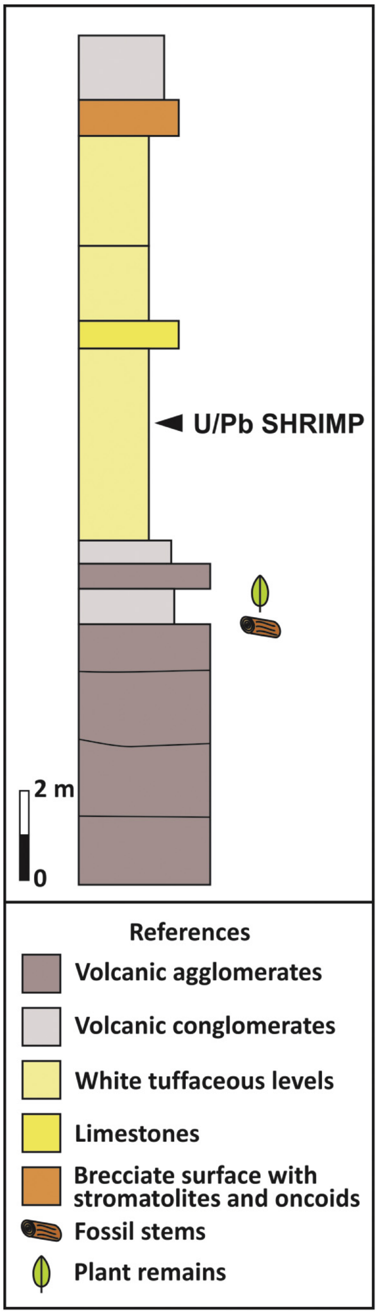

Fig. 2. Logged section of eastern Pichaihue area with fossil plants horizons. (Modified from Aguirre-Urreta et al., 2011.)

measurements; the numbers in parentheses indicate the minimum and maximum values.

The fossil wood and thin sections are deposited in the palaeontological collections of the Museo Provincial de Ciencias Naturales Profesor Dr. Juan A. Olsacher (Zapala, Neuquén Province, Argentina) (MOZ–Pb), and the palaeobotanical collection of the Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina (BAFC–Pb).

In order to improve description and make more comparisons, original pieces and thin sections of other fossil taxa (e.g. *Michelilloa*, *Vladiloxylon*, *Zamuneria*, *Neochamberlainia*, *Brunoa*, *Worsdellia*, *Wintucycas*, *Bororoa* and *Menucoa*) were examined.

3.1. Systematic palaeobotany

Order CYCADALES Dumortier, 1829
Suborder Zamiineae Stevenson, 1992
Family ZAMIACEAE Reichenbach, 1837
Subfamily Encephalartoideae Stevenson, 1992
Genus ***Wintucycas*** Martínez, Artabe et Bodnar
Type species: *Wintucycas stevensonii* Martínez, Artabe et Bodnar
Wintucycas beatrizae Martínez, Ottone et Artabe sp. nov.

Species diagnosis: Manoxylic secondary xylem and phloem with primary and secondary rays. Secondary xylem tracheids with araucarioid pitting. Primary rays with parenchymatic cells and secretory cells (mucilage canals). Secondary rays with homocellular parenchymatic cells. Secondary phloem with sieve and sclerenchymatic cells. Foliar traces with a classic omega pattern. Leaf bases with simple and unbranched trichomes in a continuous layer on the adaxial side.

Holotype: MOZ–PB 567.

Thin sections: MOZ–PB 567a, MOZ–PB 567b, MOZ–PB 567c, MOZ–PB 567d, MOZ–PB 567e, MOZ–PB 567f.

Paratypes: MOZ–PB 6264, BAFC–Pb 16956, BAFC–Pb 17029, BAFC–Pb 17030, BAFC–Pb 17031, BAFC–Pb 17032, BAFC–Pb 17033.

Type locality: Pichaihue, Loncopué Department, Neuquén Province, Argentina.

Type straum: Pichaihue Limestones.

Age: Considering that a tuff placed ca. 5 m. over the plant levels yielded a U–Pb SHRIMP age of 64.3 ± 0.9, the fossil plant horizon is referred to the basalmost Palaeocene (Danian).

Etymology: The name was given in honour to Dr. Beatriz Aguirre-Urreta in recognition of her studies on fossils of Neuquén Basin.

Figures. Plates I–V.

4. Description

The stem is columnar (pachycaulous) with an armour of persistent leaf bases, and lacks cataphylls. The diameter reaches 0.15 m in average, and its length is incomplete, varying between 0.22 m and 0.30 m, depending on the specimen (Plate I, 1–3).

In cross-section, four areas are distinguished in the stem: the pith, the polyxylic vascular cylinder, the cortex, and persistent leaf bases (Plate I, 4).

4.1. Pith

Because of its lateral compression, the pith is circular to oval in cross section, with 3.8 cm × 2.8 cm in diameter, and it occupies the centre of the stem (Plate I, 4). The pith is composed by parenchymatous cells, idioblasts, mucilage canals, and the medullary vascular system (Plate II, 1–2).

The fundamental parenchyma cells are generally isodiametric and thin walled, with an average diameter of 57.8 μm (19.3–115.9). Most of the parenchyma cells have dark contents, with probably starch grains and idioblasts with gum-like material (Plate II, 2–3).Transfusion cells were not observed, probably by the preservation state of the fossils.

The medullary vascular system displays a radial pattern from the centre to peripheral zone in the pith (Plate II, 1), close to the vascular cylinder a ring-like band of mucilage canals borders the pith (Plate II, 1–2). The medullary vascular system consists of secondary vascular bundles (Plate II, 2–3). These vascular bundles are numerous, free or sometimes anastomosed (Plate II, 3), from circular to ovoid in outline, collaterals, composed of xylem and phloem, and usually accompanied by a mucilage canal (Plate II, 2–4). In cross section, each bundle measures 383 μm (212–549.9) in radial diameter, and 515.3 μm (242.1–779.9) tangentially (Plate II, 4). The mucilage canals are circular to ovoid in outline, with a diameter of 91.7 μm (40.6–148.8). They are composed by secretory cells to form an internal lumen to store mucilage

