A new Encephalarteae trunk (Cycadales) from the Cretaceous of Patagonia (Mata Amarilla Formation, Austral Basin), Argentina

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ABSTRACT

The cycads are remnants of a flora that dominated the terrestrial ecosystems across the Mesozoic Era. The stem record of fossil cycads is scanty, with seventeen genera described around the world. From them, eight come from Argentina (Triassic to Paleogene strata), and actually six from the Cretaceous of Patagonia. In this research, we present a new fossil trunk of cycad from Upper Cretaceous beds of Patagonia. The good preservation of the permineralized stem allows to make detailed descriptions and comparisons and, accordingly, support the erection of a new taxon, *Zamuneria amyla* gen. et sp. nov. This new taxon possesses characters that fit with the Encephalarteae (e.g., columnar stem with persistent leaf bases and cataphylls, a wide pith, medullary vascular bundles, mucilage canals and idioblasts, a polyxylic vascular cylinder). Some features present in *Zamuneria* are discussed, such as the great development of parenchyma tissues with a marked amount of specialized cells (idioblasts), probably related with some protective function. Furthermore, the presence of cycads during the deposition of the Mata Amarilla Formation allows inferring climatic conditions, as well as a greater diversity of Encephalarteae in South America reinforces the endemic conditions for this group for the Cretaceous of southern continents.

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1. Introduction

The Cycadales are the most antique and basal of living seed-bearing plants. Actually, the living cycads are just small remnants of a surprisingly diverse lineage of seed plants, with an origin during the Permian (Mamay, 1969; Zhu and Du, 1981; Du and Zhu, 1982; Gao and Thomas, 1989).

Extant cycads grow in tropical and subtropical areas, between c. 30°N and 35°S (Norstog and Nicholls, 1997; Hill et al., 2004). The Order Cycadales bears today 331 living species grouped in 10 genera: *Bowenia* J.D. Hook, *Ceratozamia* Brongniart, *Cycas* L., *Dioon* Lindley, *Encephalartos* J.G.C. Lehmann, *Lepidozamia* E. Regel, *Macrozamia* Miquel, *Microcycas* (Miquel) de Candolle, *Stangeria* T.

Moore y *Zamia* L. (Stevenson, 1990, 1992; Hill et al., 2003; Hill et al., 2004; Osborne et al., 2012).

At present, the genus with the most species is *Cycas* (107 spp.), followed by *Zamia* (71 spp.), *Encephalartos* (65 spp.), *Macrozamia* (41 spp.), *Ceratozamia* (27 spp.) and *Dioon* (14 spp.); whereas other genera contain only a single (monotypic) or a few species (Osborne et al., 2012).

Fossil records indicate a more diversification and geographical distribution of Cycadales during all the Mesozoic, with a large number of genera and species. Although cycads survived the latest Cretaceous extinction, their fossil record shows a marked decline along the Cenozoic (Artabe and Stevenson, 1999; Brenner et al., 2003; Hill et al., 2003). Some authors suggest that extant genera of Cycadales have diversified recently since the Late Cretaceous to the Neogene (Nagalingum et al., 2011; Condamine et al., 2015); however, several major taxa and extant families can be recognized in the fossil record (Artabe and Stevenson, 1999; Martínez and Artabe, 2014).

The fossil record of cycads in Argentina is diverse, containing leaves, stems and reproductive structures. It is continuous across the Mesozoic, beginning in the Triassic, with a peak in the Cretaceous, to decline and even disappear in the late Paleogene (Artabe and Stevenson, 1999; Artabe et al., 2004, 2005; Martínez et al., 2012; Martínez and Artabe, 2014), following the global cooling event.

In this research, we describe a new taxon of Cycadales from the Mata Amarilla Formation (Middle Cenomanian). Its anatomical features, prompts a systematic position within or very close to Encephalarteae for the new taxon. Furthermore, the Patagonian specimen here described suggests warm climatic conditions during the deposition of the Mata Amarilla Formation.

2. Geological setting

The Mata Amarilla Formation shows the best exposures of the lower Upper Cretaceous deposits in the Austral Basin (Fig. 1). It overlies the Piedra Clavada Formation with a transitional contact, and is unconformably covered by the marine deposits of the La Anita Formation (Varela et al., 2012a).

Based on facies analysis, Varela et al. (2012b) divide the Mata Amarilla Formation into three sections: lower, middle and upper. The lower and upper sections of the Mata Amarilla Formation consist of fine-grained sediments with littoral palaeosols interbedded with shell beds interpreted as littoral marine, lagoon, and estuary palaeoenvironments (Varela et al., 2011, 2012b). In contrast, the middle section is characterized by conglomerates to coarse-grained sandstones with subordinate mudstones in the west; whereas towards the east, it consists of medium- to coarse-grained sandstones with subordinate mudstones interpreted as fluvial deposits with palaeosols development (Varela, 2015).

The new cycad stem comes from the contact between the lower and middle section of the Mata Amarilla Formation at Cerro Fortaleza locality (Fig. 2).

The time of deposition of the middle section of the Mata Amarilla Formation was U−Pb dated by means of zircons collected from a tuff layer at 96.2 ± 0.7 Ma, corresponding to the middle Cenomanian (Varela et al., 2012a).

The sedimentary palaeoenvironment of the deposit containing the new cycad stem has been interpreted as a high-sinuosity meandering fluvial system (Varela, 2015). The cycad stem fossiliferous level is represented by an important increase in the degree of amalgamation of fluvial channels interpreted as a forced regression heterogeneous surface located in the contact between the lower and middle sections of the Mata Amarilla Formation (Varela, 2015; Varela et al., 2015). Toward the north east of the basin, that surface is represented by a low-sinuosity meandering fluvial system with well-developed palaeosols containing in situ petrified forests, where large conifer fossil woods were described (Zamuner et al., 2004; Varela et al., 2015).

The Cerro Fortaleza locality provided abundant petrified trunks and woods within amalgamated sheet-like channel deposits (Fig. 1). Large conifer trunks (40−95 cm in diameter) are abundant at the same stratigraphic level (Varela et al., 2015).

Although with some degree of transportation, all known fossil trunks, including the cycad stem here studied, are interpreted as **parautochthonous**, lying close to the original living site (Varela et al., 2015). Sedimentological analyses indicate that palaeosols where the cycad grew, were moderate to well-drained (Varela et al., 2012b; Varela et al., 2015).

3. Materials and methods

The new fossil material comes from the uppermost part of the Lower Section of Mata Amarilla Formation (Austral Basin), in the Cerro Fortaleza locality (Fig. 1). The material was found associated with a petrified forest dominated by fallen Podocarpaceae trunks (Varela et al., 2015).

The fossil studied comprises a single permineralized cycad trunk fossilized with amorphous silica (opal), although a few thin cracks filled with micro-crystalline quartz are evident.

