

A new cycad stem from the Cretaceous in Argentina and its phylogenetic relationships with other Cycadales

LEANDRO CARLOS ALCIDES MARTÍNEZ^{1,2*}, ANALÍA EMILIA EVA ARTABE² and JOSEFINA BODNAR²

¹*División Paleobotánica, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Avda, Ángel Gallardo 470, Buenos Aires 1405, Argentina*

²*Facultad de Ciencias Naturales y Museo, División Paleobotánica, Universidad Nacional de La Plata, Paseo del Bosque s/n, La Plata 1900, Argentina*

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The cycads are an ancient group of seed plants. Fossil stems assigned to the Cycadales are, however, rare and few descriptions of them exist. Here, a new genus of cycad stem, *Wintucycas* **gen. nov.**, is described on the basis of specimens found in the Allen Formation (Upper Cretaceous) at the Salitral Ojo de Agua locality, Río Negro Province, Argentina. The most remarkable features of *Wintucycas* are: a columnar stem with persistent leaf bases, absence of cataphylls, a wide pith, medullary vascular bundles, mucilage canals and idioblasts; a polyxylic vascular cylinder; inverted xylem; and manoxylic wood. The new genus was included in a phylogenetic analysis and its relationships with fossil and extant genera of Cycadales were examined. In the resulting phylogenetic hypothesis, *Wintucycas* is circumscribed to subfamily Encephalartoideae, supporting the existence of a greater diversity of this group in South America during the Cretaceous. © 2012 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2012, **170**, 436–458.

ADDITIONAL KEYWORDS: Allen Formation – anatomy – Neuquén Basin – Patagonia – phylogeny – South America – systematics.

INTRODUCTION

The cycads are a monophyletic group, defined by 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).

These plants have a long evolutionary history which is well documented in the fossil record, with the earliest indisputable cycad fossils coming from the Lower Permian of China (Zhu & Du, 1981; Du & Zhu, 1982; Gao & Thomas, 1989). During the Mesozoic, cycads reached their highest point in morphological diversification, geographical distribution and taxic diversity, followed by a decline in the Early and Mid Cenozoic (Artabe & Stevenson, 1999; Brenner, Stevenson & Twigg, 2003; Hill *et al.*, 2003). However,

recent fossil-calibrated molecular phylogenetic trees indicate that all extant species (except for those in monotypic genera) could have been derived from recent divergence events that occurred in the late Miocene (Nagalingum *et al.*, 2011).

Today, there are about 305 species of Cycadales in 11 genera: *Cycas* L., *Stangeria* T.Moore, *Bowenia* J.D.Hook, *Dioon* Lindley, *Encephalartos* J.G.C.Lehmann, *Macrozamia* Miquel, *Lepidozamia* E.Regel, *Ceratozamia* Brongniart, *Microcycas* (Miquel) de Candolle, *Zamia* L. and *Chigua* D.W.Stevenson (Stevenson, 1990, 1992; Hill *et al.*, 2003; Hill, Stevenson & Osborne, 2004); they are restricted to tropical and subtropical areas (Hill *et al.*, 2004), between *c.* 30°N and 35°S (Norstog & Nicholls, 1997).

Cycadales do not currently occur in Argentina, but their fossil remains as leaf impressions, cuticles, and petrified strobili and trunks have been found throughout the country (Artabe & Stevenson, 1999; Archangelsky & Villar de Seoane, 2004). Most are Mesozoic or

*Corresponding author. E-mail: gesaghi@gmail.com

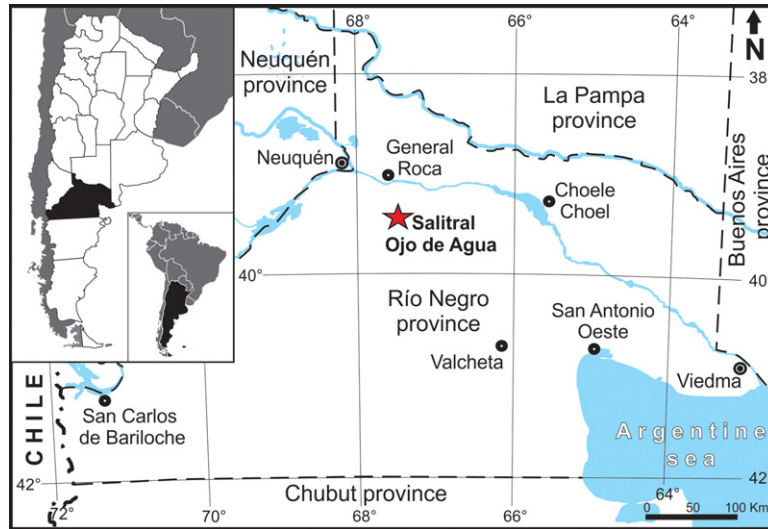


Figure 1. Location map of the fossiliferous locality, 'Salitral Ojo de Agua', Río Negro province, Argentina.

Cenozoic leaves assigned to *Almargemia* Florin, *Ctenis* Lindley & Hutton, *Kurtziana* Frenguelli emend. Petriella & Arrondo, *Mesodescolea* Archangelsky emend. Archangelsky & Petriella, *Mesosingeria* Archangelsky, *Nilssonia* Brongniart, *Pseudoctenis* Seward, *Restrepophyllum* Passalia, Del Fueyo et Archangelsky, *Sueria* Menéndez emend. Baldoni, *Ticoa* Archangelsky and *Zamia* (Berry, 1938; Archangelsky, 1963; Villar de Seoane, 1997, 2005; Artabe & Stevenson, 1999; Pasalía et al., 2010). Reproductive structures are rare and only three species of *Androstrobus* Schimper, from the Cretaceous of Patagonia, are known (*A. munku* Archangelsky & Villar de Seoane, *A. patagonicus* Archangelsky & Villar de Seoane and *A. rayen* Archangelsky & Villar de Seoane) (Archangelsky & Villar de Seoane, 2004). Six fossil cycad stems are known from Triassic to Cenozoic rocks in Argentina: *Michelilloa* Archangelsky & Brett (1963), *Menucoa* Petriella (1969), *Bororoa* Petriella (1972), *Brunoa* Artabe, Zamuner & Stevenson (2004), *Worsdellia* Artabe et al. (2004) and *Neochamberlainia* Artabe, Zamuner & Stevenson (2005, 2010). Except *Michelilloa*, all of these trunks come from sites in Patagonia, indicating a high diversity of this group during the Cretaceous and Palaeocene in South America.

The objectives of this research are the description of a new genus of cycad stem from the Allen Formation (Upper Cretaceous) and the evaluation of its phylogenetic relationships in Cycadales.

GEOLOGICAL SETTING

The permineralized stems come from Salitral Ojo de Agua in Río Negro province, (Patagonia) Argentina (Fig. 1). In this locality, the Allen Formation, which

contains a diverse record of sauropods, foraminifers, palms, conifers and cycads (Ballent, 1980; Andreis et al., 1991; Ancibor, 1995; Del Fueyo, 1998; Artabe et al., 2004, 2005; Salgado et al., 2007), is exposed (Hugo & Leanza, 2001a).

Other fossil cycad stems have been described in the Allen Formation from Bajo de Santa Rosa (c. 40°S, 60°W), north of Valcheta village, Río Negro Province, Argentina. They are *Brunoa santarosensis* Artabe, Zamuner & Stevenson, *Worsdellia bonettiae* Artabe, Zamuner & Stevenson and *Neochamberlainia pteridospermoidea* (Artabe et al., 2004, 2005).

The sedimentary succession of the Allen Formation has been interpreted as continental to deltaic with shallow marine deposits (Andreis et al., 1991). This lithostratigraphic unit is assigned to the middle Campanian to early Maastrichtian (Ballent, 1980) and is divided into two members, the lower one composed of moderate-energy sandy to muddy fluvial deposits and the upper one of lower-energy lacustrine deposits (Leanza & Hugo, 2001a, b). The cycad stems described in this paper were found in the lower member.

MATERIALS AND METHODS

The studied material comprises four cycad trunks fossilized as silicifications with a relatively well preserved state of preservation. To study wood anatomy, thin sections were made using traditional techniques; transverse (TS), radial (RLS) and tangential (TLS) sections were made. For scanning electron microscopy (SEM), the specimen was fractured, stuck to aluminium stubs using nail polish and coated with a layer of gold. Cell dimensions are based on at least 25 measurements; numbers in parentheses indicate minimum and maximum values.

The fossil wood and thin sections are deposited in the Paleontological Collection of Universidad Nacional del Comahue (MUCPb), Neuquén, and in the Paleobotanical Collection of the Paleobotany Division of Museo de La Plata (LPPB), La Plata, Argentina.

A cladistic analysis was also made to determine the phylogenetic relationships of *Wintucycas* to other genera of living and fossil Cycadales. This cladistic analysis is based on the matrix of Hermsen *et al.* (2006), with several modifications, including the addition of fossil taxa, new characters and new states for particular characters (41 taxa and 88 characters). The analysis was conducted using the program TNT (Goloboff, Farris & Nixon, 2003) given that it is the most widely used software in palaeontological phylogenetic studies.

The matrix used in this research (Appendix S1) was initially centred on the morphological matrix of Hermsen *et al.* (2006) as modified below. Also, some characters that had been considered in other cladistic analyses (Stevenson, 1990, 1992; Hilton & Bateman, 2006; Crepet & Stevenson, 2010) and new characters, such as dioecy, microsporangia in strobili, megasporangia in strobili and strobilus type, were added.

Characters were treated as non-ordered. The heuristic search was based on 1000 random addition sequences using tree-bisection-reconnection (TBR) saving 100 trees per replication; all characters were treated as unpolarized. The resulting phylogenetic trees were rooted with Lyginopteridales as the outgroup. All fossil taxa included in the matrix have one or more features that link them to Cycadales. The resultant phylogenetical hypothesis is discussed in the Cladistic and Systematic sections below.

SYSTEMATIC PALAEOBOTANY

Order CYCADALES Dumortier, 1829
Suborder ZAMIINEAE Stevenson, 1992
Family ZAMIACEAE Reichenbach, 1837
Subfamily ENCEPHALARTOIDEAE Stevenson, 1992
Genus *WINTUCYCAS* Martínez, Artabe *et* Bodnar
gen. nov.

Type species: Wintucycas stevensonii Martínez, Artabe *et* Bodnar **sp. nov.** Figures 2–5.

GENERIC DIAGNOSIS

Columnar, polyxylic stem, covered by persistent rhomboidal leaf bases. Parenchymatous central pith with mucilage canals, idioblasts and medullary vascular bundles. Cylindrical vascular system with many rings of manoxylic secondary xylem and phloem containing uni- to multiseriate rays, and centripetal vascular bundles adjacent to the innermost ring.