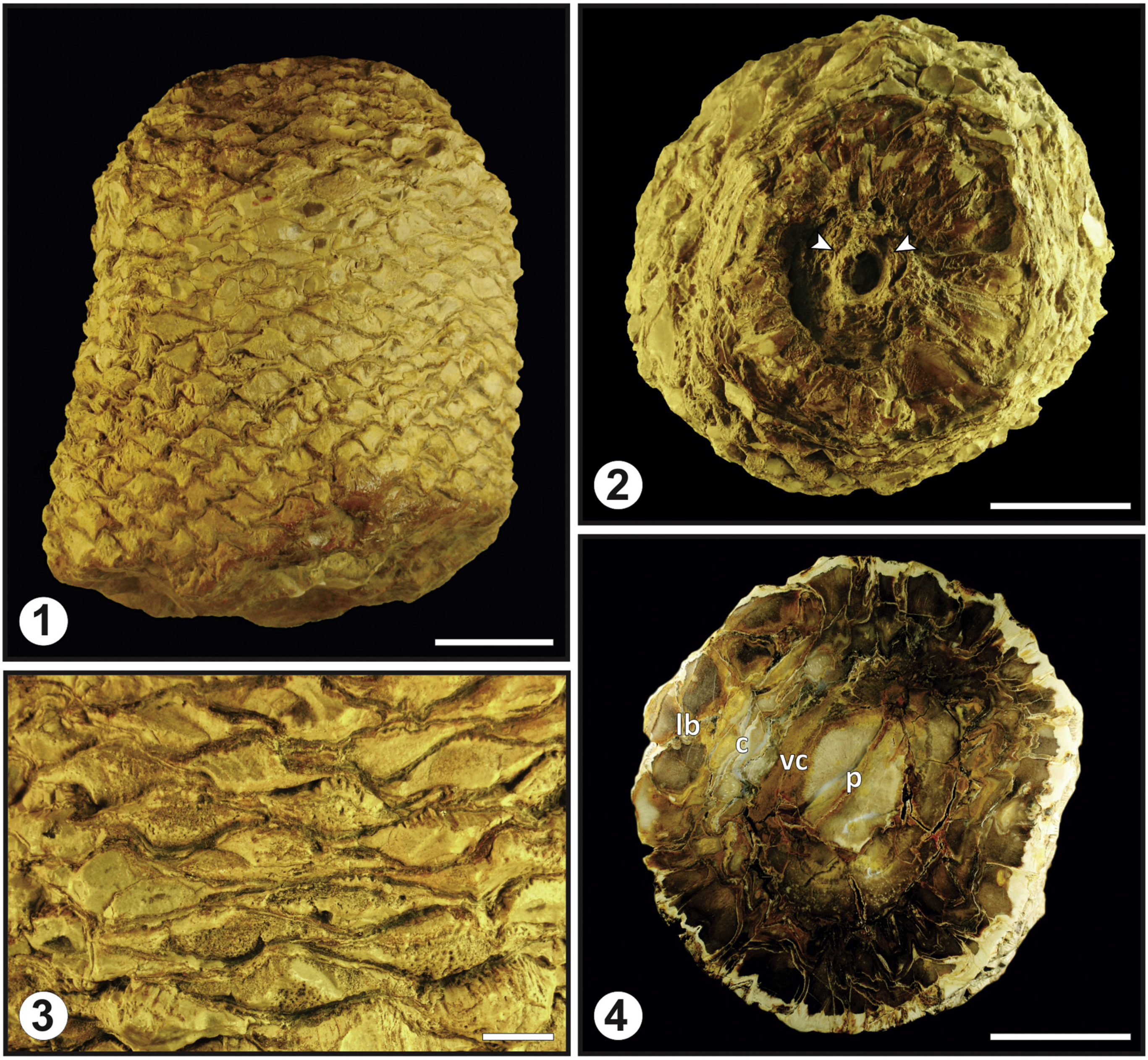

Plate I. *Wintucycas beatrizae* sp. nov. Martínez, Ottone et Artabe. Holotype (MOZ–PB 567). 1. General view of the stem. Scale bar = 5 cm. 2. Apical view of stem (arrows). Scale bar = 5 cm. 3. External views of stem, detail of leaf bases. Scale bar = 1 cm. 4. Cross-section (TS) of the stem. Detail of pith (p), vascular cylinder (vc), cortex (c) and leaf bases (lb). Scale bar = 5 cm.

(Plate II, 4–6). The epithelial cells lining the mucilage canals have the nuclei preserved (Plate II, 5–6).

The medullary bundles are not related to reproductive structures, and do not form regularly arranged rings, for these reasons they are not related to cone domes.

4.2. Cylindrical vascular system

The cylindrical vascular system has centrifugal and centripetal growth patterns (Plate II, 7 and Plate III, 1).

The centripetal growth pattern consists of a small cycle of perimedullar vascular bundles adjacent to the innermost continuous ring of the centrifugal vascular system (Plate II, 7 and Plate III, 1).

The centrifugal vascular system comprises many sympodia of endarch primary xylem in a circumferential arrangement, and it lays in the peripheral part of the pith thus forming a typical eustele. The sympodia of primary xylem and secondary rays are separated by wide multiseriate parenchymatic rays (primary rays) that continue across the centrifugal vascular system, connecting the pith to the cortex (Plate III, 1–2). Primary xylem has tracheids that are oval to square in cross section; they have an average radial diameter of 16.7 μm (8.3–29.7) and a tangential diameter of 23.4 μm (7.8–37.8) (Plate III, 1–2). The primary ring of vascular bundles is followed by several rings of secondary xylem and phloem (polyxylic). The successive rings of centrifugal secondary xylem and phloem are well developed (Plate III, 4–5, Plate IV, 4). In the holotype, the inner ring is more developed than the outermost one (Plate III, 4), and in the inner area between the first

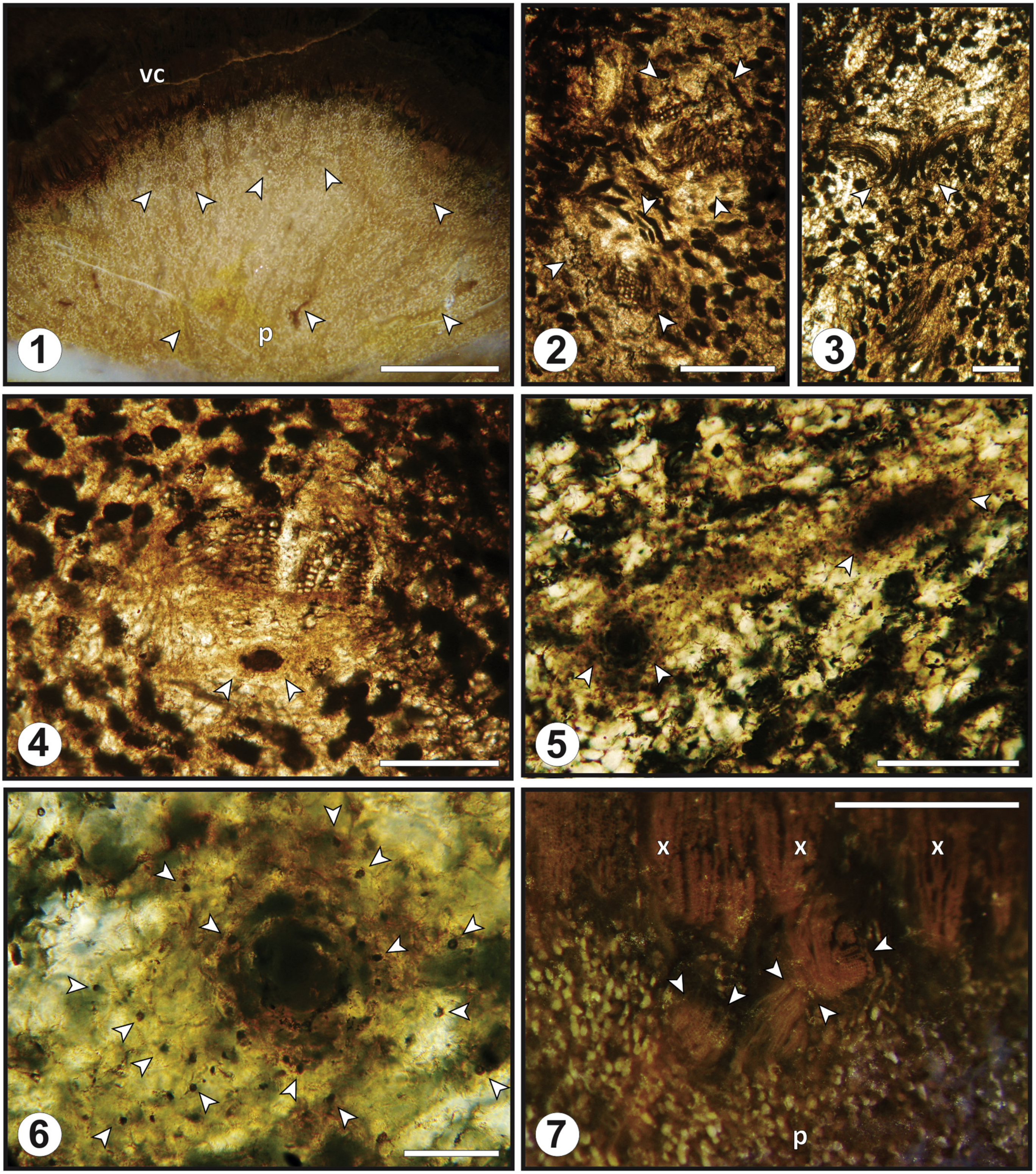

Plate II. *Wintucycas beatrizae* sp. nov. Martínez, Ottone et Artabe. Holotype. All LM. 1. TS. Pith with mucilage canals (white arrows). Scale bar = 1 cm. 2. TS. Pith. Detail of mucilage canals surrounded the pith (arrows). Scale bar = 500 μm. 3. TS. Pith. Medullary vascular bundles anastomosed (arrows). Scale bar = 500 μm. 4. TS. Pith. Medullary vascular bundle and mucilage canal (arrow). Scale bar = 500 μm. 5. TS. Pith. Mucilage canal (arrow). Scale bar = 500 μm. 6. TS. Pith. Mucilage canal, detail of cells with nuclei preserved (arrows). Scale bar = 100 μm.7. TS. Pith (p), centripetal vascular bundles (white arrows), and secondary xylem (x). Scale bar = 1 mm.

ring and the second ring, there are centripetal xylem bundles, which are triangular in cross section (Plate II, 7).

In the secondary xylem, the tracheids are rectangular to square with a mean radial diameter of 35.5 μm (11.9–63.1) and a tangential diameter of 23.4 μm (7.8–37.8) (Plate III, 3–5). The secondary phloem is composed by sieve, and sclerenchymatic cells (Plate III, 4–5). The vascular segments of secondary xylem and phloem are separated by primary rays with a width of 883 μm (639–1080) (Plate III, 3–5).