Thin sections were made using traditional techniques for wood anatomy; transverse (CS), radial (RS) and tangential (TS) sections
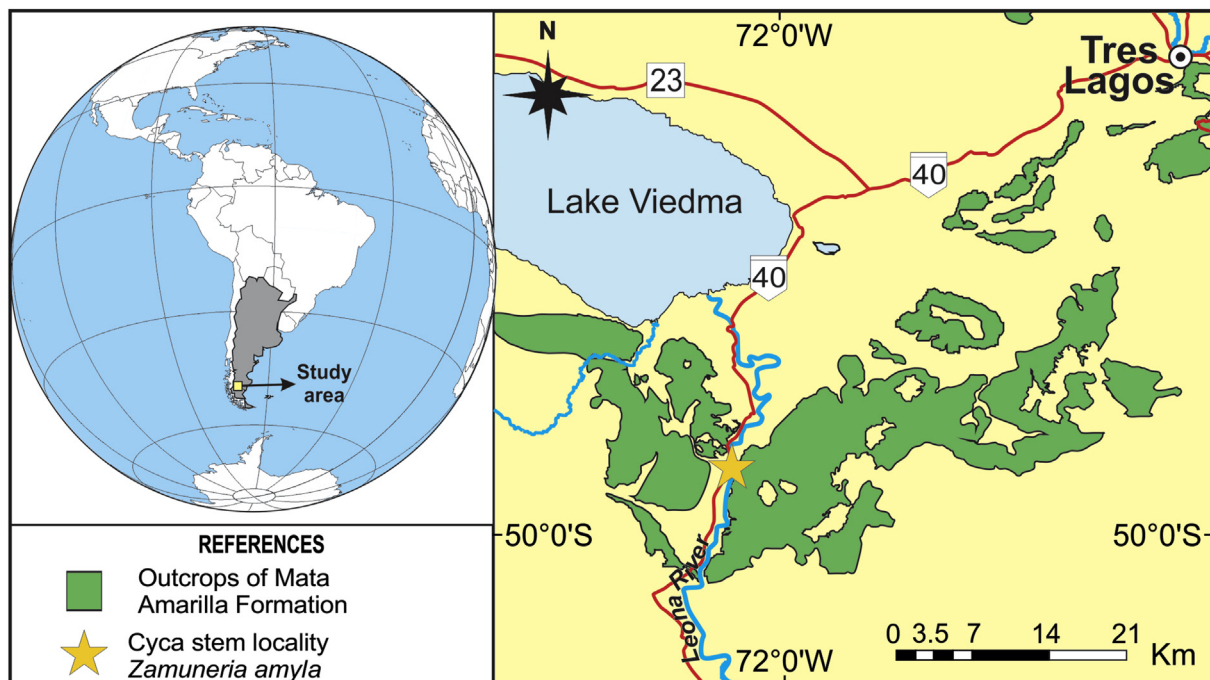

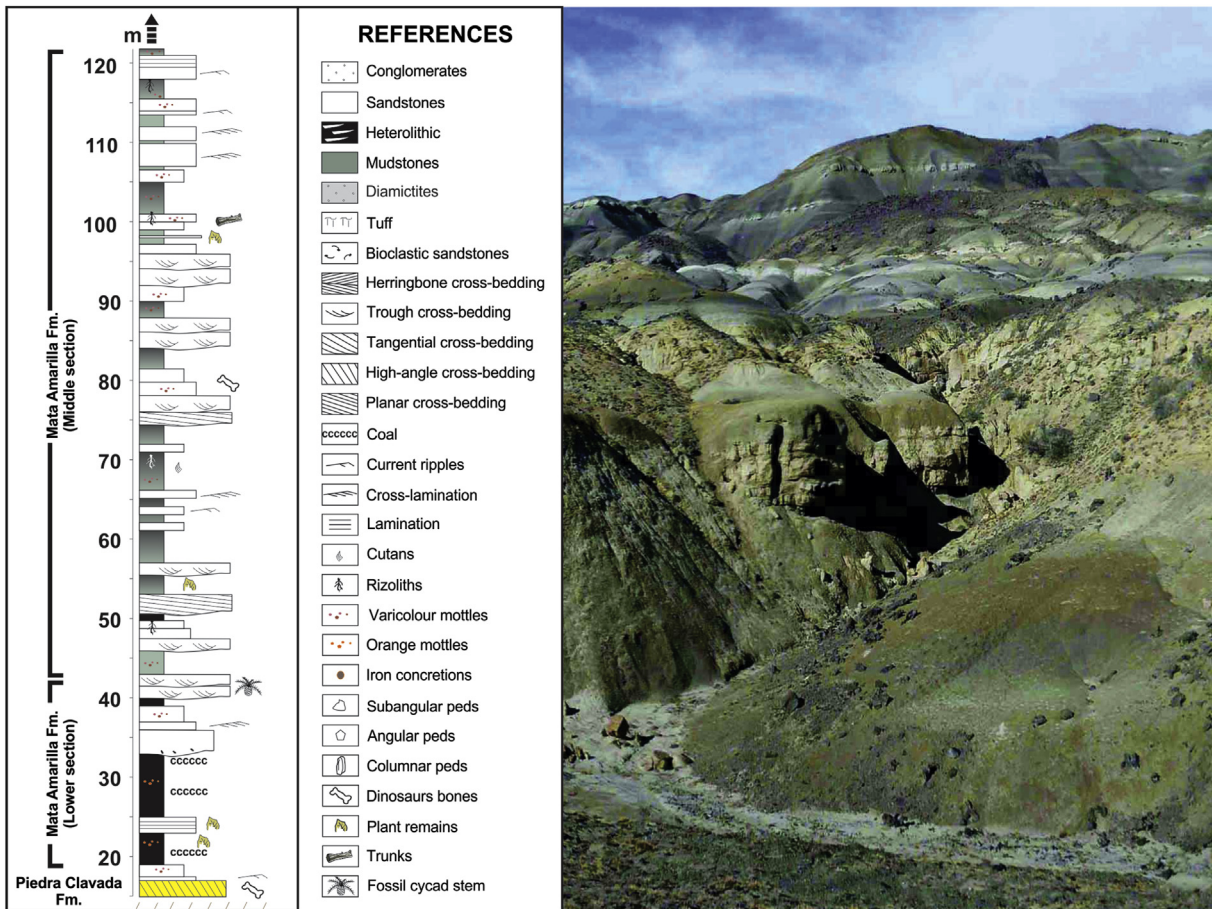**Fig. 1.** Location map of the fossil site.

Fig. 2. Sedimentological section and general view of Cerro Fortaleza locality, Santa Cruz Province, Argentina.

were made to study wood anatomy. In addition, the fossil was examined with JEOL JSM 6360 LV scanning electron microscopy (SEM); the fossil stem was fractured and adhered to aluminium stubs using nail polish, and coated with a gold layer. The measurements are based on at least 25 measurements; the numbers in parentheses indicate the minimum and maximum values.

The fossil wood and thin sections are deposited in the Palaeontological Collection of Museo Padre Molina from Santa Cruz Province (MPM-PB), and in the Collection of the Paleobotany Division of Museo de La Plata (LPPB), La Plata, Argentina.

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

3.1. Systematic palaeobotany

The extant cycads form a monophyletic group (Stevenson, 1990; Soltis et al., 2002). However, the classification of cycads presents numerous uncertainties and, at present, the molecular phylogenies are not consistent with the morphological analysis (Hill et al., 2003; Zgurski et al., 2008). Several cycad clades are strongly supported by the molecular data: including one that defines a sister group relationship between *Cycas* and all other cycads, a *Microcycas—Zamia* clade, and the Encephalarteae (*Macrozamia* (*Encephalartos*, *Lepidozamia*)) (Zgurski et al., 2008). However, for practical purposes, we follow here the classic systematic arrangement proposed by Stevenson (1992) based only on anatomical and morphological characters.

Cycadales Dumortier
Zamiineae Stevenson
Family Zamiaceae Reichenbach
Subfamily Encephalartoideae Stevenson
Tribe Encephalarteae Miquel

Genus ***Zamuneria*** Martínez, Iglesias & Artabe, gen. nov.
Type species: *Zamuneria amyla* Martínez, Iglesias & Artabe, gen. et sp. nov.