Parenchymatous cortex with mucilage canals, idioblasts and girdling leaf traces in cortex.

ETYMOLOGY

The generic name is a combination of *wintu*, which means ‘old’ in the Mapuche language, and *cycas* refers to Cycadales.

Wintucycas stevensonii Martínez, Artabe & Bodnar **sp. nov.**

SPECIES DIAGNOSIS

A columnar and polyxylic stem, covered by persistent rhomboidal leaf bases. A wide and parenchymatous central pith with mucilage canals, idioblasts and medullary vascular bundles. The secondary vascular cylinder comprises a medullary vascular system and a cylindrical vascular system. The medullary vascular system is composed of many medullary vascular bundles. The cylindrical vascular system has concentric rings of secondary xylem and phloem toward the cortex, and centripetal bundles adjacent to the innermost ring. Manoxylic secondary xylem, with homocellular, multiseriate rays one to four cells wide. Secondary phloem with parenchyma cells and abundant mucilage canals. Cortex composed of parenchyma cells and idioblasts, mucilage canals and girdling leaf traces. Foliar traces with an elaborated omega pattern. Leaf bases with simple and unbranched trichomes on the adaxial side.

Age: Late Cretaceous (Allen Formation).

Type locality: Salitral Ojo de Agua, Río Negro province, (Patagonia) Argentina.

ETYMOLOGY

The specific name is dedicated to Prof. Dennis Wm. Stevenson for his important contributions and extensive studies on the biology and systematics of Cycadales.

Holotype: MUCPb-369

Isotype: LPPB-13876, pmLPPB-1604 to pmLPPB-1608.

Paratype: MUCPb-370, MUCPb-371 and MUCPb-372.

DESCRIPTION

The stem is columnar with persistent leaf bases and lacks cataphylls. Because of its lateral compression,

one diameter reaches 0.28 m and the other only 0.20 m (Fig. 2A–C). Along the trunk, there are buds of an apparent helical distribution (Fig. 2D, E). In cross-section, four areas are distinguished in the stem: pith, polyxylic vascular cylinder, cortex, and persistent leaf bases and buds (Fig. 2C, F).

The pith is parenchymatous, with mucilage canals, idioblasts and peripheral medullary vascular bundles. As a result of compression, the pith is elliptical in cross-section, 11.0 cm × 5.5 cm in diameter (Fig. 2B, C). Parenchyma cells are generally isodiametric and thin walled and have circular to oval simple pits, with an average diameter of 89.45 μm (53.50–128.40 μm). The idioblasts are similar to parenchyma cells in size and shape, although the former have a thick wall and usually contain resin or gum-like material (Fig. 3A). Mucilage canals are scattered in the pith and circular to ovoid in outline, with a diameter of 303.42 μm (139.10–556.40 μm) (Fig. 3B).

Primary xylem is endarch or mesarch with tracheids that are oval to square in cross-section; they have an average radial diameter of 15.02 μm (8.12–24.36 μm) and a tangential diameter of 16.32 μm (6.09–24.36 μm). The medullary vascular system consists of secondary vascular bundles arranged irregularly in the outer part of the pith (Fig. 3A). Each bundle measures 589.83 μm (342.40–1070.00 μm) in radial diameter and 946.95 μm (588.50–1872.50 μm) tangentially. Some bundles are large, sometimes branching or with mucilage canals next to their distal pole. As no medullary bundles appear to be related to reproductive structures and do not form regularly arranged rings, they are not thought to be related to cone domes.

The cylindrical vascular cylinder has three successive rings of centrifugal secondary xylem and phloem (Fig. 3C). The innermost ring is more developed than the others; the outermost is incomplete. In the inner area of the first vascular cylinder (on the periphery of the pith), there are a few centripetal xylem bundles which are triangular in cross-section (Fig. 3D).

In the secondary xylem, the tracheids are rectangular to square with a mean radial diameter of 11.44 μm (8.12–18.27 μm) and a tangential diameter of 18.27 μm (10.15–30.45 μm) (Fig. 3E). Each ring of centrifugal secondary xylem is composed of vascular segments separated by wide parenchymatous rays that are up to 0.1 cm wide (Fig. 3F).

In radial section, the secondary xylem tracheids have araucarioid pitting with contiguous alternate uni-biseriate flattened pits on the radial walls. The pits have a horizontal diameter of 11.36 μm (8.12–16.24 μm) and a vertical diameter of 8.93 μm (6.09–10.15 μm) (Fig. 4A, B). The crossfields have three to five oculipores of the araucarioid type (Fig. 4C).

In radial section, the rays are composed of rectangular or quadrangular cells, with smooth vertical and horizontal walls. In tangential section, they appear multiseriate and homocellular and consist of rectangular to square cells that are commonly biseriate (uni- to quadriseriate), 53.42 μm (22.33–101.50 μm) in diameter and 1029.76 μm (117.71–2054.39 μm) in height (Fig. 4D, E). The secondary phloem is poorly preserved, but the phloem parenchyma and abundant mucilage canals, circular to oval in outline, can be distinguished (Fig. 3F).

The cortex is composed of parenchyma cells, idioblasts, mucilage canals and girdling leaf traces. There are many vascular bundles, which set off the vascular cylinder, with a curved path (girdling traces) ending in leaf bases (Fig. 4G).

The parenchyma cells and idioblasts are similar to those found in the pith. The parenchyma cells are isodiametric with an average diameter of 87.30 μm (45.00–134.98 μm). The mucilage canals are scattered among the parenchyma cells and more abundant than in the pith; their average diameter is 263.64 μm (117.71–449.40 μm) (Fig. 4F).

Wintucycas has numerous adventitious buds arranged helically on the stem (Fig. 2D–F) and surrounded by foliar bases. These buds are thought to be developed from the inner vascular tissues. They are 1.57 cm (1.44–1.65 cm) high and 2.68 cm (2.41–2.97 cm) wide. In longitudinal section, the shoot of buds have a medium length of 1.92 cm (1.65–2.10 cm) covered by a series of thin young leaves (Fig. 4H, I).

The outer part of the stem is covered with an armour of helical persistent leaf bases and lacks cataphylls (Fig. 2A, D, E). The rhomboidal leaf bases are 1.99 cm (1.73–2.24 cm) wide and 1.04 cm (0.68–1.35 cm) high. Each leaf base has three areas; the outermost is the epidermis, followed by a parenchymatous middle area and a vascular inner area (Fig. 5A, B). On the adaxial side of the leaf bases, the epidermis has a ramentum composed of separated clusters of simple and unbranched trichomes (Fig. 5A, C). Below the epidermis, there is an area composed of large parenchyma cells, mucilage canals and idioblasts. The parenchyma cells are thin-walled and compose an area that is similar to the cortical tissue (Fig. 5C, D). The vascular area is delimited by an endodermis and several layers of thickened cells. Inside the vascular area, transfusion tissue, vascular bundles, amorphous parenchyma cells, idioblasts and mucilage canals are present. Vascular bundles are numerous (>10 per leaf base) and they develop an elaborated omega pattern (Fig. 5B, C, D). The mucilage canals are linked to the vascular bundles.



Figure 2. A, general view of the stem. Scale bar = 5 cm. B,C, cross-sections of the stem. B, general view. Scale bar = 3 cm. C, detail of pith (p), vascular cylinder (vc), cortex (c) and leaf bases (lb). Scale bar = 3 cm. D,E, external views of stem. D, buds (arrows). Scale bar = 1 cm. E, buds in cross-section showing young leaves (tangential section of stem). Scale bar = 1 cm. F, bud in longitudinal section, arrows (cross-section of stem). Scale bar = 1 cm.

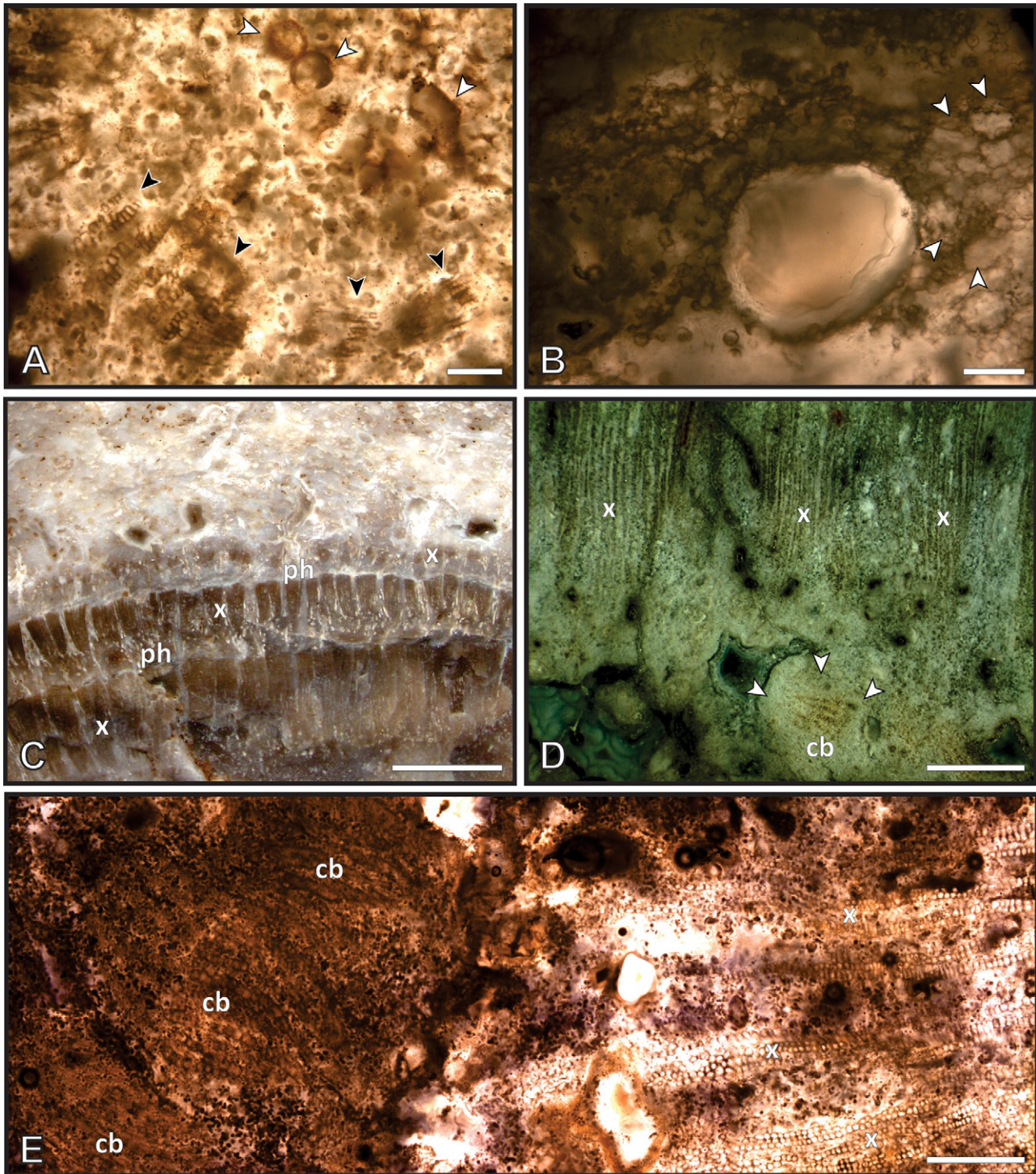


Figure 3. Cross-sections. A, pith, medullary vascular bundles (black arrows) and idioblasts (white arrows). Scale bar = 100 μ m. B, pith, mucilage canal and parenchyma cells (arrows). Scale bar = 100 μ m. C, polyxylic cylindrical vascular system, xylem (x) and phloem (ph). Scale bar = 1 cm. D, centripetal vascular bundle (cb) (arrows) and secondary xylem (x). Scale bar = 1000 μ m. E, centripetal vascular bundles (cb), detail, and secondary xylem (x). Scale bar = 200 μ m.