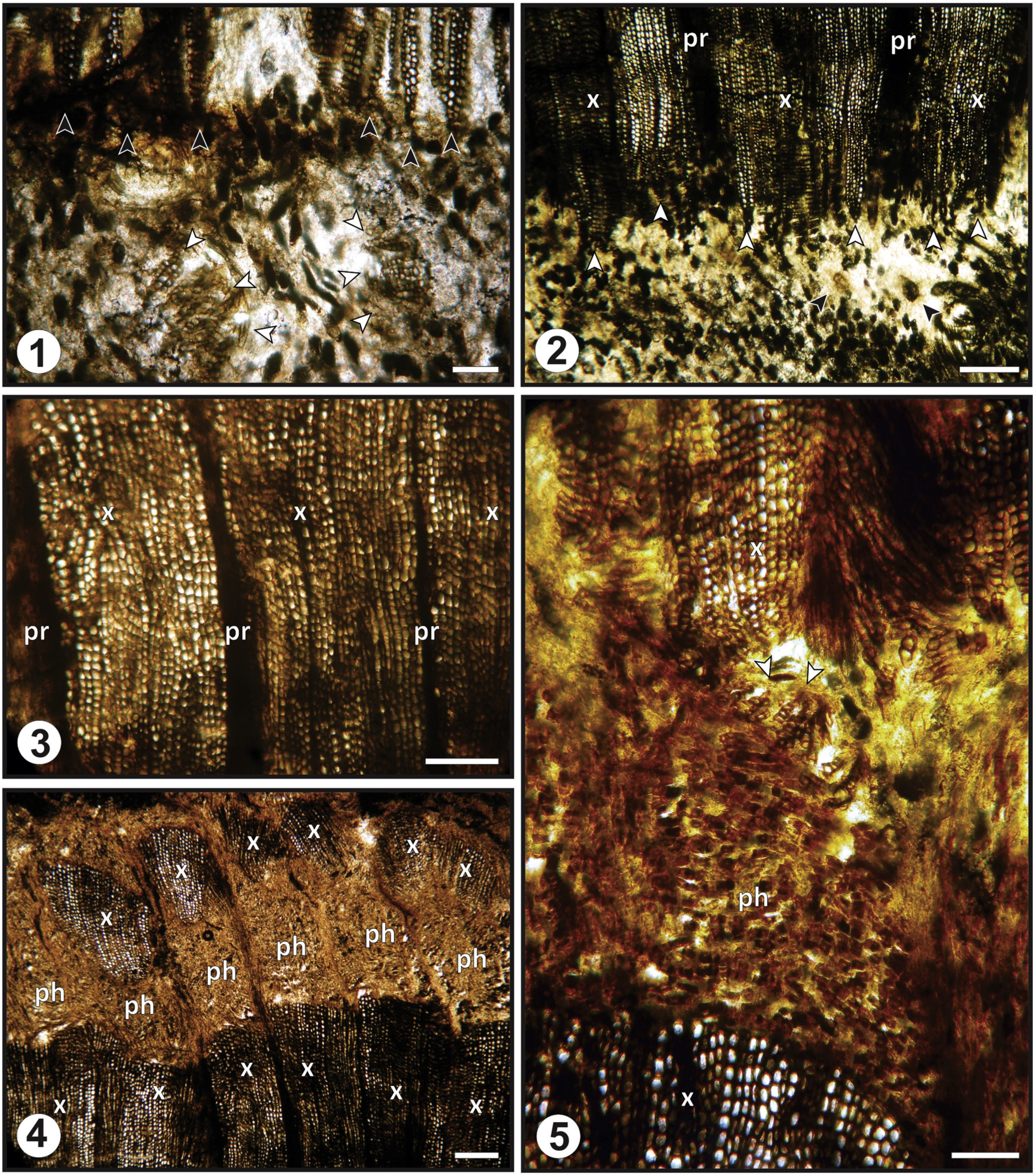

Plate III. *Wintucycas beatrizae* sp. nov. Martínez, Ottone et Artabe. Holotype. All LM. 1. TS. Pith and vascular cylinder. Centripetal vascular bundles (white arrows) and primary xylem endarch (black arrows). Scale bar = 200 μm. 2. TS. Vascular cylinder. Primary xylem endarch (white arrows), primary rays (pr), secondary xylem (x), and mucilage canals (black arrows). Scale bar = 500 μm. 3. TS. Vascular cylinder. Secondary xylem (x) and primary rays (pr). Scale bar = 300 μm. 4. TS. Vascular cylinder. Polyxylic cylindrical vascular system, xylem (x) and phloem (ph). Scale bar = 500 μm. 5. TS. Vascular cylinder. Polyxylic cylindrical vascular system (detail), xylem (x) and phloem (ph). Centripetal vascular bundle (white arrows). Scale bar = 200 μm.

In the radial section, the tracheids of secondary xylem have araucarioid pitting with contiguous alternate uniseriate to triseriate flattened and hexagonal pits on the radial walls (Plate IV, 1). The pits have a horizontal diameter of 12 μm (8.6–16.5), and a vertical diameter of 9.3 μm (6.7–13.9) (Plate IV, 1). The crossfield pitting is not preserved.

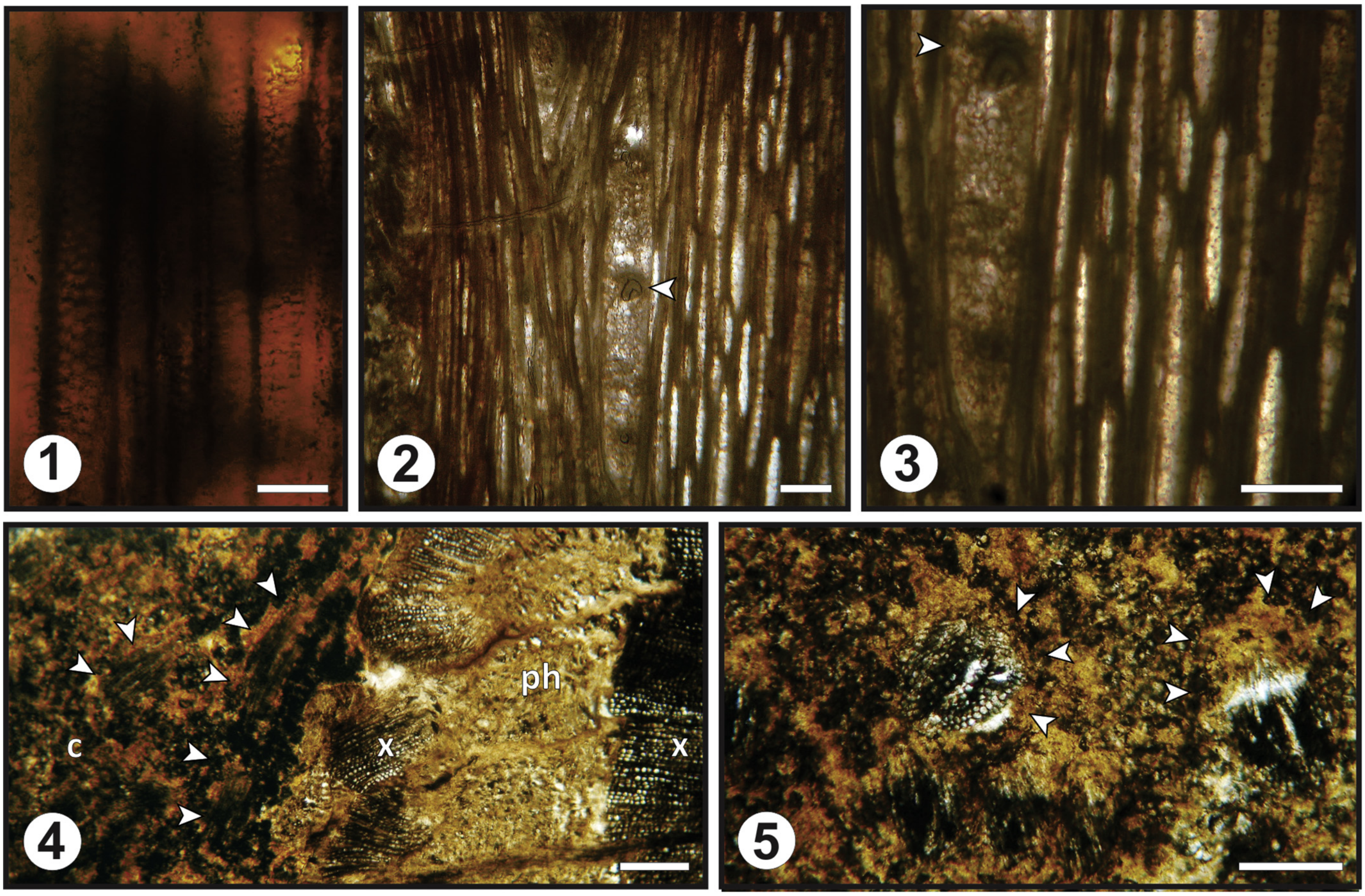

Plate IV. *Wintucycas beatrizae* sp. nov. Martínez, Ottone et Artabe. Holotype. All LM. 1. Radial section (RLS). Vascular cylinder. Xylem. Hexagonal radial pits. Scale bar = 50 μm. 2. Tangential section (TLS). Vascular cylinder. Xylem. Tracheids and rays. Primary rays with mucilage canals (arrow). Scale bar = 300 μm. 3. TLS. Vascular cylinder. Primary and secondary rays (detail). Scale bar = 300 μm. 4. TS. Vascular cylinder and cortex. Xylem (x), phloem (ph), cortex (c), and girdling traces (arrows). Scale bar = 500 μm. 5. TS. Cortex. Vascular bundles (arrows). Scale bar = 500 μm.