Figs. 3—11

Holotype. MPM-Pb-17527, *Isotype*: LPPB-14021, pmLPPB-1938 to pmLPPB-1949.
Locality. Cerro Fortaleza locality (49°56′40″S, 72°03′50″ W), Santa Cruz Province, Argentina (Fig. 1).
Stratigraphic horizon. Mata Amarilla Formation, lower Upper Cretaceous (middle Cenomanian).
Generic diagnosis. Columnar, polyxylic stem, covered by persistent rhomboidal leaf bases and cataphylls. Parenchymatous central pith with mucilage canals, idioblasts and medullary vascular bundles. Cylindrical vascular system centrifugal, with many rings of manoxylic secondary xylem and phloem, containing primary and secondary rays. Primary rays with leaf traces and a mucilage canal associated. Parenchymatous cortex with mucilage canals, idioblasts and girdling leaf traces in the cortex.
Etymology. The genus honours the late Dr. Alba B. Zamuner, an Argentinian palaeobotanist who passed away in 2012, and who made significant contributions to our knowledge of fossil floras from Argentina. She was one of the leaders of the expedition in which this fossil was discovered.
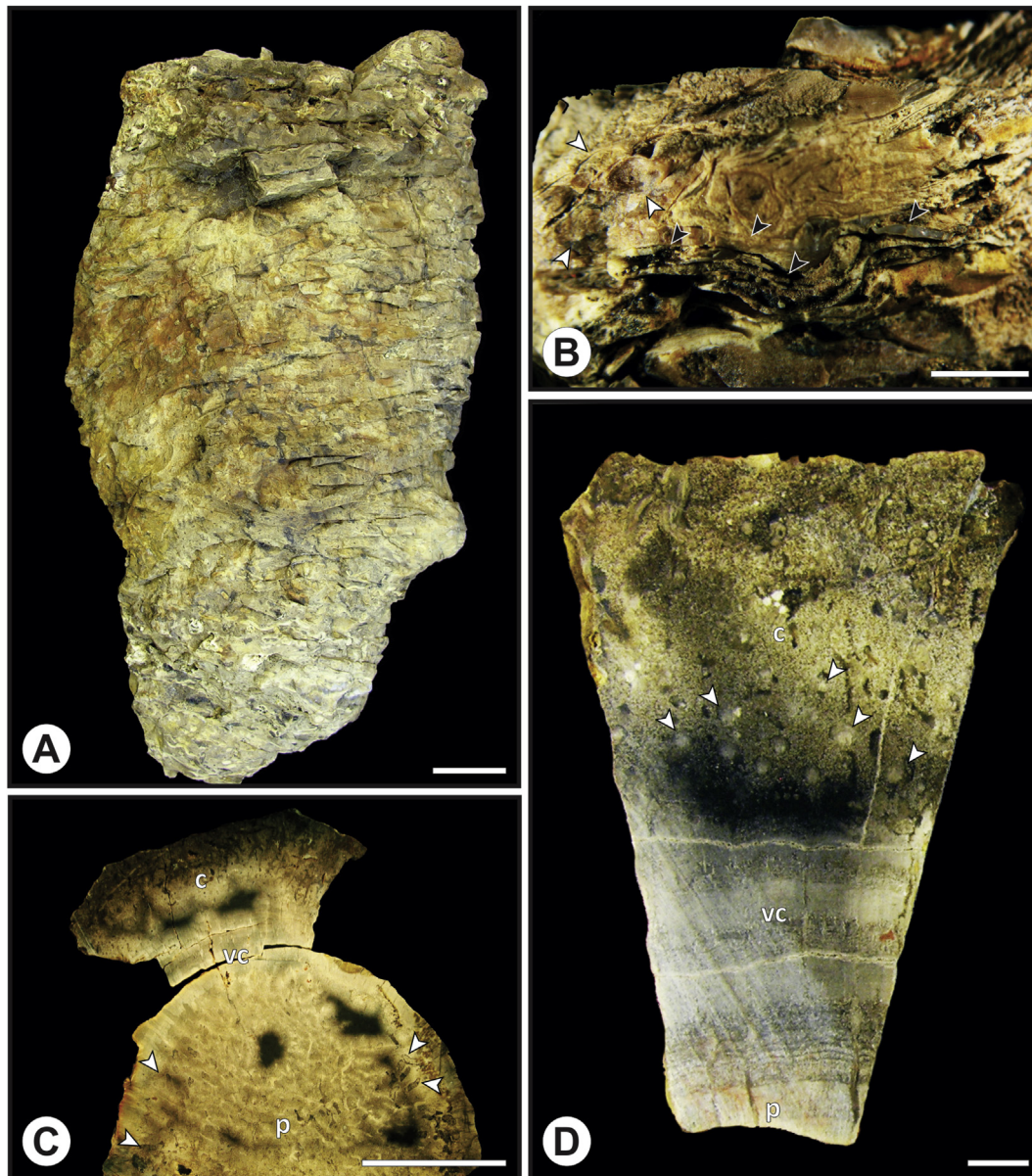
Fig. 3. _Zamuneria amyla_ gen. et sp. nov. (MPM-Pb-17527). Stem and pith. A. General view of external surface of the stem. Scale bar = 3 cm. B. Leaf bases (white arrows) and cataphylls (black arrows). Scale bar = 1 cm. C. Cross section (CS), general view. Pith (p), vascular cylinder (vc), cortex (c) and insect borings in pith (arrows). Scale bar = 5 cm. D. CS, Detail of pith (p), vascular cylinder (vc), cortex (c) and cortical bundles (arrows). Scale bar = 1 cm.

Zamuneria amyla Martínez, Iglesias & Artabe, gen. et sp. nov.

Species diagnosis. A columnar and polyxylic stem, covered by persistent rhomboidal leaf bases and cataphylls. A wide and parenchymatous central pith with mucilage canals, idioblasts and medullary vascular bundles. The vascular system comprises a medullary vascular system, and a cylindrical vascular system. The medullary vascular system is composed of many scattered medullary vascular bundles. The cylindrical vascular system has concentric rings of centrifugal secondary xylem and phloem (polyxylic) toward the cortex, separated by wide multiseriate parenchymatic rays (primary rays). Primary rays with vascular bundles and mucilage canals. Tracheids of secondary xylem with uni- to triseriate contiguous and alternate bordered pits in walls. Manoxylic secondary xylem and phloem with homocellular multiseriate rays, with one to three cells wide (secondary rays). Cortex composed of fundamental parenchyma cells and idioblasts, mucilage canals and girdling leaf traces.

Etymology. The name of species is derived from Latin noun _amylum_ (starch), by the abundance of parenchyma cells with lots of starch grains in the fossil stem.

4. Description

The stem is columnar (pachycaulous) and incomplete, with a diameter of 0.13 m and 0.31 m of length (Fig. 3A). The stem has an armour of persistent leaf bases and cataphylls. However, leaf bases and cataphylls are preserved only in a small section of the fossil (Fig. 3B).