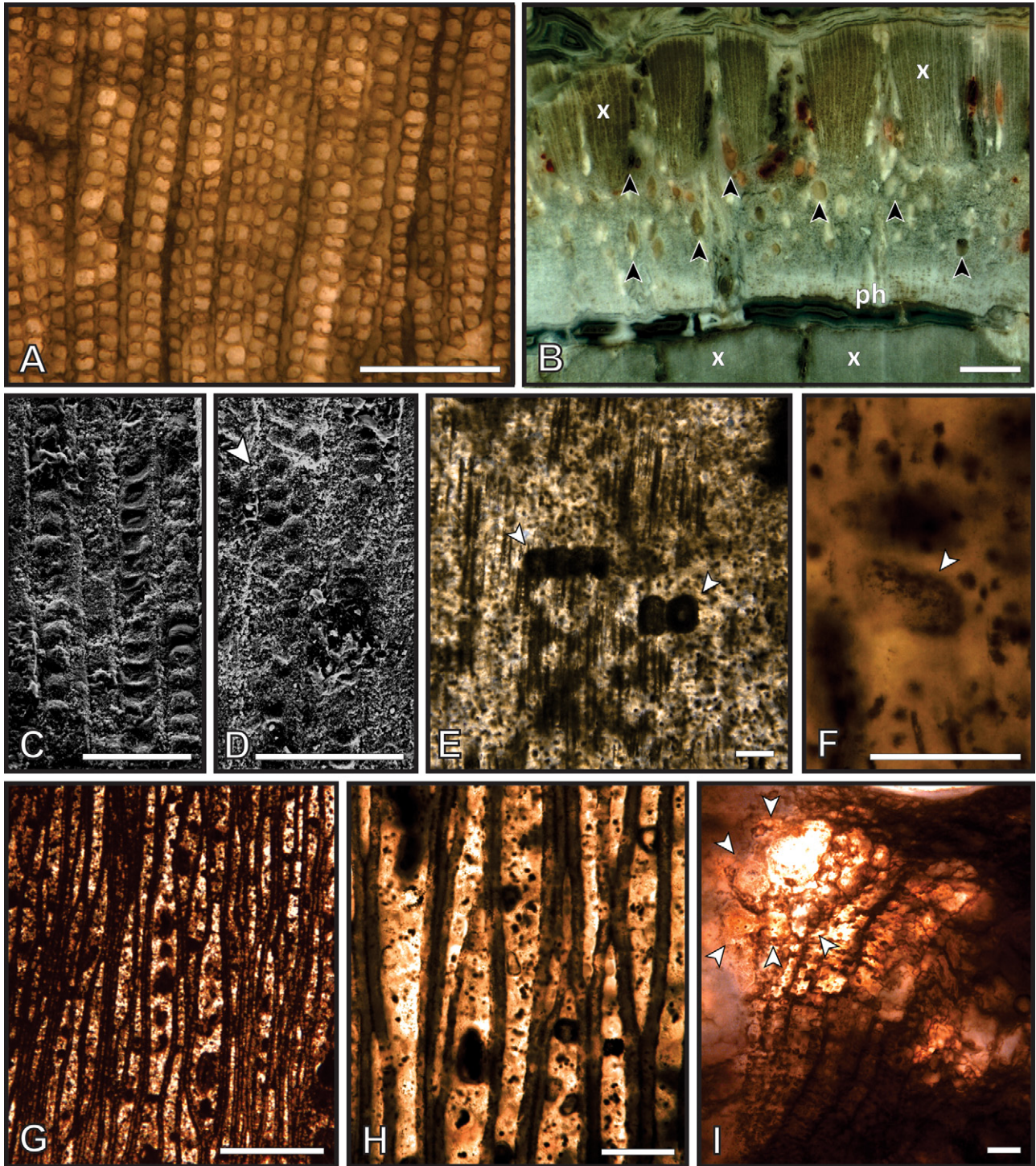


Figure 4. A,B, cross-sections. A, secondary xylem, detail. Scale bar = 100 μm . B, secondary xylem (x), secondary phloem (ph) and mucilage canals (arrows). Scale bar = 1000 μm . C–F, radial sections. C, uniseriate bordered pits. Scale bar = 50 μm . D, biseriate and alternately bordered pits (arrow). Scale bar = 50 μm . E, cross field (arrows). Scale bar = 50 μm . F, araucarioid cross field. Scale bar = 50 μm . G,H, tangential sections. G, rays, general view. Scale bar = 100 μm . H, rays, detail. Scale bar = 100 μm . I, cross-section. Cortical leaf traces and mucilage canals (arrows). Scale bar = 100 μm .

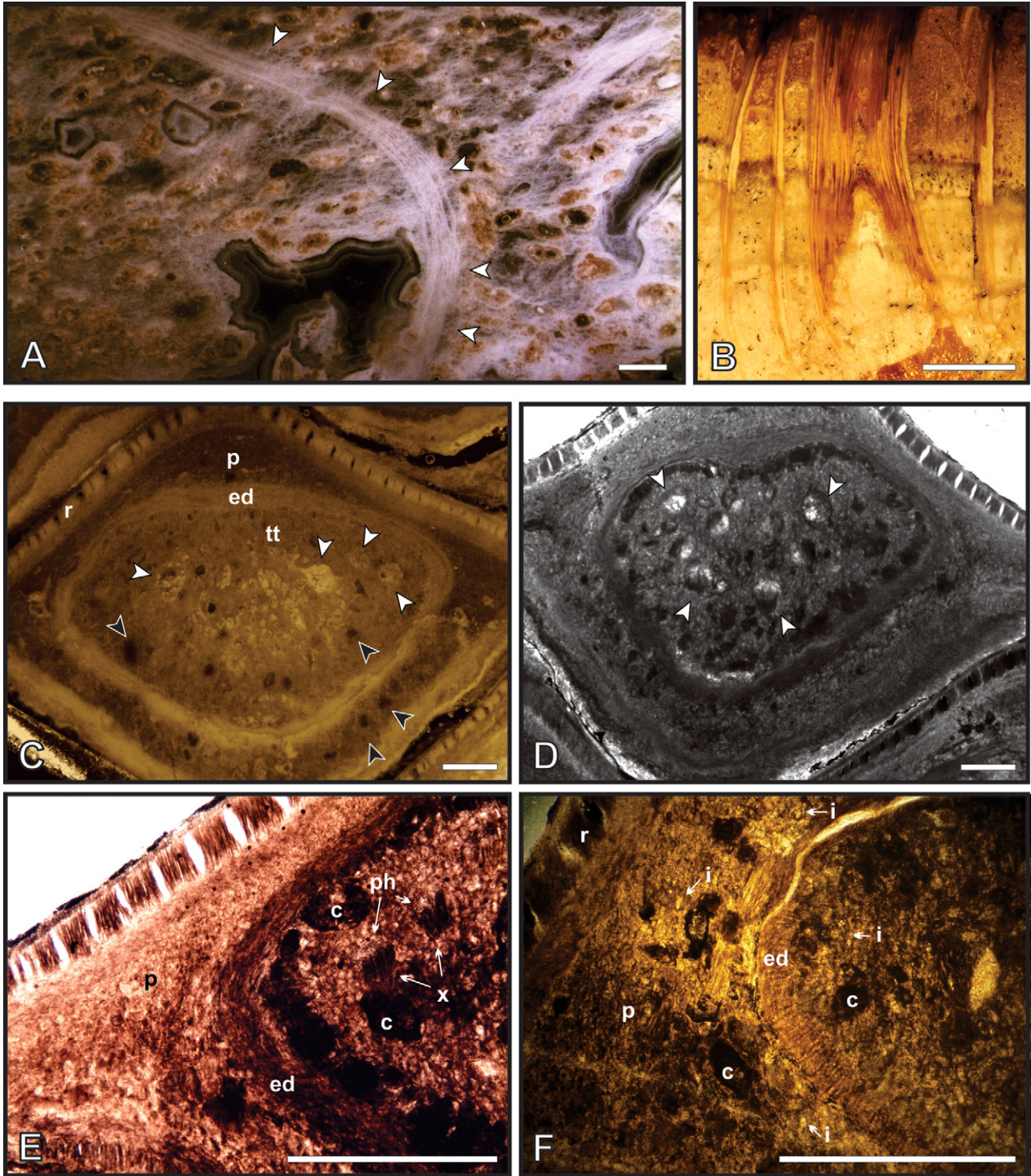


Figure 5. A, girdling trace (arrows). Scale bar = 200 μm . B, bud in longitudinal section, detail. Scale bar = 1 cm. C–F, leaf bases, cross-section. C,D, general view, ramentum (r), parenchyma (p), endodermis (ed), transfusion tissue (tt), vascular bundles (white arrows) and mucilage canals (black arrows). Scale bar = 1000 μm . E,F, details of leaf bases, rament (r), parenchyma (p), endodermis (ed), mucilage canals (c), idioblasts (i), collateral vascular bundles with xylem (x) and phloem (ph). Scale bar = 1000 μm .

DISCUSSION

COMPARISONS WITH EXTANT AND FOSSIL
CYCAD STEMS

The characters of the studied material allow us to assign it to a new genus, *Wintucycas*, in Cycadales. The new taxon has remarkable features which are briefly discussed below, and comparatively presented in Tables 1 and 2, according to their distribution among the genera of Cycadales.