In the tangential section, two types or rays are distinguished: primary and secondary rays. The primary rays are multiseriate and heterocellular, and consist of parenchymatic and secretory cells (mucilage canals). The primary rays have a mean diameter of 290 μm (170–520), and are 2033 μm (823–4014) in height. Inside the primary rays there is a mucilage canal; in the samples studied, vascular bundles were not observed (Plate IV, 2–3).

The secondary rays are commonly 1-seriate to 3-seriate and homocellular, and are composed by parenchyma cells, 44 μm (15 μm–82 μm) in diameter, and 432 μm (97–1068) in height (Plate IV, 2–3).

The parenchyma cells of rays are oval to rectangular in outline, with a mean diameter of 57 μm (28–101), and 46 μm (30–65) in height (Plate IV, 3).

4.3. Cortex

In cross section, the cortex is located between the cylindrical vascular system and the leaf bases. It has a mean diameter of 10 mm (9.4–11.3), and is composed by parenchyma cells, idioblasts, mucilage canals and leaf traces.

The parenchyma cells and idioblasts are similar to those found in the pith. The parenchyma cells are isodiametric with an average diameter of 40.4 μm (12.6–104.3). There are many vascular bundles, which set off the vascular cylinder, with a curved path (girdling traces), ending in leaf bases (Plate IV, 4–5).

4.4. Leaf bases

The outer part of the stem is covered with an armour of helical, rhomboidal, persistent leaf bases, and lacks cataphylls (Plate I, 1–3). The leaf bases are 23.3 mm (14.15–30.73) wide, and 9.3 mm (5.87–12.51) high (Plate I, 3) and has a mean diameter of 35.3 mm (31.4–41.42) (Plate I, 4) in cross section.

In each leaf base we can differentiate four areas: the outermost is the epidermis with hairs (ramentum), followed by the hypodermis, a parenchymatous area, and the vascular inner area (Plate V, 1–2).

On the adaxial side of the leaf bases, the epidermis is covered by a continuous ramentum, and a thick cuticle (Plate V, 4). The ramentum is composed of a continuous stratum of simple and unbranched trichomes (Plate V, 3–4). The epidermis is supported by a 3-layered hypodermis of cells with thick walls (Plate V, 2–3). The leaf bases have vascular bundles, amorphous parenchyma cells, idioblasts and mucilage canals. Vascular bundles are numerous (more than 10 per leaf base) and develop an omega pattern (Plate V, 5). Close to vascular bundles, mucilage canals are also scattered inside the parenchyma of the leaf bases (Plate V, 5).

5. Discussion

The anatomical features present in the fossil stems described herein, such as the presence of a pachycaulous stem enclosed by an armour of

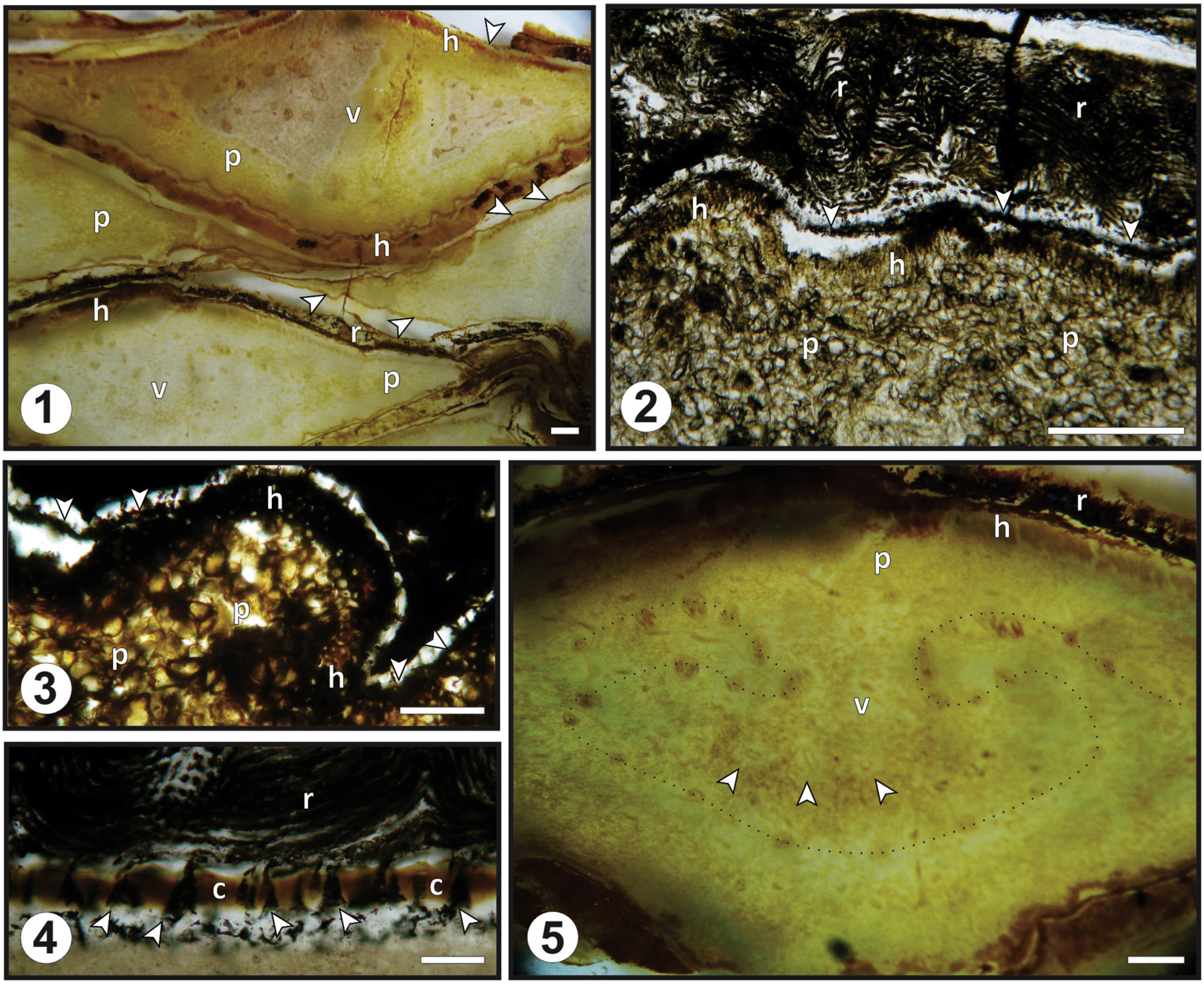

Plate V. *Wintucycas beatrizae* sp. nov. Martínez, Ottone et Artabe. Holotype. All LM. 1. TS. Leaf bases. General view, epidermis (arrows) with ramentum (r), hypodermis (h), parenchymatous area (p) and a vascular inner area (v). Scale bar = 1 mm. 2–3. CS. Leaf bases. Detail of ramentum with hairs (r), epidermis (arrows), hypodermis (h) and parenchymatous area (p). Scale bar = 300 µm. 4. TS. Leaf bases. Ramentum (r) with hairs with conical bases (arrows) and cuticle (c). Scale bar = 200 µm. 5. TS. General view, ramentum (r), hypodermis (h), parenchyma (p), vascular bundles in classic omega pattern (dotted line) and mucilage canals (arrows). Scale bar = 1 mm.

leaf bases with vascular bundles in an omega pattern, a parenchyma cortex with girdling traces, a centrifugal polyxylic vascular cylinder, centripetal and medullar vascular system with vascular bundles and mucilage canals in a parenchymatous pith, link our material to the Cycadales (Artabe and Stevenson, 1999; Greguss, 1968; Martínez et al., 2017; Stevenson, 1990, 1992).

5.1. Comparison among fossil stems

Several cycadalean stems around the world have been described from the Triassic to the Palaeogene. Five were recovered from Triassic beds: *Michelilloa* Archangelsky et Brett (1963) in Argentina; *Vladiloxylon* Lutz, Crisafulli, et Herbst (2003) in Chile; *Lyssoxylon* Daugherty (Gould, 1971) and *Charmorgia* Ash (1985) in the United States of America; and *Antarcticycas* Smoot, Taylor et Delevoryas (1985) emend. Hermsen, Taylor, Taylor et Stevenson (2006) in Antarctica. These genera have a monoxylic stem, a feature that clearly distinguishes them from the new species described herein.