In cross-section, the stem can be divided into four regions: the pith, cylindrical vascular system, the cortex (Fig. 3B), and persistent leaf bases (Fig. 3C).
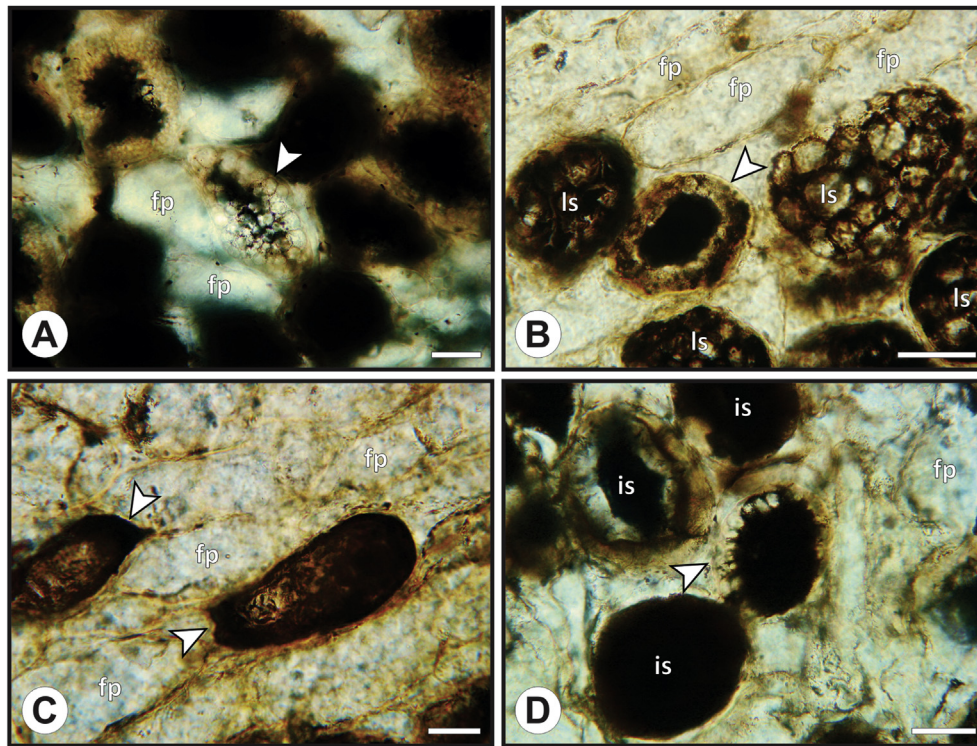
Fig. 4. *Zamuneria amyla* gen. et sp. nov. (pmLPPB-1938). All light microscope (LM). Pith, CS. A. Details of parenchyma cell with lots of possible starch grains (arrows) and fundamental parenchyma cells (fp). Scale bar = 100 μm. B. Idioblastic sclereid (arrows), fundamental parenchyma cells (fp), and parenchyma cells with lots of possible starch grains (ls). Scale bar = 100 μm. C. Secretory idioblasts (arrows) and fundamental parenchyma cells (fp). Scale bar = 100 μm. D. Pitted idioblastic sclereid (arrow) and idioblastic sclereid (is). Scale bar = 100 μm.

4.1. Pith

In cross section, the pith is circular to oval in outline, with a diameter of 0.10 m, occupying the largest portion of the stem (Fig. 3C, D). The pith is composed of parenchymatous cells, idioblasts, numerous medullary vascular bundles (medullary vascular system), and mucilage canals (Fig. 3C, D). The fundamental parenchyma cells are thin-walled, and isodiametric, with an average diameter of 70 μm (50−110 μm). Usually, the parenchyma cells have circular to oval simple pits, and most of these cells contain lots of possible starch grains (Fig. 4A, B). Among the parenchyma cells, there are many idioblasts characterized by the presence of lignified thick secondary cell walls, and can be classified (*sensu* Vovides, 1991) into: secretory idioblasts, idioblastic sclereids and pitted idioblastic sclereids (Fig. 4B−D).

The medullary vascular system consists of secondary vascular bundles that are randomly arranged in the pith. The bundles are numerous, with a mean diameter of 1205 μm (810−2160 μm). They are collateral, composed of xylem and phloem, commonly accompanied by a mucilage canal (Fig. 5A, B). In longitudinal section, the vascular bundles are large, irregular in course, and sometimes branching. 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. The cone domes are a sequence of dome-like vascular bundle patterns in a longitudinal section of the cycad stems with terminal strobili (Chamberlain, 1911; Norstog and Nicholls, 1997).

In cross section, the mucilage canals are circular of ovoid in outline, with a diameter of 170 μm (80−270 μm). They are composed by secretory cells to form an internal lumen to store mucilage (Fig. 5A, B). The epithelial cells lining the mucilage canals have the nuclei preserved (Fig. 5C). Some transfusion cells are occasionally observed adjacent to the vascular bundles on the outer part of pith, close to vascular cylinder (Fig. 5D, E).

4.2. Cylindrical vascular system

The cylindrical vascular system has a centrifugal growth pattern, and consists of many sympodia of endarch primary xylem in a circumferential arrangement (Fig. 6A, B). The primary xylem is followed by alternative rings of secondary xylem and phloem (polyxylic), and secondary rays, separated by wide multiseriate parenchymatic rays (primary rays) (Fig. 6C). In cross section, the primary xylem has oval to square tracheids; with a mean radial diameter of 14 μm (6−35 μm), and a tangential diameter of 14 μm (6−19 μm) (Fig. 6A, B).

The secondary vascular cylinder is polyxylic, composed of three successive rings of xylem, cambium and phloem; and segmented by primary rays that connect the pith with the cortex (Fig. 6C). The secondary xylem has rectangular to square tracheids with a mean radial diameter of 23 μm (14−35 μm) and a tangential diameter of 21 μm (13−29 μm) (Fig. 6D). The vascular cambium is located between secondary xylem and phloem, and comprises a series of two to four rectangular cells with thin walls (Fig. 6C, E). The phloem possesses sieve, parenchyma and sclerenchymatous cells (Fig. 7A). The sieve and parenchyma cells (thin-walled cells) are positioned among fibre bands (thick-walled cells) (Fig. 7A, B).

Each ring of centrifugal secondary xylem and phloem is composed of many vascular segments separated by wide parenchymatous rays (primary rays); between them, there are many thin rays (secondary rays) (Fig. 6D). Parenchyma cells essentially constitute the primary and secondary rays (Fig. 7C). Pitted idioblastic sclereids and secretory idioblasts are commonly present in the rays (Fig. 7C, D).
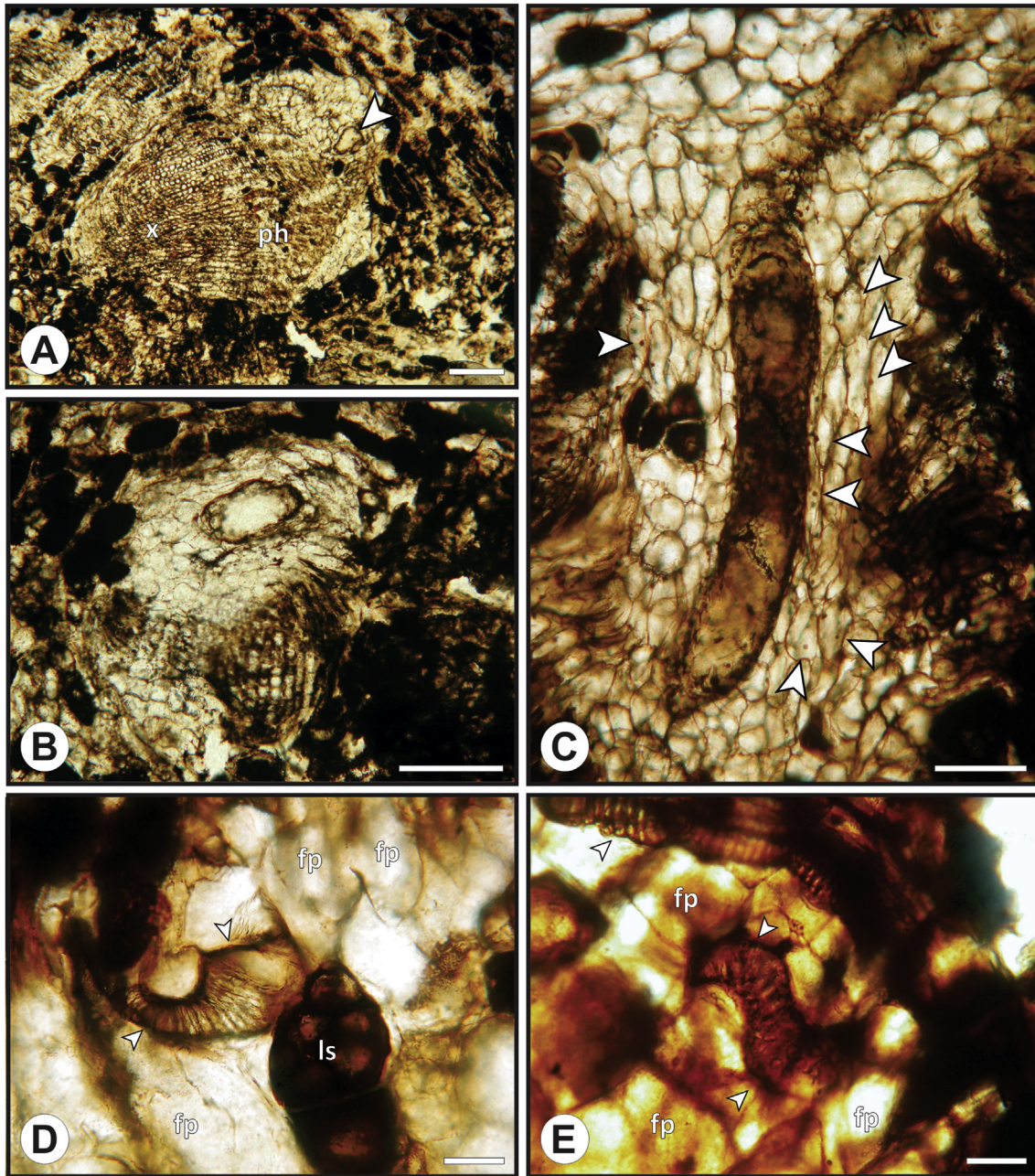
Fig. 5. *Zamuneria amyla* gen. et sp. nov. (pmLPPB-1938 − pmLPPB-1940). All LM. Pith. A−B. CS, Pith, medullary vascular bundle: xylem (x), phloem (ph), and mucilage canal (arrow). Scale bars = 400 μm. C. Longitudinal section (LS), Mucilage canal in detail. Well-preserved secretory cells where nuclei are clearly visible (arrows). Scale bar = 500 μm. D−E. Transfusion cells (arrows), fundamental parenchyma cells (fp), and parenchyma cells with lots of possible starch grains (ls). Scale bars = 100 μm.