A total of 14 fossil genera of cycad stems have been described. Five genera were found in Triassic beds: *Michelilloa* in Argentina; *Vladiloxylon* Lutz, Crisafulli & Herbst (2003) in Chile; *Lyssoxylon* Daugherty (Gould, 1971) and *Charmorgia* Ash (1985) in the USA; and *Antarcticycas* Smoot, Taylor & Delevoryas (1985) emend. Hermsen *et al.* (2006) in Antarctica. Taxa from younger strata include *Lioxylon* Zhang *et al.* (2006) from the Jurassic of China and India and *Fascisvarioxylon* Jain (1962) from the Late Jurassic–Early Cretaceous of India. Cretaceous forms include *Sanchucycas* Nishida, Nishida & Tanaka (1991) from Japan, *Centricycas* Cantrill (2000) from Antarctica and three genera from Argentina, i.e. *Worsdellia*, *Brunoa* and *Neochamberlainia*. Finally, *Bororoa* and *Menucoa* are known from the Palaeogene of Argentina.

Wintucycas has a pachycaul trunk with a persistent armour of leaf bases. According to Stevenson (1990), all extant cycads have a primary thickening meristem, and woody stems or trunks that are more or less succulent with well-developed pith and cortex and a small amount of secondary wood. The oldest fossil stems are interpreted as slender and often branched, and thus the pachycaul habit that appeared later would be derived from these (Delevoryas & Hope, 1976). Regarding the medullary broadness, previously described fossil forms are quite variable. Hence, the pith/vascular tissue ratio is high in *Antarcticycas*, *Charmorgia*, *Lioxylon* and *Worsdellia*, moderate in *Michelilloa*, *Fascisvarioxylon*, *Neochamberlainia* and *Bororoa* and low in all the other genera. This character has not been quantified in extant forms.

Among extant arborescent forms, only *Cycas*, *Dioon*, *Encephalartos*, *Macrozamia* and *Lepidozamia* have a persistent armour of cataphylls and old leaf bases covering the trunk for many years or indefinitely, whereas *Microcycas*, *Ceratozamia* and *Zamia* have smooth trunks (Artabe *et al.*, 2005). *Stangeria*, *Bowenia* and *Chigua* do not have persistent leaf bases. Both *Stangeria* and *Bowenia* have completely naked subterranean stems (Norstog & Nicholls, 1997). *Chigua* stems are subterranean with few erect fronds that have fern-like pinnae. Concerning fossil genera, persistent leaf bases are present in *Charmorgia*, *Lyssoxylon*, *Lioxylon*, *Fascisvarioxylon*, *Worsdel-*

lia, *Brunoa*, *Neochamberlainia*, *Bororoa*, *Menucoa* and the new genus described here. Stems of *Antarcticycas* are small and have ephemeral leaf bases (Hermsen, Taylor & Taylor, 2009). In *Sanchucycas*, *Michelilloa*, *Vladiloxylon* and *Centricycas*, the leaf bases are unknown. All extant Cycadales possess petiole-rachides with an omega-shaped pattern of vascular bundles, each one with an exarch protoxylem pole. The latter feature is considered a synapomorphy for the order, and the omega-shaped pattern an autapomorphy of Cycadales with respect to other seed plant groups (Hermsen *et al.*, 2006). Only *Bowenia*, *Encephalartos* and *Stangeria* have a pattern of vascular bundles that does not clearly appear to be omega-shaped in transverse section; however, serial sections of petiole-rachides show an elaborated inverted omega arrangement in the trace departure to the pinnae (Matte, 1904). This is considered an apomorphic feature in Cycadales, suggesting that the unmodified inverted-omega is the plesiomorphic pattern in the group (e.g. Stevenson, 1990; Hermsen *et al.*, 2006). Among fossil genera, only *Antarcticycas* and *Charmorgia* have petioles with an unmodified inverted-omega arrangement of vascular bundles (Ash, 2001; Hermsen *et al.*, 2006, 2007). *Lioxylon*, *Brunoa*, *Bororoa*, *Menucoa* and *Wintucycas* are interpreted as having an elaborated omega-shaped pattern (Hermsen *et al.*, 2007). Cataphylls have been reported on vegetative axes of all extant cycad taxa, except for *Stangeria* and *Bowenia* (Stevenson, 1990). The fossil genera *Charmorgia*, *Antarcticycas*, *Lioxylon*, *Fascisvarioxylon* (Jain, 1962), *Brunoa* and *Worsdellia* (Artabe *et al.*, 2004) have cataphylls. Moreover, these seem to be present in *Bororoa* and occasionally in *Menucoa*, although this is not mentioned in the original diagnoses (Petriella, 1969, 1972). *Wintucycas* and *Lyssoxylon* do not have cataphylls. The anatomy of cataphylls is known in *Charmorgia*, *Antarcticycas* and *Lioxylon* (Ash, 2001; Hermsen *et al.*, 2006; Zhang *et al.*, 2006). In comparison with leaf bases, cataphylls have a similar anatomy, but are smaller with a decreased number of vascular bundles.

Cycadales are also characterized by centrifugal polyxylic stems. The extant genera *Dioon*, *Stangeria*, *Bowenia*, *Ceratozamia*, *Zamia*, *Chigua* and *Microcycas* do not develop more than one centrifugal vascular cylinder. Among the fossil genera, *Michelilloa*, *Charmorgia*, *Lyssoxylon*, *Antarcticycas*, *Vladiloxylon*, *Fascisvarioxylon* and *Centricycas* have only one centrifugal vascular cylinder as well. The presence of a centrifugal polyxyly has been shown in *Cycas*, *Encephalartos*, *Lepidozamia* and *Macrozamia* (Greguss, 1968), although not all species of these genera have this character, which is more developed in arborescent taxa (Stevenson, 1990). Centrifugal polyxyly is found in *Wintucycas* and the Cretaceous

Table 1. Comparisons among *Winitucycas* and extant genera stems of Cycadales

	Cone domes	Medullary bundles	Cortical steles	Secondary centrifugal polyxyly	Wood parenchyma	Petiole bundle pattern	Cataphylls in vegetative axes	Centripetal polyxyly (additive)	Mucilage
<i>Winitucycas</i>	Absent	Present	Absent	Present	Abundant	Omega elaborate	Absent	Random or discontinuous cycles	Canals
gen. nov.									
<i>Bowenia</i>	Present	Absent	Present	Absent	Abundant	Omega elaborate	Absent	Absent	Canals
<i>Stangeria</i>	Present	Absent	Absent	Absent	Abundant	Omega elaborate	Absent	Absent	Canals
<i>Ceratozamia</i>	Present	Absent	Absent	Absent	Abundant	Omega classic	Present	Absent	Canals
<i>Chigua</i>	Present	Absent	Absent	Absent	Abundant	Omega classic	Present	Absent	Canals
<i>Cycas</i>	Present	Absent	Present	Present	Abundant	Omega classic	Present	Random or discontinuous cycles	Canals
<i>Dioon</i>	Present	Absent	Absent	Absent	Scanty	Omega classic	Present	Absent	Canals
<i>Encephalartos</i>	Absent	Present	Present	Present	Abundant	Omega elaborate	Present	Random or discontinuous cycles	Canals
<i>Lepidozamia</i>	Absent	Present	Present	Present	Abundant	Omega classic	Present	Random or discontinuous cycles	Canals
<i>Macrozamia</i>	Absent	Present	Present	Present	Abundant	Omega classic	Present	Random or discontinuous cycles	Canals
<i>Microcycas</i>	Present	Absent	Absent	Absent	Abundant	Omega classic	Present	discontinuous cycles	Canals
<i>Zamia</i>	Present	Absent	Absent	Absent	Abundant	Omega classic	Present	Absent	Canals

Table 2. Comparisons among fossil genera stems of Cycadales

	Cone domes	Medullary bundles	Cortical steles	Secondary centrifugal polyxyly	Wood parenchyma	Petiole bundle pattern	Cataphylls in vegetative axes	Centripetal polyxyly	Mucilage
<i>Antarcticycas</i>	Present	Absent	Absent	Absent	Abundant	Omega	Present	Absent	Cavities and canals
<i>Bororoa</i>	Present	Absent	Absent	Present	Abundant	Omega elaborate	Present	Absent	Canals
<i>Brunoa</i>	Present	Absent	Absent	Present	Scanty	Omega elaborate	Present	Absent	Cavities
<i>Centricycas</i>	Absent	Present	?	Absent	Abundant	?	?	Absent	Canals
<i>Charmorgia</i>	Absent	Present	Absent	Absent	Abundant	Omega	Present	Absent	Canals
<i>Fascisvarioxylon</i>	Present	Absent	Absent	Absent	Abundant	?	Present	Continuous cycle	Cavities
<i>Lioxylon</i>	Absent	Present	Absent	Absent	Abundant	Omega elaborate	Present	Continuous cycle	Cavities
<i>Lyssoxylon</i>	Absent	Absent	Absent	Absent	Scanty	?	Absent	Absent	Canals
<i>Menucoa</i>	Absent	Present	Absent	Present	Abundant	Omega elaborate	Present	Random or discontinuous cycles	Canals
<i>Michelilloa</i>	Absent	Absent	Absent	Absent	Scanty	?	?	Absent	Canals
<i>Neochamberlainia</i>	Absent	Present	Present	Present	Abundant	?	Present	Random or discontinuous cycles	Canals
<i>Sanchucyas</i>	Absent	Absent	?	Present	Scanty	?	?	Absent	Cavities
<i>Vladiloxylon</i>	Absent	Absent	Absent	Absent	Abundant	?	?	Absent	Canals
WINTUCYCAS gen. nov.	Absent	Present	Absent	Present	Abundant	Omega elaborate	Absent	Random or discontinuous cycles	Canals
<i>Worsdellia</i>	Absent	Present	Present	Present	Abundant	?	Present	Random or discontinuous cycles	Canals

taxa *Neochamberlainia*, *Sanchucyas*, *Brunoa* and *Worsdellia* and persists through the Cenozoic in *Bororoa* and *Menucoa*.

Wintucycas, as in some extant and fossil Cycadales, has centripetal xylem bundles. Among fossil forms, *Lioxylon* and *Fascisvarioxylon* have centripetal polyxylic stems with two cambial rings, which develop centrifugal secondary xylem and centripetal secondary xylem around the mesarch primary xylem. It should be noted that *Fascisvarioxylon* and *Lioxylon* are the only genera of the order developing a complete ring of centripetal (inversed) xylem. The remaining stems of Cycadales have isolated centripetal bundles. Thus, *Neochamberlainia* and *Worsdellia* have small centripetal bundles linked to the first centrifugal vascular ring. In *Wintucycas* and *Menucoa*, the presence of centripetal xylem is rare, whereas in extant forms it is sporadic and occurs on the stem base of some species of *Macrozamia*, *Lepidozamia*, *Encephalartos* and *Cycas*.