Two genera of cycadealean stems have been described from the Jurassic of China: *Lioxylon* Zhang, Wang, Saiki, Li et Zheng (2006), and *Sinocycadoxylon* Zhang, Yang, Fu, Zheng et Wang (2012). These taxa share some features with the new species here described, such as the presence of polyxyly, and centripetal and centrifugal vascular systems; however, whereas the vascular centripetal system in the cycad trunk here described is undeveloped, both Chinese genera have a well-developed and continuous vascular centripetal system. The Indian fossil *Fascisvarioxylon* Jain (1962) is differentiated from the new species in possessing a monoxylic stem, cone domes and mucilage cavities.

In the Cretaceous, there are a considerable number of records and a diversity of cycad stems. *Sanchucycas* Nishida, Nishida et Tanaka (1991) is an incomplete stem from Japan assigned to Cycadales; this genus, which only preserves the vascular cylinder and the pith, differs from the Patagonian species in possessing mucilage cavities and in lacking a centripetal vascular system. *Centricycas* Cantrill (2000) from Antarctica is another incomplete stem that lacks polyxylic centrifugal vascular system, as in the fossil described above.

The rest of the Cretaceous/Palaeogene cycad trunks have been reported from Patagonia. All these taxa, *Menucoa* Petriella (1969), *Bororoa* Petriella (1972), *Worsdellia* Artabe, Zamuner et Stevenson (2004), *Brunoa* Artabe, Zamuner et Stevenson (2004), *Neochamberlainia* Artabe, Zamuner et Stevenson (2005, 2010), *Wintucycas* Martínez, Artabe et Bodnar (2012), and *Zamuneria* Martínez, Iglesias and Artabe (2017) are polyxylic, and display most of the features present in the new fossil described herein. However, *Brunoa* and *Bororoa* have cone domes, and the rest of the taxa, with the exception of *Wintucycas*, have cataphylls. The absence of cataphylls is a feature that distinguishes *Wintucycas* from other fossil genera, especially those from Patagonia (Martínez et al., 2012).

Wintucycas has a columnar stem covered by persistent, rhomboidal leaf bases. The parenchymatous cortex has mucilage canals, idioblasts and girdling leaf traces. The centrifugal vascular system is polyxylic, and the centripetal vascular system has small vascular bundles adjacent to the innermost ring. The pith is parenchymatous with mucilage canals, idioblasts and medullary vascular bundles. All those features presented in the generic diagnosis of *Wintucycas* match with the new species described herein.

Wintucycas was described from the Allen Formation (Upper Cretaceous) of the Neuquén Basin, with a single species: *Wintucycas stevensonii* Martínez, Artabe et Bodnar (Martínez et al., 2012). The fossil here described was assigned to a new species within this genus, *Wintucycas beatrizae* sp. nov. Martínez, Ottone et Artabe, which differs from *W. stevensonii* in having a smaller diameter of stems, leaf bases with a vascular bundles in an omega classic pattern, a continuous layer of hairs on the adaxial side of the leaf bases, and in lacking mucilage canals in the phloem.

5.2. Relationships among extant and fossil cycads

As *Wintucycas stevensonii*, and several of the cycad fossil stems from the Patagonia, *Wintucycas beatrizae* n. sp. is related to the Encephalarteae, by a group of characters such as the presence of a columnar stem, an arborescent habit, a persistent armour of leaf bases, centrifugal polyxyly, manoxyly, and a medullary vascular system (see Artabe et al., 2004, 2005a, 2005b; Martínez et al., 2017).

Wintucycas beatrizae sp. nov. has a stem covered by an armour of leaf bases, as well as the extant *Cycas*, *Dioon*, *Encephalartos*, *Lepidozamia* and *Macrozamia*, in contrast to *Microcycas*, *Ceratozamia* and *Zamia*, which show smooth stems, or *Bowenia* and *Stangeria*, which display naked and subterranean stems (Artabe et al., 2005a, 2005b; Norstog and Nicholls, 1997).

Wintucycas beatrizae sp. nov. shows centrifugal polyxyly and a centripetal vascular system. The centrifugal polyxyly is a common feature that is well developed in *Cycas* and in the Encephalarteae Tribe (e.g. *Encephalartos*, *Macrozamia* and *Lepidozamia*) (Greguss, 1968; Stevenson, 1990). A scanty development of the centripetal vascular system also occurs on the stem base of some species of *Cycas*, *Macrozamia*, *Lepidozamia* and *Encephalartos* (Worsdell, 1896, 1906). Furthermore, the medullar vascular system, a synapomorphy of the Tribe Encephalarteae (Stevenson, 1990, 1992), is well developed in *W. beatrizae*. Besides, the genus *Wintucycas* can be clearly distinguished from extant and fossil genera of Encephalarteae by the absence of cataphylls in the stem.

5.3. Palaeogeography, plant distribution and extinction

Plant communities with conifers, and occasional palms and cycads (zamiaceous forms) are known from the Early Cretaceous of Argentina (Del Fueyo et al., 2007; Passalía et al., 2010; Martínez et al., 2016). However, distinct plant assemblages of conifers, cycads (Encephalartoideae) and palms are characteristic of the Upper Cretaceous–Palaeocene of north Patagonia (Ottone, 2009; Andreis et al., 1991).

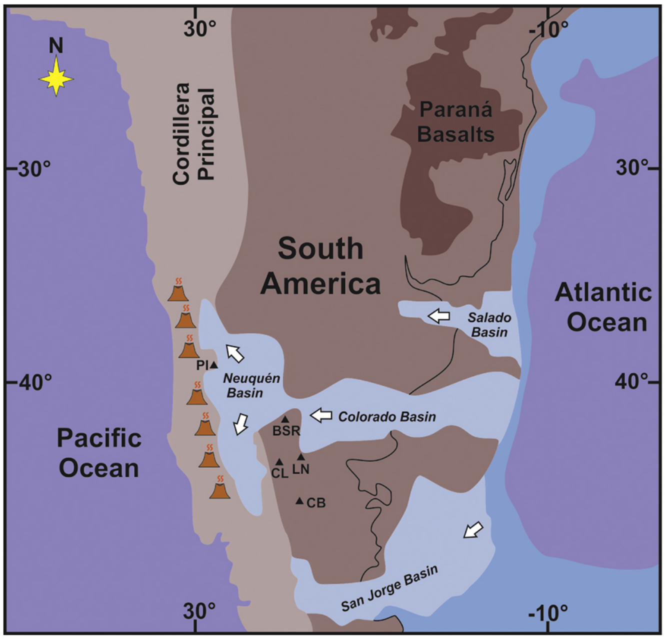

Fig. 3. Late Cretaceous palaeogeography and coeval Maastrichtian–Palaeocene localities of north Patagonia with similar palaeofloras: Bajo de Santa Rosa (BSR), Cari Laufquen Grande (CL), and Limen Niyeu (LN), Río Negro Province, and Cerro Bororó (CB), Chubut Province. Base map modified from Aguirre-Urreta et al. (2011).

This type of palaeoflora is present at Pichaihue, in one of the westernmost outcrops of the Malargüe Group in the Neuquén Province (Fig. 1), with conifer fossil woods, Encephalartoideae (*Wintucycas beatrizae* sp. nov.) and palms (*Palmoxylon pichaihuensis* Ottone) (Ottone, 2007, 2009; Aguirre-Urreta et al., 2011). Similar fossil assemblages are also present at Bajo de Santa Rosa (BSR), north of the Río Negro Province, in outcrops of the Allen Formation (Fig. 3), with Arecaceae, Podocarpaceae and Encephalartoideae (Andreis et al., 1991; Ancibor, 1995; Del Fueyo, 1998; Artabe et al., 2004, 2005a, 2005b; Ottone, 2009; Martínez et al., 2012); and, to the south of the Río Negro Province, at Limen Niyeu (LN) and Cari Laufquen Grande (CLG), in levels related to the Angostura Colorada Formation (Fig. 3), with Encephalartoideae and petrified wood, but without palms (Petriella, 1969, 1972, 1978; Artabe and Stevenson, 1999; Remesal et al., 2001; Ottone, 2009). Cycadales, Arecaceae and Podocarpaceae, together with abundant angiosperms were also recovered southward, at the Cerro Bororó Formation, Chubut Province (Fig. 3) (Arguijo, 1978, 1981; Petriella, 1969, 1972).

The distribution of cycads, conifers and palms in the Late Cretaceous/Palaeocene of north Patagonia was evidently constrained not only by climate, but also by the palaeogeography. The palaeofloras of the Pichaihue, the Allen and the Angostura Colorada formations progressed in an extended region located at about 38–42°S, relatively close to the margins of an inland sea formed by an Atlantic marine transgression that flooded the Colorado and Neuquén Basins (Aguirre-Urreta et al., 2011). The taphoflora of Pichaihue was developed on the Andean foothills, towards the west coast, whilst the palaeofloras of the Allen and Angostura Colorada formations progressed to the south of this epeiric sea (Ottone, 2009). The palaeoflora of Cerro Bororó was located more to the south, between the Neuquén and the San Jorge Basins (Fig.3).