In radial section, the secondary xylem has tracheids with araucarioid pitting. The pits are uni- to tri-seriate and bordered, flattened to hexagonal in outline, with a contiguous and alternate disposition (Figs. 7E, 8A, B). The pits have a horizontal diameter of 9 μm (6−12 μm) and a vertical diameter of 8 μm (5−12 μm) (Fig. 8A, B). The apertures are circular to oval in outline. The crossfields have a mean of 8 (6−10) oculipores of the araucarioid type (Fig. 7F).

In tangential section, the secondary rays are fusiform composed of parenchyma cells, and few secretory idioblasts. There is a mean of 25 (9−35) secondary rays between the two primary rays. The high number of secondary rays (parenchyma) makes the wood manoxylic.

The primary rays are heterocellular, composed of parenchyma cells, idioblasts, and secretory cells (mucilage canals). The primary rays have a mean diameter of 1130 μm (720−1440 μm), and 5140 μm (4350−5710 μm) in height. Inside the primary rays there is a leaf trace (vascular elements) with a mucilage canal associated (Fig. 9A, B). The secondary rays are 1- to 3-seriate, with a mean diameter of 101 μm (35−168 μm) and a height of 1705 μm (71−470 μm) (Fig. 9C).

The ray cells are oval to rectangular in outline, with a diameter of 38 μm (19−80 μm) and a height of 40 μm (20−70 μm) (Fig. 9C).The parenchyma cells are commonly circular, elliptic, upright or occasionally procumbent. The idioblasts are generally circular to oval, however some of them are fusiform to elongate.
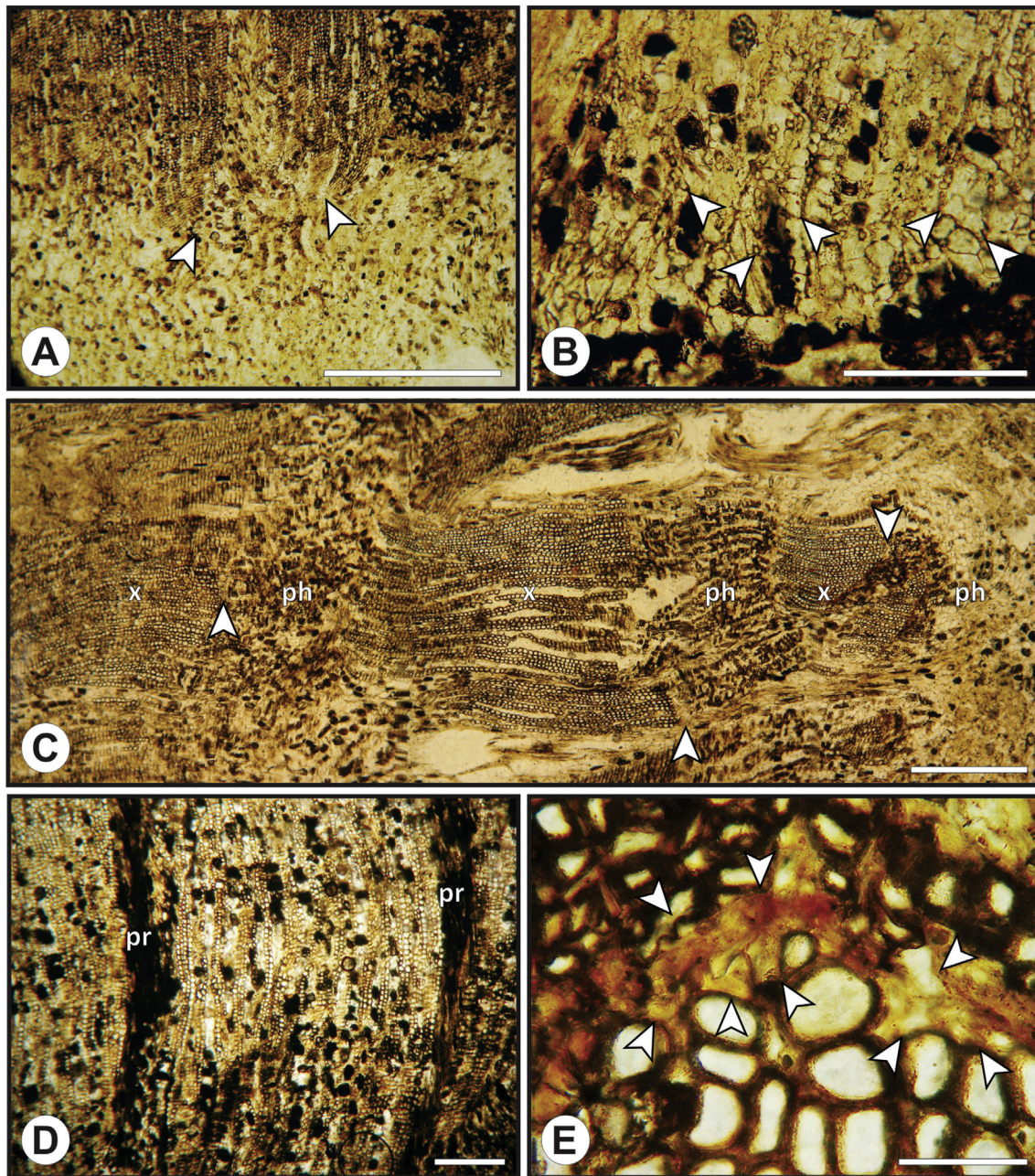
Fig. 6. *Zamuneria amyla* gen. et sp. nov. (pmLPPB-1941 − pmLPPB-1943). All LM. Vascular cylinder, CS. A. Primary xylem endarch (arrows). Scale bar = 1000 μm. B. Primary xylem, detail. Scale bar = 500 μm. C. Polyxylic secondary vascular cylinder, xylem (x), cambium (arrows) and phloem (ph). Scale bar = 1000 μm. D. Secondary xylem and primary rays (pr). Scale bar = 500 μm. E. Detail of cambium cells (arrows). Scale bar = 50 μm.