The medullary vascular system is present in extant (*Encephalartos*, *Macrozamia* and *Lepidozamia*) and fossil cycads (*Charmorgia*, *Lioxylon*, *Fascisvarioxylon*, *Worsdellia*, *Neochamberlainia*, *Centricycas* and *Menucoa*). As originally suggested by Worsdell (1896, 1906), and later by Artabe *et al.* (2005), the medullary vascular system originates from a cylindrical vascular system. This has been verified in *Neochamberlainia* and *Worsdellia*, showing how centripetal secondary xylem branches and splits at the inner part of the first centrifugal vascular ring and gives rise to the medullary vascular system. This feature is also present in *Wintucycas*.

The new genus shares the occurrence of mucilage canals with all fossil forms, except for *Sanchucyas*, *Lioxylon*, *Fascisvarioxylon* and *Brunoa*, which have mucilage reservoirs (cavities). Only *Antarcticycas* has both canals and cavities (Hermsen *et al.*, 2009). Extant forms show mainly mucilage canals which are considered an apomorphic character (Artabe *et al.*, 2005).

The manoxylic wood is widespread among Encephalartoideae; only *Dioon* has dense wood resembling pycnoxyly (Chamberlain, 1911; Stevenson, 1990). *Wintucycas*, *Neochamberlainia*, *Charmorgia*, *Lioxylon*, *Fascisvarioxylon*, *Worsdellia*, *Centricycas*, *Bororoa* and *Menucoa* have manoxylic wood, while *Lyssoxylon*, *Michelilloa*, *Brunoa* and *Sanchucyas* have compact pycnoxylic-like wood. According to Artabe *et al.* (2005), the pycnoxylic-like dense wood is considered an apomorphic feature.

Cycads with terminal strobili show, in a longitudinal section of the stem, a sequence of dome-like vascular bundle patterns or cone domes (Chamberlain, 1911; Norstog & Nicholls, 1997). In cross-section, the cone domes (*sensu* Chamberlain, 1911) are seen as a

normal vascular ring of small size inside the main vascular ring. Cone domes have been observed in extant genera such as *Dioon*, *Zamia*, *Ceratozamia*, *Stangeria* and (in microsporangiata stems) *Cycas* (Stevenson, 1990; Norstog & Nicholls, 1997). *Microcycas*, *Chigua* and *Bowenia* also have terminal strobili, and are therefore considered to possess cone domes. *Macrozamia*, *Lepidozamia* and *Encephalartos* only have lateral cones; consequently, they lack cone domes (Norstog & Nicholls, 1997). The presence of cone domes in *Brunoa* and *Bororoa* provides evidence for the hypothesis that these cycads produced terminal cones. In *Fascisvarioxylon*, we assume the presence of cone domes, because some medullary bundles are concentric, like those present in the reproductive axis. In *Antarcticycas*, cone domes were described; however, their probable peduncle has an inverse anatomy in comparison with the typical cone-dome structure (Hermsen *et al.*, 2009).

Extrascicular vascular bundles are found in the stems of some Cycadales such as *Cycas*, *Bowenia*, *Encephalartos*, *Macrozamia* and *Lepidozamia* (Worsdell, 1901; Stevenson, 1990). Among fossil forms, extrascicular vascular bundles have been observed in *Neochamberlainia* and *Worsdellia* (Artabe *et al.*, 2004, 2005). *Wintucycas* does not have extrascicular vascular bundles.

The presence of sclerotic nests is considered a plesiomorphic feature because it is present in Lyginopteridales and Medullosales, the putative ancestors of modern Cycadales (Stein & Beck, 1978; Taylor & Taylor, 1993; Artabe *et al.* 2005). This character is present only in *Encephalartos*, *Macrozamia* and *Lepidozamia* (Stevenson, 1990). Among the fossil forms, only *Fascisvarioxylon* has sclerotic nests; *Lyssoxylon*, *Vladiloxylon*, *Lioxylon* and *Bororoa* have isolated sclerotic cells.

Many Cycadales produce adventitious buds between foliar bases at any point on the stem. Stevenson (1988) distinguished adventitious buds from bulbils as the former are arranged helically, whereas the latter exhibit an irregular pattern. Adventitious buds are present in *Wintucycas*, *Neochamberlainia* and probably in *Bororoa* (Artabe *et al.*, 2005).

All these comparisons indicate that *Wintucycas* shows a combination of anatomical features similar to those present in Encephalartoideae, characterized by the presence of centripetal polyxyly and medullary vascular bundles.

RELATIONSHIPS AMONG EXTANT AND FOSSIL CYCADS

Most published phylogenetic analyses show gymnosperms as a monophyletic group, and Cycadales appear as sister to the crown group composed of Ginkgoales, Gnetales and Coniferales (Stevenson,

1990; Chaw *et al.*, 2000; Qiu *et al.*, 2000; Palmer, Soltis & Chase, 2004; de la Torre *et al.*, 2006). However, the phylogenetic hypotheses that include fossil forms place the seed ferns as the stem group of seed plants, and suggest that cycads originated from pteridosperms (Crane, 1996). It is significant to note that, although the parentage of Cycadales and some seed ferns such as Medullosales has been postulated by many authors (Worsdell, 1906; Delevoryas, 1955; Stewart & Rothwell, 1993), these orders only appear in the same lineage (Crane, 1985) or closely linked to the medullosans as basal to Cycadales (Nixon *et al.*, 1994; Rothwell & Serbet, 1994) in some cladistic analyses. In the phylogenetic approaches of Doyle (1996), Hilton & Bateman (2006) and Bateman, Hilton & Rudall (2006), cycads are included in the stem group of seed plants together with pteridosperms, but they do not appear directly related to Medullosales.

The classification of living cycads suggested and formalized by Stevenson (1990, 1992) places families and genera in a hierarchical structure, based on cladistic analyses of morphological, anatomical, karyological, physiological and phytochemical data. This classification scheme is in some disagreement with molecular analyses. For example, Hill *et al.* (2003) showed certain groups to be strongly supported, such as the segregation of *Cycas* in Cycadinae, the clade of Encephalartoideae (*Encephalartos*, *Lepidozamia* and *Macrozamia*) and the clade of *Zamia*, *Ceratozamia* and *Microcycas*, all well supported. However, additional studies seem to be necessary to clarify the position of *Stangeria*, *Dioon* and *Bowenia* and to obtain a natural classification of Cycadales. Furthermore, knowledge of fossil genera, which has improved over the last years, should be integrated with the general classification of cycads.

In this paper, we use Stevenson's proposal (1992) that acknowledges two suborders (Cycadineae and Zamiineae) and three families (Cycadaceae, Stangeriaceae and Zamiaceae) with 11 extant genera (Stevenson, 1990, 1992; Hill *et al.* 2004). Today, Cycadineae are distributed in Australia, Asia and Africa, and four synapomorphies characterize the clade (megasporephylls not in cones, leaflets with a single unbranched midrib and no lateral veins, platyspermic seeds and multi-ovulate megasporephylls with two to 12 ovules). The suborder includes a single family, Cycadaceae, and only one genus: *Cycas* L. (Stevenson, 1992).

Zamiineae have representatives in America, Africa and Australia, and include the remaining cycad genera. Their synapomorphies are megasporephylls in cones, leaflets with multiple branching veins, radiospermic seeds, bi-ovulate megasporephylls with

coronula and inverted ovules (Stevenson, 1992). The suborder includes Stangeriaceae and Zamiaceae.

Note that, on the basis of their molecular analysis, Hill *et al.* (2003) believe that *Epicycas* (De Laubenfels & Adema, 1998) and *Chigua* could be superfluous and should be included in *Cycas* and *Zamia*, respectively. Other molecular studies carried out by Chaw *et al.* (2005) show that *Dyerocycas* could be included in *Cycas* and *Chigua* in *Zamia*.

Some authors (e.g. Brenner *et al.*, 2003; Hermsen *et al.*, 2006; Cúneo *et al.*, 2010) have developed phylogenetic trees, combining extant and extinct cycad genera. Although most fossil taxa included in these cladistic analyses correspond to morphotaxa, such as leaves, stems and reproductive structures, they have one or more features that definitively link them to Cycadales. Among the extinct taxa considered in these studies, there are only two reconstructions of whole fossil plants: NILAMBE and *Antarcticycas*. NILAMBE is a composite terminal taxon that includes *Nilssonia* Brongn., *Androstrobus* Schimper and *Beania* Carruthers morphotaxa, which Harris (1941) suggested represented a single whole-plant genus. More strictly, Thomas & Harris (1960) associated *Nilssonia tenuinervis*, *Androstrobus wonnacotti*, *Beania mamayi* and *Deltolepis* sp. into a plant, and *Pseudoctenis lanei*, *Androstrobus wonnacotti* and *Beania mamayi* into another.

Other reconstructions used in these studies and based on a close association of shared anatomical features were made by Florin (1933). He reconstructed the Late Triassic cycad *Bjuvia simplex* as a pachycaul plant with an armoured trunk, persistent leaf bases and a terminal crown of megasporephylls, all of which superficially resemble those of *Cycas*. Today, this reconstruction is not accepted because it is based on fragmentary material of associated megasporephylls (without seeds) and leaves. The phylogenetic hypothesis mentioned above has only taken into account the cuticular characteristics and morphology of the *Bjuvia* leaves (Axsmith *et al.*, 2003; Taylor, Taylor & Krings, 2009).

Other important records from the Lower Permian of China belong to megasporephylls, which are similar to those of some extant cycads and were assigned to *Crossozamia* (Zhu & Du, 1981). These megasporephylls were found in association with leaves, *Taeniopteris* Brongniart, *Tianbaolinia* Gao & Thomas and *Yuania* H.C.Sze, but not in attachment (Du & Zhu, 1982; Gao & Thomas, 1989). The morphological features of the leaves suggest that the plant that produced *Crossozamia* megasporephylls had immature foliage of the *Yuania* type and mature leaves of the *Tianbaolinia* type. Both *Tianbaolinia* and *Yuania* are pinnate (Gao & Thomas, 1989).