After the Eocene, there are no records of cycads in Patagonia (Wilf et al., 2016). Their extinction could have been influenced by abiotic and biotic factors occurring in the Cretaceous. Among the abiotic factors, the Andean uplift (forming a topographic barrier) and global cooling (decrease atmospheric CO_2, inception of the Antarctic Circumpolar

Current) caused a drastic climatic change (from humid and template to cold and dry) (Martínez and Artabe, 2014; Iglesias et al., 2011).

The extinction of animals and the diversification of flowering plants would probably be some of the biotic factors related to the extinction of cycads in Patagonia and other areas. The extinction of some animals (e.g., dinosaurs), would have produced alterations in seed dispersal strategies, and limited the migration of cycads to refuges or tropical areas during periods of earth cooling (Butler et al., 2009; Martínez et al., 2014; Salgado et al., 2017). Floristic changes involving the diversification of the Magnoliophyta, with the appearance of groups that competed for the same habitat (and even with a similar life-form as the palms), also constrained the cycad populations.

5.4. Plants assemblages and palaeoecological inferences

At present, Cycadales, conifers and palms inhabit common areas of Asia, North America, South America, Africa and Australia, and in some cases, they grow in the same communities. In the case of Encephalarteae, Arecaceae with Podocarpaceae and/or Araucariaceae, these are restricted to Africa and Australia (Jones, 1993; Dalling et al., 2011; Farjon and Filer, 2013; Norstog and Nicholls, 1997; Sabato, 1990; White, 1983; Blach-Overgaard et al., 2010; Dowe, 2010).

In Africa, there are clearly two regions that involved cycads, palms and conifers. The first are southern South Africa and southern Mozambique, with a vegetation of a complex mosaic of forest, scrub forest, and evergreen and semi-evergreen bushland and thicket in a matrix of secondary grassland and wooded grassland (White, 1983). In this area, the cycas *Stangeria eriopus* (Kunze) Baill., *Encephalartos* spp., and *Afrocarpus falcate* (Thunb.) C. N. Page, grow with conifers *Podocarpus latifolius* (Thunb.) R. Br. ex Mirb., and *Podocarpus henkelii* Stapf ex Dallim. et A. B. Jacks, and palms *Jubaeopsis* Becc., *Phoenix* L., and *Raphia* P. Beauv (Palmweb, 2016; Midgley et al., 1995; Norstog and Nicholls, 1997; White, 1983; Blach-Overgaard et al., 2010). The second region follows a discontinuous mountainous belt from Cameroon to Angola to the West, and from Ethiopia in the northeast to the southern Cape in South Africa. Several genera of conifers inhabit this region, [*Juniperus* L., *Podocarpus* Lavill., *Afrocarpus* (Buchanan-Hamilton and N. E. Gray) C. N. Page and *Widdringtonia* Endl.], with numerous species of *Encephalartos* and some palms. *Encephalartos* spp. and *Widdringtonia* ssp. developed as part of the associated flora typical of Fynbos. There also grow some Podocarpaceae, Cupressaceae and palms, in a cool tropical montane with abundant precipitation to a tropical montane climate, and a prolonged dry season (Palmweb, 2016; Farjon and Filer, 2013; Farjon, 2005; Midgley et al., 1995; White, 1983).

In Australia, the association of Encephalarteae, Araucariaceae, Podocarpaceae and Arecaceae is mainly restricted to the humid tropical and subtropical northeast and southwest of the country, from rainforest, sclerophyllous woodlands to grasslands (Palmweb, 2016; Farjon and Filer, 2013; Bowman, 2000; Dowe, 2010; Norstog and Nicholls, 1997). However, *Macrozamia macdonnellii* (F. Muell. ex Miq.) A. DC., *Callitris columellaris* F. Muell. and *Livistona mariae* F. Muell are the exception, growing in sandstone canyons and dry stream beds, where their roots can reach seepage or deep ground water in the Northern Territory (dry interior of Australia) (Ingham et al., 2013; Farjon, 2005; Bowman, 2000; Dowe, 2010). However, several hypotheses about the occurrence of these taxa have attributed this to relictualism, and habitat fragmentation or long-distance dispersal (Ingham et al., 2013; Bowman, 2000; Byrne et al., 2008).

With these data, we can infer than cycads as well as palms and some conifers are typical plants of tropical to subtropical regions from forests to semi-arid environments, indicating warm climates; however, they do not add any data about the humidity levels. In this sense, we can only infer a warm climate for the palaeoflora of the Pichaihue Limestone, probably similar to those developed in Africa or Australia today.

6. Conclusions

Wintucycas beatrizae sp. nov. Martínez, Ottone and Artabe is a distinct species that encompass medium sized, columnar and manoxylic stems, which display foliar traces with simple and unbranched trichomes in a continuous layer and a classic omega pattern. Several anatomical features present in the cycad stems studied herein, allow us to include them in the Zamiineae (Encephalarteae).

This new taxon was recovered at Pichaihue together with palms (*Palmoxylon pichaihuensis* Ottone) and araucaroid woods. Taphophloras with conifers, cycads, and palms are characteristic in the Upper Cretaceous–Palaeocene of north Patagonia. These fossil plant assemblages represent communities that progressed under a warm climate relatively near the margin of the inland sea formed by an Atlantic marine transgression that flooded the Colorado and Neuquén Basins reaching the Andean foothills at about 38–42°S.

There are no records of cycad stems in Patagonia after the Eocene; therefore, their extinction was perhaps influenced by abiotic (Andean uplift, temperature fall, drop of atmospheric CO_2, inception of the Antarctic Circumpolar Current and climate change) and biotic (extinction of animals, and diversification of flowering plants) factors that occurred from the Cretaceous to the Latest Eocene–early Oligocene.

Nonetheless, the cycads still grow in some warm regions of the Earth. This is an interesting group of seed plants, with a long history, that survived several extinction events from the Palaeozoic to the present.

Acknowledgements

The authors wish to thanks A. Garrido for their valuable assistance in palaeontological collection of the Museo Provincial de Ciencias Naturales Profesor Dr. Juan A. Olsacher. We thank R. R. Pujana for his help in processing the samples, M.B. Aguirre-Urreta and P. Rawson for their advice on the fossil locality, and Mr. and Mrs. Rivera and family for their kind hospitality at Pichaihue. This research was supported by grants PICT–2011–2324 (Agencia Nacional de Promoción Científica y Tecnológica) and PIP 112 – 201501 – 00613 – CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas). This is the R–256 contribution of the Instituto de Estudios Andinos Don Pablo Groeber.

References

Aguirre-Urreta, B., Tunik, M., Naipauer, M., Pazos, P., Ottone, E., Fanning, M., Ramos, V.A., 2011. Malargüe Group (Maastrichtian–Danian) deposits in the Neuquén Andes, Argentina: implications for the onset of the first Atlantic transgression related to Western Gondwana break-up. Gondwana Res. 19, 482–494.

Ancibor, E., 1995. Palmeras fósiles del Cretácico Tardío de la Patagonia argentina (Bajo de Santa Rosa, Río Negro). Ameghiniana 32, 287–299.

Andreis, R.R., Ancibor, E., Archangelsky, S., Artabe, A., Bonaparte, J., Genise, J., 1991. Asociación de vegetales y animales en estratos del Cretácico Tardío del norte de la Patagonia. Ameghiniana 28, 201–202.

Archangelsky, S., Brett, D.W., 1963. Studies on Triassic fossil plants from Argentina. Ann. Bot. 27, 147–156.

Arguijo, M.H., 1978. *Palmoxylon bororoense* n. sp. de la Formación Cerro Bororó (Paleoceno), provincia de Chubut, Argentina. Physis 38, 87–96.

Arguijo, M.H., 1981. *Palmoxylon vaterum*, n. sp. del Paleoceno (Daniano) de la provincia de Chubut, Argentina. Physis 39, 49–59.

Artabe, A.E., Stevenson, D.W., 1999. Fossil Cycadales of Argentina. Bot. Rev. 65, 219–238.

Artabe, A.E., Zamuner, A.B., Stevenson, D.W., 2004. Two new petrified cycad stems, *Brunoa* gen. nov. and *Worsdellia* gen. nov., from the Cretaceous of Patagonia (Bajo de Santa Rosa, Río Negro Province), Argentina. Bot. Rev. 70, 121–133.

Artabe, A.E., Zamuner, A.B., Stevenson, D.W., 2005a. A new genus of late cretaceous cycad stem from Argentina, with reappraisal of known forms. Alcheringa 29, 87–100.

Artabe, A.E., Zamuner, A.B., Stevenson, D.W., 2005b. *Neochamberlainia*, a new name for *Chamberlainia* Artabe, Zamuner & D. W. Stev. (Zamiaceae) non *Chamberlainia* Grout (Brachytheciaceae). Brittonia 62, 95.

Ash, S., 1985. A short thick cycad stem from the Upper Triassic of Petrified Forest National Park, Arizona, and vicinity. Mus. North. Ariz. Bull. 54, 17–32.