4.3. Cortex

In cross section, the cortex is composed of parenchyma cells, idioblasts, mucilage canals and leaf traces. The features and dimensions of parenchyma cells and idioblasts are similar to those present in the pith (Fig. 10A−D). The parenchyma cells are isodiametric with an average diameter of 70 μm (50−12 μm). The leaf traces comprise many collateral vascular bundles and girdling traces scattered in the cortex (Fig.11A−B). They are commonly associated with a mucilage canal. The mucilage canals are scattered among the parenchyma cells and more abundant than in the pith; their average diameter is 550 μm (360−930 μm) (Fig.11A−B).

4.4. Leaf bases

Most of the outer part of the stem is not preserved; however, in a small area it is possible to observe helical persistent leaf bases and cataphylls (Fig. 3B). The leaf bases are rhomboidal and small, with a 1.2 cm (0.8−1.4 cm) wide and 0.5 cm (0.3−0.7 cm) high.

4.5. Animal activity

The stem bears tunnels and galleries bored by animal activity into their different tissues. The tunnels were bored into the cortex, vascular tissue (phloem) or between the vascular tissue and the
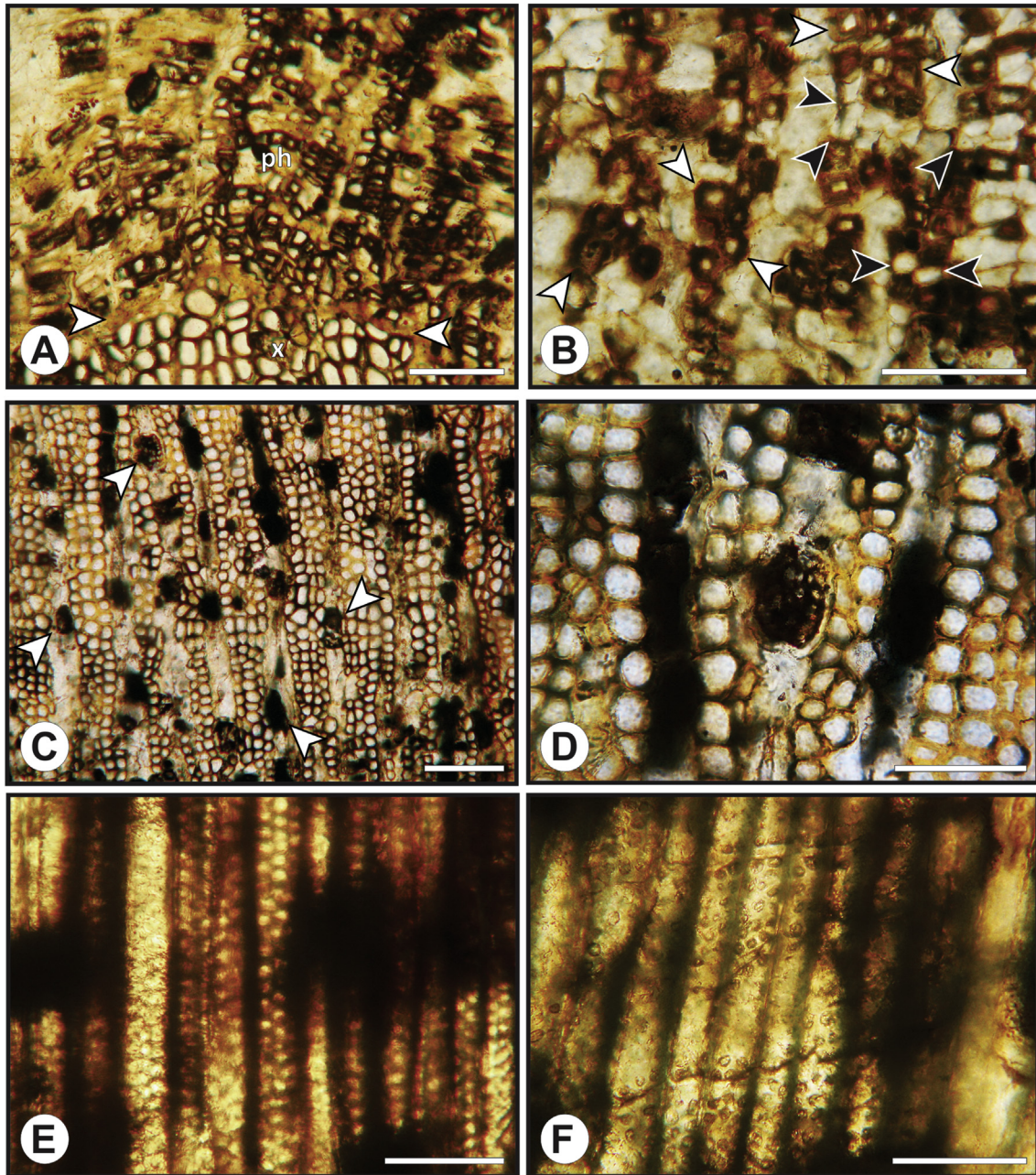
Fig. 7. *Zamuneria amyla* gen. et sp. nov. (pmLPPB-1939 − pmLPPB-1944). All LM. Vascular cylinder. A. CS. Xylem (x), cambium (arrows) and phloem (ph). Scale bar = 100 μm. B. CS. Phloem details. Sieve cells (black arrows), fibres (white arrows) and ray cells. Scale bar = 100 μm. C. CS. Secondary rays and idioblasts (arrows), general view. Scale bar = 250 μm. D. CS. Secondary rays, detail of idioblast. Scale bar = 100 μm. E. Radial section (RS). Secondary xylem, tracheids with uni- to tri-seriate bordered pits. Scale bar = 100 μm. F. RS. Araucariod cross fields. Scale bar = 100 μm.

pith. The galleries are circular, oval to irregular in outline, and generally filled with abundant frass (Fig. 3C).

5. Discussion

The features described for the fossil stem are characteristic of the Cycadales, such as pachycaulous stem, an armour of leaf bases, parenchymatous cortex with girdling traces, centrifugal polyxylic vascular cylinder, and a large parenchymatous pith with vascular bundles and mucilage canals (Greguss, 1968; Stevenson, 1990, 1992; Artabe and Stevenson, 1999). In order to classify and assign the fossil trunk here described into a taxonomic category of the Order Cycadales, it was compared with extant and fossil cycads. The

characters of the studied material allow us to assign it to a new genus *Zamuneria*. The new taxon has numerous characters that are argued below, and displayed in Tables 1 and 2.