Although not used in these cladistic studies, the reconstruction of *Leptocycas gracilis* Delevoryas & Hope is important, due to its role in the clarification of the habit of some early cycads. *Leptocycas gracilis* (Upper Triassic) from the United States of America was reconstructed as a slender-stemmed plant with pinnately compound leaves of the *Pseudoctenis* type (Delevoryas & Hope, 1971). The petiole bases are persistent on the stem surface. Cataphylls are intermixed with the leaves. The cones resemble pollen cones and are located on the stem apex. A new species, *Leptocycas yangcaogouensis* Zhang, Yao, Chen & Li, was described in Late Triassic China (Zhang *et al.*, 2010). The fossil remains belong to the upper part of the stem, which has leaves, cataphylls and a female cone. The pinnately compound leaves (*Pseudoctenis* type) are attached in a crown on the stem top. The leaflets are linear, with parallel veins and decurrent bases on the rachis. The leaf bases are persistent and the cataphylls intermix with the leaves. The female cone is ovoid in shape.

Several recent discoveries made in Asia have not been included in the cladistic analyses mentioned above. The fossil whole-plant cycad (*Holozamites hongtaoi*) from Upper Triassic China is one of the most surprising findings, but only a preliminary study, where the plant is briefly described, has been made (Wang *et al.*, 2009). The plant is preserved intact on a sandstone slab, including some leaves and a male cone physically attached to the stem apex. Analysis of the morphology, the arrangement and venation of the leaves and leaflets, and the male cone and its relationship to other parts indicates that this taxon is closely related to living Zamiaceae in Cycadales. In China, various fossils have been found, including cycad-like stems (*Lioxylon liaoningense* Zhang *et al.*, 2006) in Mid Jurassic sediments (Wang *et al.*, 2005), megasporophylls of *Mediocycas kazuoensis* Li, Fu, Zhang, Zheng & Cao from the Lower Triassic (Li *et al.*, 2005), leaves of the *Taeniopteris* type of *Yixianophyllum jinjiagouense* Zheng, Li, Li, Zhang & Bian from the Upper Jurassic (Zheng *et al.*, 2005) and leaves and a pollen cone of *Jurastrobus chenii* from the Lower Jurassic (Wang, Li & Cui, 2006).

In recent years, Hermsen *et al.* (2009) provided a reconstruction of the whole *Antarcticycas* plant (Smoot *et al.*, 1985), which had been considered basal in previous phylogenetic hypotheses (Hermsen *et al.*, 2006). This reconstruction was based on stems of *Antarcticycas schopfii*, leaves of *Yelchophyllum ome-gapetiolaris* and male strobili of *Delemaya spinulosa* found in the Fremouw Formation, from the early Mid Triassic of Antarctica (Hermsen *et al.*, 2009). The discovery of these closely associated (same assemblage) morphotaxa and the presence of shared characters in

different morphogenera allowed these authors to accept that they belonged to the same plant. *Antarcticycas* is reconstructed as a small plant, possibly with an underground habit, similar to some current *Zamia* spp. Its anatomy is comparable with extant cycads, although the contractile tissue and coralloid roots have still to be identified.

CLADISTIC ANALYSIS AND SYSTEMATIC POSITION OF *WINTUCYCAS*

From this phylogenetic analysis, 22 most-parsimonious trees of 211 steps were obtained with a strict consensus shown in Figure 6. The strict consensus tree has a polytomy that includes the Permian *Crossozamia*, the Triassic *Bjuvia*, *Charmorgia*, *Vladiloxylon*, *Michelilloa* and *Lyssoxylon*, the Cretaceous *Nilssoniocladus* and the extant *Cycas*; all of them occur in the early branching part of the clade containing all extant and fossil cycads, a position supported by the five classical synapomorphies that delimit the Cycadales (Stevenson, 1990, 1992) and the presence of microsporophylls in strobili.

In this analysis, the early branching position of *Antarcticycas* is remarkable, as regards the rest of Cycadales (NILANBE and Zamiineae), demarcated by leaflets with multiple branching veins and an alveolar pollen wall.

Encephalartoideae have anastomosing veins in leaflets and cataphylls in the peduncle of the strobilus (*sensu* Stevenson, 1992). However, in our analysis, some additional characters allowed us to group other members in this subfamily, such as overarching accessory cells, a number of accessory cell layers, perforated epidermal cells, the position of stomata and leaflets articulated at the rachis. Other characters, such as a secondary centrifugal polyxyly and a petiole bundle pattern in an elaborate omega, link the fossils *Bororoa*, *Sanchucycas*, *Brunoa*, *Lioxylon* and *Fascivarioxylon* with tribe Encephalarteae.

The presence of pith bundles, and megasporophylls with lateral and adaxially thickened lobes, are important characters to delimit Encephalarteae. In this tribe, the fossil genera *Wintucycas*, *Menucoa*, *Worsdelia* and *Neochamberlainia* and the extant *Encephalartos*, *Macrozamia* and *Lepidozamia* are included.

Wintucycas and *Menucoa* can be separated from the rest of the Encephalartae because they lack cortical steles. Finally, as noted above, *Wintucycas* does not have cataphylls, thus differing from *Menucoa* and the rest of Encephalarteae.

CONCLUSIONS

The results of our phylogenetic analysis expose an unresolved polytomy at the base of Cycadales. Nev-

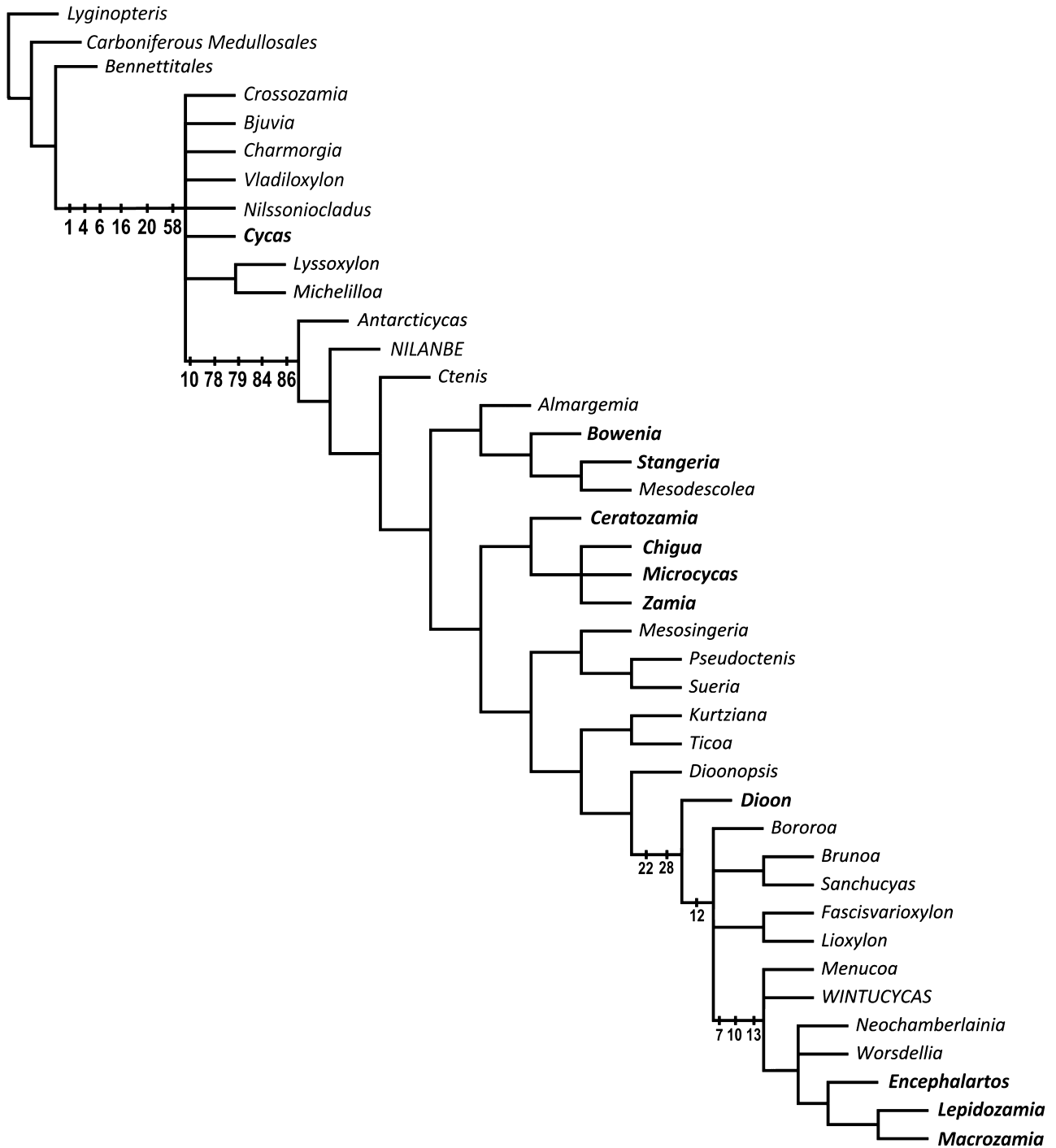


Figure 6. Strict consensus of 22 most-parsimonious trees found in the results of the cladistic analysis. Extant taxa are indicated with bold type.

ertheless, this cladogram is broadly concordant as to the age of most extinct genera of the order (*Crossozamia*, *Bjuvia*, *Charmorgia*, *Vladiloxylon*, *Michelilloa* and *Lyssoxylon*). Moreover, this polytomy includes the fossil *Nilssoniocladus* and extant *Cycas*. *Cycas* probably occupies this position due to a set of features

considered plesiomorphic. However, the ‘absence’ of strobili in *Cycas* would suggest a condition derived through the reduction and simplification of loose strobili from a hypothetical ancestor such as *Crossozamia*, in agreement with Gao & Thomas (1989), diverging into the less diverse Cycadineae.

In contrast, Zamiineae are a more diversified lineage, in the past as well as at present. The current analysis shows *Antarcticycas* at the base of Zamiineae, which would indicate an origin of this suborder in the Triassic in Gondwana. NILANBE also has a remarkable early branching position in Zamiineae; the presence of loose strobili (e.g. *Beania*) supports the hypothesis of Gao & Thomas (1989).

Wintucycas has features that clearly allow us to erect a new genus, with affinities to fossil and living Zamiaceae, included in Encephalarteae due to their manoxylic wood, centripetal polyxyly, parenchymatous pith, centrifugal polyxyly and medullary vascular bundles. The cladistic analysis sets *Wintucycas* and *Menucoa* in a lateral position as regards Encephalarteae, according to the morphological and anatomical studies because these fossil genera have polyxyly and lack extrafascicular vascular bundles.

This new taxon highlights the diversity of Cycadales and specially Encephalartoideae in the Upper Cretaceous of Patagonia. Despite this, in the Palaeocene of Patagonia, the record of Cycadales is represented only by *Menucoa* and *Bororoa* (Encephalarteae).