Barrio, C.A., 1990. Paleogeographic control of the Upper Cretaceous tidal deposits, Neuquén Basin, Argentina. J. S. Am. Earth Sci. 3, 31–49.

Blach-Overgaard, A., Svenning, J.C., Dransfield, J., Greve, M., Balslev, H., 2010. Determinants of palm species distributions across Africa: the relative roles of climate, non-climatic environmental factors, and spatial constraints. Ecography 33, 380–391.

Bowman, D.M.J.S., 2000. Australian Rainforests: Islands of Green in a Land of Fire. Cambridge University Press, Cambridge, UK.

Butler, R.J., Barrett, P.M., Kenrick, P., Penn, M.G., 2009. Testing co-evolutionary hypotheses over geological timescales: interactions between Mesozoic non-avian dinosaurs and cycads. Biol. Rev. Camb. Philos. Soc. 84 (1):73–89. https://doi.org/10.1111/j.1469-185X.2008.00065.x.

Byrne, M., Yeates, D.K., Joseph, L., Kearney, M., Bowler, J., Williams, M.A.J., Cooper, S., Donnellan, S.C., Keogh, J.S., Leys, R., Melville, J., Murphy, D.J., Porch, N., Wyrwoll, K.H., 2008. Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. Mol. Ecol. 17, 4398–4417.

Cantrill, D.J., 2000. A petrified cycad trunk from the Late Cretaceous of the Larsen Basin, Antarctica. Alcheringa 24, 307–318.

Carbone, O., Franzese, J., Limeres, M., Delpino, D., Martínez, R., 2011. El Ciclo Precuyano (Triásico Tardío-Jurásico Temprano) en la Cuenca Neuquina. In: Leanza, H.A., Arregui, C., Carbone, O., Danielli, J.C., Vallés, J.M. (Eds.), Geología y recursos naturales de la provincia del Neuquén. 18 Congreso Geológico Argentino, Relatorio, Asociación Geológica Argentina, Buenos Aires, pp. 63–76.

Chase, M.W., Soltis, D.E., Olmstead, R.G., Morgan, D., Les, D.H., Mishler, B.D., Duvall, M.R., Price, R.A., Hills, H.G., Qiu, Y.-L., Kron, K.A., Rettig, J.H., Conti, E., Palmer, J.D., Manhart, J.R., Sytsma, K.J., Michaels, H.J., Kress, W.J., Karol, K.G., Clark, W.D., Hedren, M., Gaut, B.S., Jansen, R.K., Kim, K.-J., Wimpee, C.F., Smith, J.F., Furnier, G.R., Strauss, S.H., Xiang, Q.-Y., Plunkett, G.M., Soltis, P.S., Swensen, S.M., Williams, S.E., Gadek, P.A., Quinn, C.J., Eguiarte, L.E., Golenberg, E., Learn, G.H., Graham Jr., S.W., Barrett, S.C.H., Dayanandan, S., Albert, V.A., 1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene rbcL. Ann. Mo. Bot. Gard. 80, 528–580.

Cúneo, N.R., Escapa, I., Villar De Seoane, L., Artabe, A.E., Gnaedinger, S., 2010. Review of the Cycads and Bennettitaleans from the Mesozoic of Argentina. In: Gee, C.T. (Ed.), Plants in Mesozoic Time: Morphological Innovations, Phylogeny, Ecosystems. Indiana University Press, pp. 187–212.

Dalling, J.W., Barkan, P., Bellingham, P.J., Healey, J.R., Tanner, E.V.J., Toro Murillo, J., 2011. Ecology and distribution of Neotropical Podocarpaceae. In: Turner, B.L., Cernusak, L. (Eds.), Ecology of Podocarpaceae in Tropical Forests. Smithson. Contrib. Bot. 95. Smithsonian Institution Press, Washington, DC, pp. 43–56.

Del Fueyo, G.M., 1998. Coniferous woods from the Upper Cretaceous of Patagonia, Argentina. Rev. Esp. Paleont. 13, 43–50.

Del Fueyo, G.M., Villar de Seoane, L., Archangelsky, A., Guller, V., Llorens, M., Archangelsky, S., Gamerro, J.C., Mussachio, E.A., Passalía, M., Barreda, V.D., 2007. Biodiversidad de las Paleofloras de Patagonia Austral durante el Cretácico Inferior. Asociación Paleontológica Argentina. Publicación Especial 11. Ameghiniana 50 Años, pp. 101–122.

Dowe, J.L., 2010. Australian Palms: Biogeography, Ecology and Systematics. CSIRO Publishing, Collingwood. Australia.

Du, X., Zhu, J., 1982. The emendation of a cycad genus *Yuania* and the discovery of *Y. chinensis* sp. nov. Memoirs of the Beijing Natural History Museum 17, 1–6.

Farjon, A., 2005. A monograph of Cupressaceae and *Sciadopitys*. Royal Botanical Gardens, Kew.

Farjon, A., Filer, D., 2013. An Atlas of the World's Conifers: An Analysis of Their Distribution, Biogeography, Diversity, and Conservation Status. Brill Academic Publishers, Leiden. The Netherlands.

Gao, Z., Thomas, B.A., 1989. A review of fossil cycad megasporophylls, with new evidence of *Crossozamia* Pomel and its associated leaves from the lower Permian of Taiyuan, China. Rev. Palaeobot. Palynol. 60, 205–223.

Garrido, A.C., 2011. El Grupo Neuquén (Cretácico Tardío) en la Cuenca Neuquina. In: Leanza, H.A., Arregui, C., Carbone, O., Danielli, J.C., Vallés, J.M. (Eds.), Geología y recursos naturales de la provincia del Neuquén. 18 Congreso Geológico Argentino, Relatorio. Asociación Geológica Argentina, Buenos Aires, pp. 231–244.

Gould, R.E., 1971. *Lyssoxylon grigsbyi*, a cycad trunk from the Upper Triassic of Arizona and New Mexico. Am. J. Bot. 58, 239–248.

Greguss, P., 1968. Xylotomy of the living Cycads with a description of their leaves and epidermis. Budapest. Akadémiai Kiadó.

Groeber, P., 1952. Ándico. Geografía de la República Argentina. Tomo 2. Primera Parte. Sociedad Argentina de Estudios Geográficos GAEA, Buenos Aires, pp. 349–536.

Hermsen, E.J., Taylor, T.N., Taylor, E.L., Stevenson, D.W., 2006. Cataphylls of the Middle Triassic cycad *Antarcticycas schopfii* and new insights into cycad evolution. Am. J. Bot. 93, 724–738.

Hill, K.D., Chase, M.W., Stevenson, D.W., Hills, H.G., Schutzman, B., 2003. The families and genera of cycads: a molecular phylogenetic analysis of Cycadophyta based on nuclear and plastid DNA sequences. Int. J. Plant Sci. 164, 933–948.

Howell, J.A., Schwarz, E., Spalletti, L., Veiga, G.D., 2005. The Neuquén Basin: an overview. In: Veiga, G.D., Spalletti, L.A., Howell, J.A., Schwarz, E. (Eds.), The Neuquén Basin: A Case Study in Sequence Stratigraphy and Basin Dynamics. Vol. 252, pp. 1–14 The Geological Society, Special Publication.

Iglesias, A., Artabe, A.E., Morel, E.M., 2011. The evolution of Patagonian climate and vegetation from the Mesozoic to the present. Biol. J. Linn. Soc. 103, 409–422.

Ingham, J.A., Forster, P.I., Crisp, M.D., Cook, L.G., 2013. Ancient relicts or recent dispersal: how long have cycads been in central Australia? Divers. Distrib. 19:307–316. https://doi.org/10.1111/j.1472-4642.2012.00936.x.

Jain, K.P., 1962. *Fascivarioxylonmehtae* gen. et sp. nov., a new petrified cycadean wood from the Rajmahal Hills, Bihar, India. The. Palaeobotanist 11, 138–143.

Jones, D.L., 1993. Cycads of the World. Ancient Plants in Today's Landscape. Reed, Chatswood (312 p.).

Leanza, H.A., Hugo, C.A., 2005. Hoja Geológica 3969-I Zapala. Provincia del Neuquén. Programa Nacional de Cartas Geológicas de la República Argentina 1:250.000. Servicio Geológico Minero Argentino, Boletín 275, 132 (Buenos Aires).

Legarreta, L., Gulisano, C., 1989. Análisis estratigráfico secuencial de la Cuenca Neuquina (Triásico superior-Terciario inferior). In: Chebli, G., Spalletti, L. (Eds.), Cuencas Sedimentarias Argentinas: Facultad de Ciencias Naturales, Universidad Nacional de Tucumán, Correlación Geológica Serie, 6, pp. 221–243.