5.1. Comparisons

5.1.1. Comparisons with extant cycad stems
Zamuneria has a columnar stem, arborescent habit, persistent armour of leaf bases and cataphylls, like some living cycad genera: *Cycas*, *Dioon*, *Encephalartos*, *Lepidozamia* and *Macrozamia* (Norstog and Nicholls, 1997; Artabe et al., 2005). On the other hand, *Micro-cycas*, *Ceratozamia* and *Zamia* have smooth trunks (Norstog and Nicholls, 1997; Artabe et al., 2005); whereas *Bowenia* and
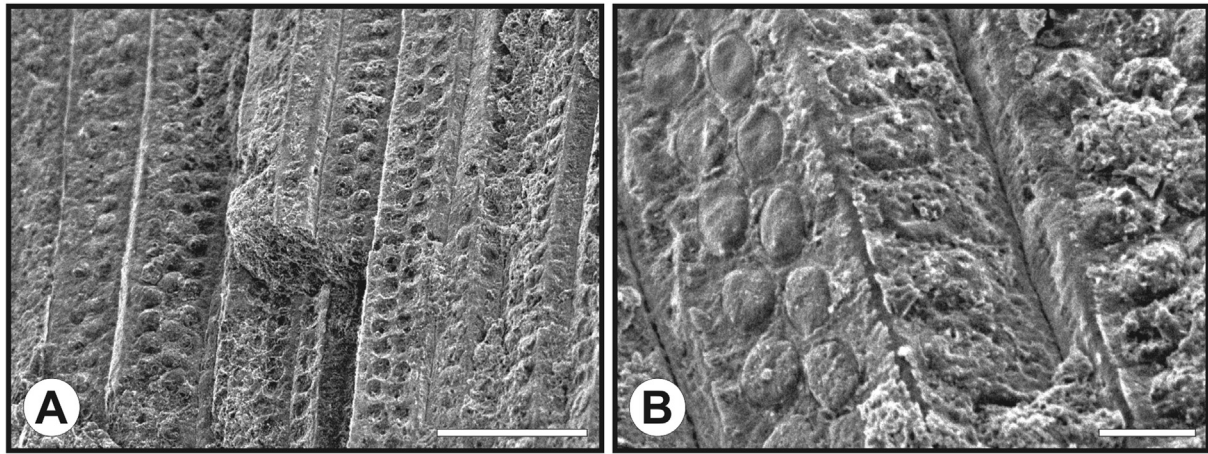
Fig. 8. *Zamuneria amyla* gen. et sp. nov. Vascular cylinder, RS. SEM images. A. Secondary xylem, tracheids with bi- to triseriate bordered pits. Scale bar = 50 μm. B. Bordered pits (detail). Scale bar = 10 μm.
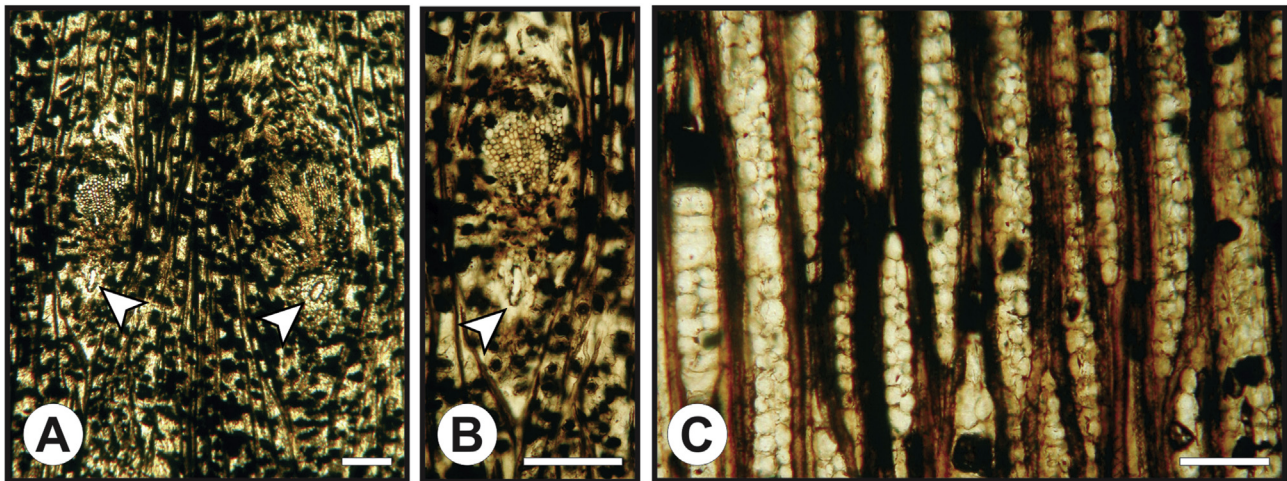

Fig. 9. *Zamuneria amyla* gen. et sp. nov. (pmLPPB-1945 − pmLPPB-1946). Vascular cylinder. Tangential sections (TS). A. Primary rays with leaf traces and mucilage canals (arrows). Scale bar = 1000 μm. B. TS. Primary rays (detail). Scale bar = 500 μm. C, TS. Secondary rays. Scale bar = 250 μm.

Stangeria have naked subterranean stems (Norstog and Nicholls, 1997). The presence of cone domes and lack of a medullary vascular system distinguish *Cycas*, *Dioon*, *Stangeria*, *Bowenia*, *Ceratozamia*, *Microcycas* and *Zamia* from *Zamuneria* (Worsdell, 1896, 1906; Greguss, 1968; Stevenson, 1992; Artabe et al., 2005).

The centrifugal polyxyly, manoxyly and medullary vascular system are characters present in *Zamuneria*, and in *Encephalartos*, *Macrozamia* and *Lepidozamia* (Worsdell, 1896, 1906; Artabe et al., 2005).

Although, the presence of a centripetal vascular system is rare or sporadic in extant forms, it is treated as a regular character in systematic studies, and occurs on the stem base of some species of *Macrozamia*, *Lepidozamia*, *Encephalartos*, and *Cycas* (Worsdell, 1896, 1906). However, *Zamuneria* do not have any evidence of a centripetal vascular system.

Zamuneria shares the presence of the medullary vascular bundle system and the centrifugal polyxyly with *Encephalartos*, *Lepidozamia*, and *Macrozamia*. (Stevenson, 1992). It is interesting to note that the medullary vascular system is a synapomorphy of Tribe Encephalarteae (Stevenson, 1990, 1992), allowing the inclusion of *Zamuneria* among members of this Tribe. However, *Zamuneria* differs from the living members of Encephalarteae in the absence of cortical steles and centripetal vascular system. The comparisons among *Zamuneria* and living cycads are summarized in Table 1.

5.1.2. Comparisons with fossil cycad stems

The fossil cycad stems are scarce, with 17 fossil genera described from Triassic to Paleogene, of which eight are from Argentina (Martínez et al., 2012; Zhang et al., 2012).

Five cycad fossil stems were described from the Triassic: *Michelilloa* Archangelsky et Brett (1963) from Argentina; *Vladiloxylon* Lutz, Crisafulli, et Herbst (2003) from Chile; *Lyssoxylon* Daugherty (Gould, 1971) and *Charmorgia* Ash (1985) from the United States of America; and *Antarcticycas* Smoot, Taylor et Delevoryas (1985) emend. Hermsen, Taylor, Taylor et Stevenson (2006) of Antarctica. The Jurassic taxa are: *Lioxylon* Zhang, Wang, Saiki, Li et Zheng (2006) and *Sinocycadoxylon* Zhang, Yang, Fu, Zheng et Wang (2012) from China, and *Fascisvarioxylon* Jain (1962) from the Upper Jurassic−Lower Cretaceous of India. Among the Cretaceous forms, there are *Sanchucycas* Nishida, Nishida et Tanaka (1991) from Japan, *Centricycas* Cantrill (2000) from Antarctica, and there are four genera from Argentina; *Worsdellia* Artabe, Zamuner et Stevenson (2004), *Brunoa* Artabe, Zamuner et Stevenson (2004), *Neochamberlainia* Artabe, Zamuner et Stevenson (2005, 2010) and *Wintucycas* Martínez, Artabe et Bodnar (2012). Finally, *Bororoa* Petriella (1972, 1978) and *Menucoa* Petriella (1969) are known from the Paleogene of Argentina.