Today, Encephalarteae are extinct in South America. However, there are numerous species in tropical Africa. The extinction of this group in Patagonia could have been influenced by climatic change, from warm and humid to cold and dry conditions. This situation would have occurred during the Cenozoic during the Andean uplift (Howell *et al.*, 2005), which may have constituted an important topographic barrier and climate control for the Patagonian region.

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CHARACTER LIST (ALL CHARACTERS ARE NON-ADDITIVE)

1. Cycasin (0, absent; 1, present) (character 1.1 of Stevenson, 1990). The presence of cycasin is an autapomorphy of Cycadales (Stevenson, 1992).
2. Mucilage (0, absent; 1, present). The occurrence of mucilage characterizes all cycadales.
3. Mucilage structures (0, cavities; 1, channels). Modified from character 47 of Hermsen *et al.* (2006). Extant forms show mainly mucilage canals which are considered to be the derived state (Artabe *et al.*, 2005).
4. Coralloid roots (0, absent; 1, present) (character 1.3 of Stevenson, 1990). The ageotropic roots containing nitrogen-fixing cyanobacteria (= coralloid roots) are found in all extant cycads.
5. Root buds (0, absent; 1, present) (character 1 of Hermsen *et al.*, 2006). Root buds were considered an autapomorphy of Stangeriaceae by Stevenson (1992).
6. Primary thickening meristem (0, internal derivatives; 1, external derivatives) (character 1.5 of Stevenson, 1990). All living cycads have a unique primary thickening meristem, which lies next to the pith and produces most of its derivatives centrifugally. This feature has also been found in most fossil cycads.
7. Medullary bundles (0, absent; 1, present) (character 1.27 of Stevenson, 1990). These vascular bundles are not linked to cone domes, but they are the result of inverted cambial activity (Stevenson, 1990; Artabe *et al.*, 2005). They were found in the pith of *Encephalartos*, *Lepidozamia*, *Macrozamia* and several fossil forms. It is considered as an autapomorphy of Encephalarteae (Stevenson, 1992).
8. Medullary sclerenchyma (0, sclerotic nests; 1, sclerotic cells; 2, absent). Sclerotic nests composed of sclereids is not a generalized character in extant cycads (Stevenson, 1990) being present only in *Encephalartos*, *Macrozamia* and *Lepidozamia*. Among fossil forms, only *Fascivarioxylon* has sclerotic nests, while *Lyssoxylon* and *Bororoa* have sclerotic cells. On the other hand, the occurrence of sclereids in the pith is widespread in seed ferns.
9. Primary xylem (0, mesarch; 1, endarch). From character 18 of Doyle (1996).
10. Cone domes (0, absent; 1, present) (character 3 of Hermsen *et al.*, 2006). In cycads with terminal cones, longitudinal sections of stems show a sequence of a dome-like vascular bundle, arrangements or cone domes (Chamberlain, 1911; Norstog & Nicholls, 1997). The presence of these structures has been reported in *Brunoa*, *Menucoa* and *Antarcticycas* (Artabe *et al.*, 2005; Hermsen *et al.*, 2009). However, the supposed cone domes of *Antarcticycas* could represent a branch trace (see discussion above).
11. Wood parenchyma (0, abundant; 1, scanty). Taken from character 7 of Hermsen *et al.* (2006).

12. Secondary centrifugal polyxyly (0, absent; 1, present). Equivalent to character 1.18, 'Polyxylic stele', of Stevenson (1990).
13. Centripetal polyxyly (0, absent; 1, continuous cycle; 2, random or discontinuous cycles). Modified from character 46, 'Inverse polyxyly', of Hermsen *et al.* (2006).
14. Cortical sclerenchyma (0, sparganum/dictyoxylon; 1 absent) (character 30 of Hilton & Bateman, 2006). The alternating strands of sclerenchyma and parenchyma in the cortex of basal pteridosperms and some cordaitalean coniferophytes are lost in derived groups.
15. Cortical steles (0, absent; 1, present). This character is modified from character 1.29 'Extrafascicular vasculature' of Stevenson (1990).
16. Leaf traces (0, radial; 1, girdling) (character 10 of Hermsen *et al.*, 2006). Girdling leaf traces are considered an automorphy of Cycadales (Stevenson, 1992).
17. Nodal anatomy (0, one trace to each leaf; 1, more than three traces; 2, leaf traces from two or more protoxylem strands or bundles over a substantial length of stem). Modified from character 20 of Hilton & Bateman (2006).
18. Leaf trace (0, mesarch; 1, endarch). From character 12 of Doyle (1996).
19. Axillary buds (0, present; 1, absent). All cycads lack axillary buds, which distinguish them from other gymnosperms.
20. Omega pattern (0, absent; 1, present). Another autapomorphy of Cycadales is the arrangement of the vascular bundles in an inverted omega pattern (Stevenson, 1992).
21. Type of omega pattern (0, simple; 1, elaborate; 2, secondarily absent). The omega pattern of vascular bundles on a petiole base is an autapomorphy of the Cycadales (Stevenson, 1990). In some living and extinct genera, a modified pattern is present, which was referred to as 'obscure omega' by Hermsen *et al.* (2006) or 'elaborate omega' (this work).
22. Leaf bases (0, persistent; 1, ephemeral). Taken from character 45 of Hermsen *et al.* (2006).
23. Stipules in leaf bases (0, absent; 1, present). Modified from character 14 of Hermsen *et al.* (2006). Stipules are present on the leaf bases of several cycad genera, and they are of two types: fleshy and vascularized or diminutive and unvascularized (Stevenson, 1990).
24. Division of leaf lamina (0, simple; 1, pinnate; 2, bipinnate). Recodified from character 58 of Hermsen *et al.* (2006).
25. Leaves truncate (0, absent; 1, present). Leaves with a truncated apex characterize *Microcycas* (Stevenson, 1992).
26. Lamina position (0, lateral; 1, adaxial). From character 57 of Hermsen *et al.* (2006).
27. Pinna attachment (0, decurrent; 1, articulate) (character 60 of Hermsen *et al.*, 2006). Modified from character 1.17, 'Articulate pinna', of Stevenson (1990). The position and mode of leaflet attachment to the rachis exhibit some variability in Cycadales. There are two basic patterns of leaflet attachment: decurrent and articulate. In the latter, the leaflets tend to abscise before the leaf (Stevenson, 1990).
28. Terminal pinna (0, all stages; 1, seedlings; 2, absent). From character 59 of Hermsen *et al.* (2006). The absence of terminal leaflets in seedlings and adult plants is an autapomorphy of Zamioideae (Stevenson, 1992).
29. Acroscopic basal callus (0, absent; 1, present) (character 17 of Hermsen *et al.*, 2006). *Lepidozamia* and *Macrozamia* have decurrent leaflets with a yellow swollen callous area near their base (Stevenson, 1990), called acroscopic basal callus by Hermsen *et al.* (2006).
30. Leaflet venation (0, uninerve; 1, multinerve). A difference between Cycadineae and Zamieae is the number of veins in the leaflet (Stevenson, 1992).
31. Pinna traces (0, one; 1, two or more) (character 18 of Hermsen *et al.*, 2006). Stevenson (1992) proposed that leaflet traces derived from more than one rachis bundle is an autapomorphy of Stangeriaceae.
32. Pinna midrib (0, alethopteroid, pectopteroid or neuropteroid type; 1, absent; 2, *Cycas* type; 3, *Chigua* type midrib). Adapted from character 61 of Hermsen *et al.* (2006). Midribs occur in the pinnae of *Cycas*, *Chigua*, *Stangeria* and *Bowenia*. *Chigua* has leaflets with midrib and parallel longitudinal secondary veins. This pattern is also present in *Stangeria* and *Bowenia* (Stevenson, 1990).
33. Veins (0, free; 1, anastomosing). From character 62 of Hermsen *et al.* (2006).
34. Whole leaf ptyxis (0, circinate; 1, non-circinate) (character 15 of Hermsen *et al.*, 2006). In his contributions, Stevenson (1990) argued that, within cycads, only *Bowenia* has circinate whole-leaf ptyxis.
35. Pinna ptyxis [0, circinate; 1, conduplicate; 2, adplicate (flat); 3, involute] (character 16 of Hermsen *et al.*, 2006). Developing flat pinnae was considered a derivation by Stevenson (1981, 1990). In carboniferous medullosans, the pinna ptyxis are interpreted as involute.
36. Prickles (0, absent; 1, present). Prickles are sharp epidermal projections on rachis and petiole (from character 1.25 of Stevenson, 1990) (character 12 of Hermsen *et al.*, 2006).