Legarreta, L., Uliana, M.A., 1991. Jurassic–Cretaceous marine oscillations and geometry of back-arc basin fill, central Argentine Andes. Int. Assoc. Sedimentol. Spec. Publ. 12, 429–450.

Legarreta, L., Uliana, M.A., 1999. El Jurásico y Cretácico de la Cordillera Principal y la Cuenca Neuquina. In: Caminos, R. (Ed.), Geología Argentina: Servicio Geológico Minero Argentino, Anales, 29, pp. 399–417.

Lutz, A.I., Crisafulli, A., Herbst, R., 2003. *Vladiloxylon troncosi* nov. gen. et sp. (Cycadales) de la Formación La Ternera (Triásico Superior), 3° Región, Chile. Rev. Mus. Argent. Cienc. Nat. 5, 31–38.

Mamay, S.H., 1969. Cycads: fossil evidence of Late Paleozoic origin. Science 164, 295–296.

Martínez, L.C.A., Archangelsky, S., Prámparo, M.B., Archangelsky, A., 2016. Early Cretaceous palm pollen tetrads from Patagonia, Argentina. Cretac. Res. 59, 129–139.

Martínez, L.C.A., Artabe, A.E.E., 2014. The fossil cycads of Argentina: new taxa, evidences and relationships about their evolutionary history. 4° International Palaeontological Congress. Abstract volume: 572.

Martínez, L.C.A., Artabe, A.E.E., Bodnar, J., 2012. A new cycad stem from the Cretaceous in Argentina and its phylogenetic relationships with other Cycadales. Bot. J. Linn. Soc. 170, 436–458.

Martínez, L.C.A., Artabe, A.E.E., Canudo, J.I., Garrido, A.C., Salgado, L., 2014. 4° International Palaeontological Congress. Abstract volume: 750.

Martínez, L.C.A., Iglesias, A., Artabe, A.E., Varela, A., Apesteguía, S., 2017. A new Encephalarteae trunk (Cycadales) from the Cretaceous of Patagonia (Mata Amarilla Formation, Austral Basin), Argentina. Cretac. Res. 72, 81–94.

Midgley, J.J., Bond, W.J., Geldenhuys, C.J., 1995. The ecology of Southern African conifers. In: Enright, N.J., Hill, R.S. (Eds.), Ecology of Southern Conifers. Melbourne University Press, Melbourne, pp. 64–80.

Nishida, H., Nishida, M., Tanaka, K., 1991. Petrified plants from the Cretaceous of the Kwanto Mountains, Central Japan. III. A polyxylic cycadean trunk, *Sanchucycas gigantea* gen. et sp. nov. Bot. Mag. (Tokyo) 104, 191–205.

Norstog, K.J., Nicholls, T., 1997. The Biology of the Cycads. Cornell University Press, Ithaca.

Ottone, E.G., 2007. A new palm trunk from the Upper Cretaceous of Argentina. Ameghiniana 44, 719–725.

Ottone, E.G., 2009. La flora cretácica de Cuenca Neuquina, su significado paleoambiental y paleoclimático. Rev. Asoc. Geol. Argent. 65, 373–386.

Palmweb, 2016. Palmweb: Palms of the World Online. Published on the Internet. http://www.palmweb.org (Accessed on date – 03/08/2016).

Passalía, M., Del Fueyo, G.M., Archangelsky, S., 2010. An Early Cretaceous zamiaceous cycad of South West Gondwana: *Restrepophyllum* nov. gen. from Patagonia, Arg. Cretac. Res. 161, 137–150.

Petriella, B., 1969. *Menucoa cazaui* nov. gen. et sp., tronco petrificado de Cycadales, prov. de Río Negro, Argentina. Ameghiniana 6, 291–302.

Petriella, B., 1972. Estudio de Maderas Petrificadas del Terciario Inferior del área central de Chubut (Cerro Bororó). Rev. Mus. La Plata (Nueva serie). Sección Paleontología 41, 159–254.

Petriella, B., 1978. Nuevos hallazgos de Cycadales fósiles en Patagonia. Boletín de La Sociedad Latinoamericana de Paleobotánica y Palinología 5, 13–16.

Ramos, V.A., 1999. Plate tectonic setting of the Andean Cordillera. Episodes 22, 183–190.

Remesal, M., Salani, F., Ardolino, A., 2001. Hoja Geológica 4169-IV Maquinchao. Provincia de Río Negro. Programa Nacional de Cartas Geológicas de la República Argentina 1: 250.000. Servicio Geológico Minero Argentino, Boletín 312 (Buenos Aires, 68 p.).

Rodríguez, M.F., 2011. El Grupo Malargüe (Cretácico Tardío-Paleógeno temprano) en la Cuenca Neuquina. In: Leanza, H.A., Arregui, C., Carbone, O., Danielli, J.C., Vallés, J.M. (Eds.), Geología y recursos naturales de la provincia del Neuquén. 18 Congreso Geológico Argentino, Relatorio. Asociación Geológica Argentina, Buenos Aires, pp. 245–264.

Sabato, S., 1990. West Indian and South America cycads. Mem. N. Y. Bot. Gard. 57, 173–185.

Salgado, L., Canudo, J.I., Garrido, A.C., Moreno Azanza, M., Martínez, L.C.A., Coria, R.A., Gasca, J.M., 2017. A basal ornithopod dinosaur from the Middle Jurassic of Patagonia preserving evidence on its diet. Sci. Rep. 7, 42778. https://doi.org/10.1038/srep42778.

Smoot, E.L., Taylor, T.N., Delevoryas, T., 1985. Structurally preserved fossil plants from Antacrtica. I. *Antacticycas*, gen. nov., a Triassic Cycad stem from the Beardmore Glacier Area. Am. J. Bot. 72, 1410–1423.

Soltis, D.E., Soltis, P.A., Zanis, M.J., 2002. Phylogeny of seed plants based on evidence from eight genes. Am. J. Bot. 89, 1670–1681.

Stevenson, D. Wm, 1992. A formal classification of the extant cycads. Brittonia 44, 220–223.

Stevenson, D.Wm., 1990. Morphology and systematics of the Cycadales. Mem. N. Y. Bot. Gard. 57, 8–55.

Uliana, M.A., Dellapé, D.A., 1981. Estratigrafía y evolución paleoambiental de la sucesión Maastrichtiana-eoterciaria del engolfamiento Neuquino (Patagonia Septentrional). 8° Congreso Geológico Argentino, Actas 3, 673–711.

Weaver, C., 1927. The Roca Formation in Argentina. Am. J. Sci. 13, 417–434.

White, F., 1983. The Vegetation of Africa: A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa. UNESCO, Paris (356 pp. + map).

Wilf, P., Wm, Stevenson D., Cúneo, R.N., 2016. The last Patagonian cycad, *Austrozamia stockeyi* gen. et sp. nov., early Eocene of Laguna del Hunco, Chubut, Argentina. Botany 94, 817–829.

Worsdell, W.C., 1896. The anatomy of the stem of *Macrozamia* compared with that of other genera of Cycadaceae. Ann. Bot. 10, 601–620.

Worsdell, W.C., 1906. The structure and origin of Cycadaceae. Ann. Bot. 20, 129–155.

Zamora Valcarce, G., Rapalini, A.E., Spagnuolo, C.M., 2007. Reactivación de estructuras cretácicas durante la deformación miocena, faja plegada del Agrio, Neuquén. Rev. Asoc. Geol. Argent. 62, 299–308.

Zamora Valcarce, G., Zapata, T., Del Pino, D., Ansa, A., 2006. Structural evolution and magmatic characteristics of the Agrio fold-and-thrust belt. In: Kay, S.M., Ramos, V.A. (Eds.), Evolution of an Andean Margin: A Tectonic and Magmatic View from the Andes to the Neuquén Basin (35°–39°S Latitude): Geological Society of America, Special Paper, 407, pp. 125–145.

Zgurski, J.M., Rai, H.S., Fai, Q.M., Bogler, D.J., Francisco-Ortega, J., Graham, S.W., 2008. How well do we understand the overall backbone of cycad phylogeny? New insights from a large, multigene plastid data set. Mol. Phylogenet. Evol. 47, 1232–1237.

Zhang, W., Wang, Y., Saiki, K.S., Li, N., Zheng, S., 2006. A structurally preserved cycad-like stem, *Lioxylon liaoningense* gen. et sp. nov., from the Middle Jurassic in Western Liaoning, China. Prog. Nat. Sci. 16, 236–248.

Zhang, W., Yang, X.-J., Fu, X.-P., Zheng, S.-L., Wang, Y.-D., 2012. A polyxylic Cycad trunk from the Middle Jurassic of western Liaoning, China, and its evolutionary implications. Rev. Palaeobot. Palynol. 183, 50–60.

Zhu, J.-N., Du, X.-M., 1981. A new cycad — *Primocycas chinensis* gen. et sp. nov. from the Lower Permian in Shanxi, China, and its significance. Acta Bot. Sin. 23, 401–404.