37. Gradual transition from foliar to spinose leaflets (0, absent; 1, present) (character 1.24 of Stevenson, (1990). *Cycas* and the genera of Encephalartoideae exhibit, in their leaves, a gradual transitional series between leaflets, reduced leaflets and true spines or spinose leaflets in the petiole (Stevenson, 1990).
38. Vascularized stipules (0, absent; 1, present) (character 1.13 of Stevenson, 1990). Large, fleshy and vascularized stipules in the leaf base only occur in *Stangeria* and *Bowenia*, among living cycads (Stevenson, 1990). We cannot verify its presence in fossil forms.
39. Cataphylls in vegetative axes (0, absent; 1, present) (character 22 of Hermsen *et al.*, 2006). The presence of vegetative cataphylls is normal for Cycadales.
40. Irregular production of cataphylls (0, absent; 1, present). Modified from character 22 of Hermsen *et al.* (2006). Another trait exclusive of Stangeriaceae is that the stems produce cataphylls in a discontinuous mode (Stevenson, 1992).
41. Peduncular cataphylls (0, absent; 1, present) (character 23 of Hermsen *et al.*, 2006). Cataphylls borne directly along the peduncle characterize only a few extant genera: *Dioon*, *Encephalartos*, *Lepidozamia* and *Macrozamia* (Stevenson, 1990).
42. Trichomes (0, transparent; 1, coloured; 2, absent) (character 19 of Hermsen *et al.*, 2006). Coloured trichomes are considered apomorphic by Stevenson (1990), as they are present in all cycads except for *Cycas*, and are absent in the other gymnosperms.
43. Curved trichomes (0, absent; 1, present) (character 20 of Hermsen *et al.*, 2006). Coloured trichomes in cycads are of two types: long-slender and short-curved. The second type is exclusive of the genera *Bowenia*, *Lepidozamia* and *Macrozamia* (Stevenson, 1990).
44. Branched trichomes (0, absent; 1, unequally branched; 2, equally branched) (character 21 of Hermsen *et al.*, 2006). Branched trichomes are found only in *Cycas*, *Microcycas* and *Zamia* (Stevenson, 1981). All branched trichomes in *Cycas* are unequally branched, being different from equally branched trichomes found in *Zamia* and *Microcycas* (Stevenson, 1990).
45. Epidermal cells (0, without perforations; 1, with perforations; 2, corner only) (character 52 of Hermsen *et al.*, 2006). Perforations in cell walls of leaf epidermis are a unique feature present in fossil and extant Cycadales (Artabe & Stevenson, 1999).
46. Epidermal thickened cells (0, uniformly thickened cells; 1, differentially thickened cells). From character 56 of Hermsen *et al.* (2006).
47. Cuticular lamellae (0, absent; 1, present) (character 54 of Hermsen *et al.*, 2006). The surface of the epidermal cells of several extant and fossil forms is covered by radially arranged cuticular lamellae (Greguss, 1968).
48. Anticlinal pegs (0, absent; 1, present) (character 53 of Hermsen *et al.*, 2006). Plants grouped in Encephalartaeae exhibit specialized thickenings of the cuticular layer at the area of the anticlinal cell walls.
49. Stomate position (0, hypostomatic; 1, amphistomatic) (character 55 of Hermsen *et al.*, 2006). The position of the stomates on the leaf surfaces is highly variable in Cycadales (Greguss, 1968).
50. Stomata (0, sunken; 1, flush) (character 63 of Hermsen *et al.*, 2006). Sunken stomata are quite generalized among gymnosperms. The flush stomata of Stangeriaceae is considered to be the derived state in the present contribution.
51. Stomatal shape (0, circular; 1, oblong) (character 65 of Hermsen *et al.*, 2006). Another peculiar feature of Stangeriaceae is the circular morphology of the stomata.
52. Guard cell orientation (0, irregular; 1, longitudinal) (character 64 of Hermsen *et al.*, 2006). *Cycas* and *Stangeria* differ from other cycadales because of the randomly scattered stomata on the leaflet surfaces (Greguss, 1968).
53. Number of accessory cell layers (0, zero; 1, one; 2, two; 3, more than two) (character 50 of Hermsen *et al.*, 2006).
54. Guard cell corona (0, absent; 1, present) (character 49 of Hermsen *et al.*, 2006). Among extant and fossil forms, only *Stangeria* and *Mesodescolea* exhibit guard cells with a circular cutine thickening.
55. Accessory cell corona (0, absent; 1, present) (character 48 of Hermsen *et al.*, 2006). Accessory cells in several Zamiaceae have a ring-shaped cutine thickening that projects over the guard cells.
56. Overarching accessory cells (0, absent; 1, present). From character 51 of Hermsen *et al.* (2006).
57. Dioecy (0, absent; 1, present). Cycadales, Ginkgoales and Gnetales are all dioecious; therefore, the dioecy is interpreted as an autapomorphy of seed plants and a symplesiomorphy of the subordinate gymnosperm taxa (Loconte and Stevenson, 1990).
58. Microsporophyll in strobili (0, absent; 1, present). This is a synapomorphy of Cycadineae and Zamiineae.
59. Microsporophyll arrangement (0, imbricate; 1, vertical rows). The Cycadales bear microsporophylls in a helical arrangement, but this can become manifest in two different patterns: strobilus of Cycadaceae and some Zamiaceae

- (Encephalarteae and Diooaeae) display an overlapping spiral, whereas those in Stangeriaceae and other Zamieae (Zamieae and Ceratozamieae) have vertical rows. All fossil cycad cones known to date display an imbricating arrangement of microsporophylls with rhomboidal faces, which is the more generalized pattern among cycads. (Klavins *et al.*, 2003).
60. Microsporophyll faced shape (0, rhomboid; 1, hexagonal) (character 51 of Hermsen *et al.*, 2006). A peculiar feature of the cycad microsporophylls is the morphology of the distal face, which could be at least of two morphotypes: rhomboid and hexagonal. *Cycas*, *Stangeria*, Encephalarteae and some fossil forms are characterized by the first shape, being considered as the basal condition (Klavins *et al.*, 2003).
 61. Microsporangia clustering (0, clustered with all fused; 1, free; 2, clustered with some fused). Modified from feature 67 of Hermsen *et al.* (2006). We interpreted that microsporangia grouped in synangia is the ancestral state as it is present in basal seed ferns.
 62. Pollen sacs per sorus (0, eight or more; 1, two to five). The number of pollen sacs per sorus is quite uniform among living Cycadales. However, some fossil genera show a greater number of pollen sacs (Klavins *et al.*, 2003).
 63. Microspore/pollen with (0, proximal tetrad scar; 1, distal sulcus). Adapted from character 85 of Crepet & Stevenson (2010).
 64. Proximal pollen shape (0, convex; 1, concave). Taken from character 37 of Hermsen *et al.* (2006).
 65. Pollen shape (0, circular; 1, oblong; 2, elliptical). Modified from character 41 of Hermsen *et al.* (2006).
 66. Pollen wall (0, spongy; 1, alveolar; 2, granular). Adapted from character 68 of Hermsen *et al.*, 2006). *Cycas* exhibits a less specialized exine structure, especially when compared with other cycad genera which have an alveolate exine layer, unique among seed plants (Audran & Masura, 1977; Stevenson, 1990).
 67. Pollen exine (0, psilate; 1, fossulate; 2, foveolate) (character 43 of Hermsen *et al.*, 2006).
 68. Sperm number (0, two; 1, four to eight). Modified from character 44 of Hermsen *et al.* (2006). Both *Ceratozamia* and *Microcycas* differ from the rest of the cycadales in producing more than two sperm cells.
 69. Megasporophyll arranged in strobili (0, absent; 1, present). This is an autapomorphy of Zamiineae (Stevenson, 1992).
 70. Strobilus type (0, absent; 1, loose; 2, compact). While megasporophyll organized in a strobilus clearly distinguishes living Zamiineae from Cycadineae, some fossil genera show a halfway arrangement, which is referred to as 'loose strobilus'.
 71. Megasporangium-bearing structure (0, simple; 1, pinnatifid; 2, pinnate; 3, modified). Modified from character 34 of Hilton & Bateman (2006).
 72. Megasporophyll skirt (0, absent; 1, above; 2, below) (character 29 of Hermsen *et al.*, 2006).
 73. Megasporophyll shape (0, flat; 1, peltate; 2, adaxially thickened) (character 29 of Hermsen *et al.*, 2006).
 74. Megasporophyll lobing (0, absent; 1, lateral) (character 27 of Hermsen *et al.*, 2006). In the sterile tips of megasporophylls of *Encephalartos*, *Lepidozamia* and *Macrozamia*, there are two lateral lobes (Stevenson, 1990).
 75. Megasporophyll spines (0, absent; 1, single; 2, two) (character 27 of Hermsen *et al.*, 2006). The megasporophylls of *Macrozamia* and *Lepidozamia* have a spinose sterile tip. On the other hand, *Ceratozamia* has megasporophylls with a distinctive apex composed of two prominent spines (Stevenson, 1990).
 76. Sporophyll vasculature (0, planar; 1, three dimensional; 2, *Macrozamia*-type) (character 25 of Hermsen *et al.*, 2006). This character is related to the vascular pattern of the laminar type of megasporophylls. *Cycas*, *Dioon* and *Stangeria* have an open dichotomous venation pattern with all the dichotomies occurring on one plane. On the other hand, the vascular pattern in the peltate form (present in *Bowenia*, *Ceratozamia*, *Chigua*, *Encephalartos*, *Lepidozamia*, *Macrozamia*, *Microcycas* and *Zamia*) consists of an open dichotomous system with successive dichotomies occurring at right angles to the previous dichotomy. It results in a three-dimensional arrangement.
 77. Sporophyll pubescence (0, absent; 1, present) (character 24 of Hermsen *et al.*, 2006). This trait is present in almost all extant cycadales.
 78. Ovule position (0, lateral; 1, above; 2, below) (character 30 of Hermsen *et al.*, 2006). Ovule position on the megasporophyll stalk is one of the differences between the three families of Cycadales, being lateral in Cycadaceae, adaxial in Zamiaceae and abaxial in Stangeriaceae (Stevenson, 1992).
 79. Ovule number (0, more than two; 1, two) (character 31 of Hermsen *et al.*, 2006). The presence of megasporophylls with two ovules is an autapomorphy of Zamiineae (Stevenson, 1992).
 80. Integument vasculature (0, single; 1, double) (character 34 of Hermsen *et al.*, 2006). Another autapomorphy of Cycadales is the double vascularization of the integument, which is not homolo-

gous to that present in seed ferns (Crane, 1988; Stevenson, 1990).

81. Ovule vasculature (0, simple; 1, medullosan; 2, cycadean) (character 33 of Hermsen *et al.*, 2006). The two bundles that enter the ovule of all extant cycads always originate from one common bundle by two anisotomous branches of that bundle. The fact that both bundles entering the ovule contribute with branches to both the outer and inner vasculature of the ovule is quite different from that of medullosans (Stevenson, 1990; Norstog & Nicholls, 1997).
82. Endospermic jacket (0, absent; 1, present) (character 36 of Hermsen *et al.*, 2006).
83. Buffer cells (0, absent; 1, present) (character 37 of Hermsen *et al.*, 2006).
84. Micropyle (0, distal; 1, proximal) (character 35 of Hermsen *et al.*, 2006). One further distinction between Cycadinae and Zamiineae is the position of the ovule micropyle, which is distal in the former, and proximal in the latter (Stevenson, 1992).
85. Pollen chamber (0, hydrasperman; 1, non-hydrasperman). Adapted from Crepet & Stevenson (2010). The hydrasperman pollen chamber is characterized by the presence of a membranous floor and a central column (Hilton & Bateman, 2006).
86. Seed (0, radiospermic; platyspermic, 1). Modified from character 1.9 of Stevenson (1990). The two suborders of Cycadales differ from each other in their seed symmetry, as Cycadinae have platyspermic seeds and Zamiineae have radiospermic seeds (Stevenson, 1992).
87. Cotyledon bundle (0, collateral; 1, bicollateral) (character 40 of Hermsen *et al.*, 2006). Adapted from character 1.28, 'Concentric vascular bundles in cotyledons', of Stevenson (1990). Bicollateral (= concentric) bundles are exclusive to Stangeriaceae (Stevenson, 1990).
88. Coronula (0, absent; 1, distinct; 2, indistinct) (character 39 of Hermsen *et al.*, 2006). Seeds of plants included in Zamiineae have a distinctive area or sclerotesta in the seed coat at the micropylar end (Stevenson, 1992; Nixon *et al.*, 1994).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Character matrix.

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