All Triassic taxa described have a monoxylic stem with a centrifugal vascular system such *Michelilloa*, *Vladiloxylon*, *Lyssoxylon*,
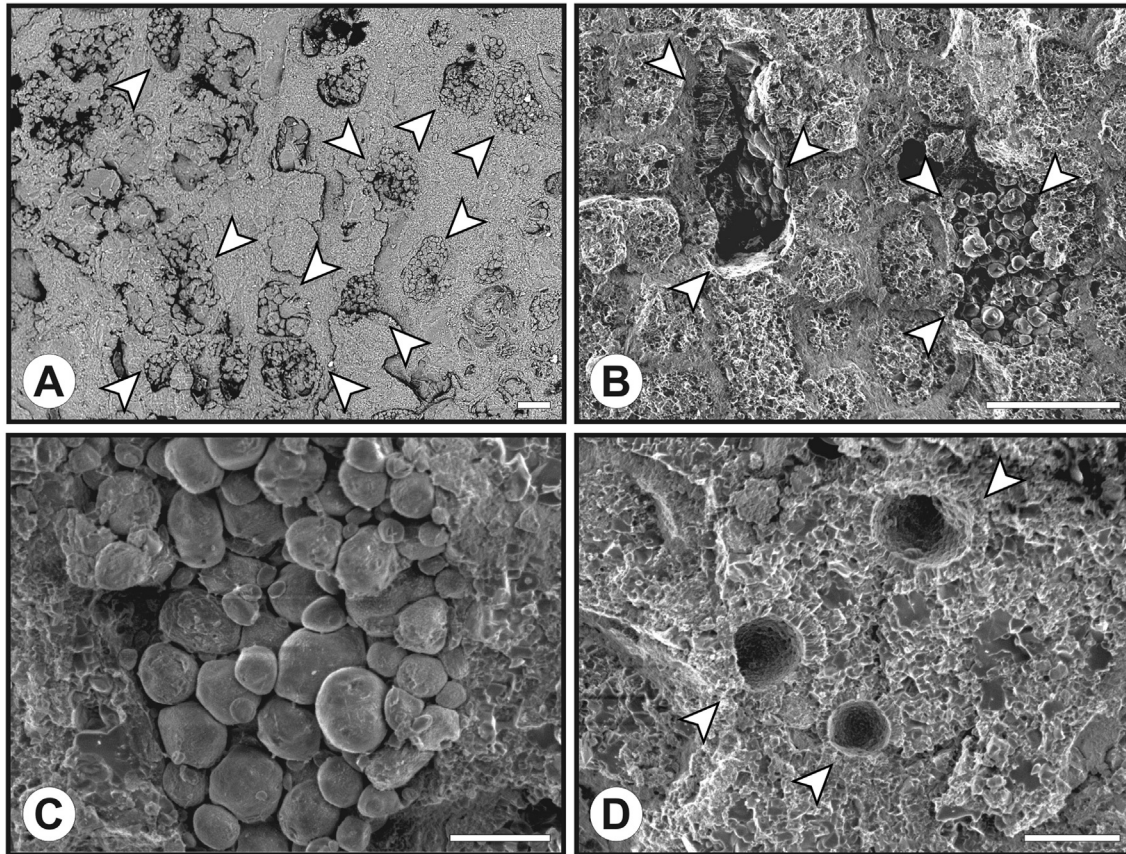
Fig. 10. *Zamuneria amyla* gen. et sp. nov. SEM images. Cortex. A–B. CS. Parenchyma cells with possible starch grains (arrows). Scale bar = 50 μm. C. Possible starch grains enlarged. Scale bar = 10 μm. D. Idioblasts with thick secondary cell walls (arrows). Scale bar = 10 μm.
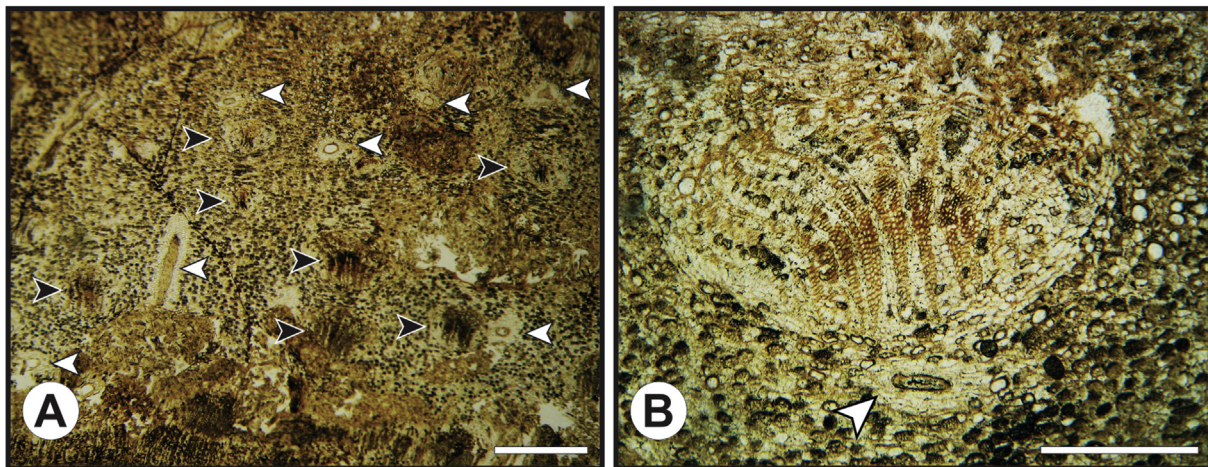

Fig. 11. *Zamuneria amyla* gen. et sp. nov. (pmLPPB-1943). Cortex, CS. A. Cortex with traces (black arrows) and mucilage canals in primary rays (white arrows). Scale bar = 1000 μm. B. Detail of a vascular trace and mucilage canal (arrow). Scale bar = 500 μm.

Charmorgia and *Antarcticycas*, features that essentially distinguish *Zamuneria* from those genera.

The Jurassic genera also have characters that easily segregate *Zamuneria*. *Lioxylon* and *Sinocycadoxylon* are distinguished by the possession of polyxylic stems with centripetal and centrifugal vascular systems, whereas *Fascisvarioxylon* has a monoxylic stem, cone domes and mucilage cavities.

The Cretaceous genera are numerous and diverse. *Sanchucycas* has mucilage cavities, and *Centricycas* possesses monoxylic stems, these features contrasts with those present in the fossil studied here. The remaining Cretaceous genera come from Patagonia and, in some way, they are closer to *Zamuneria*. On one hand, *Brunoa* has cone domes and mucilage cavities, features that clearly permit the distinction from *Zamuneria*. On the other hand,

Table 1
Comparisons among *Zamuneria* and extant genera stems of Cycadales (characters shared by those of *Zamuneria* are in italics).

	Mucilage	Medullary bundles	Centripetal polyxyly	Cone domes	Secondary centrifugal polyxyly	Wood parenchyma	Cortical steles	Petiole bundle pattern	Cataphylls in vegetative axes
Cycas	*Canals*	Absent	Random or discontinuous cycles	Present	*Present*	*Abundant*	Present	Omega classic	*Present*
Stangeria	*Canals*	Absent	*Absent*	Present	Absent	*Abundant*	*Absent*	Omega elaborate	Absent
Bowenia	*Canals*	Absent	*Absent*	Present	Absent	*Abundant*	Present	Omega elaborate	Absent
Dioon	*Canals*	Absent	*Absent*	Present	Absent	Scanty	*Absent*	Omega classic	*Present*
Encephalartos	*Canals*	*Present*	Random or discontinuous cycles	*Absent*	*Present*	*Abundant*	Present	Omega elaborate	*Present*
Macrozamia	*Canals*	*Present*	Random or discontinuous cycles	*Absent*	*Present*	*Abundant*	Present	Omega classic	*Present*
Lepidozamia	*Canals*	*Present*	Random or discontinuous cycles	*Absent*	*Present*	*Abundant*	Present	Omega classic	*Present*
Ceratozamia	*Canals*	Absent	*Absent*	Present	Absent	*Abundant*	*Absent*	Omega classic	*Present*
Microcycas	*Canals*	Absent	*Absent*	Present	Absent	*Abundant*	*Absent*	Omega classic	*Present*
Zamia	*Canals*	Absent	*Absent*	Present	Absent	*Abundant*	*Absent*	Omega classic	*Present*
ZAMUNERIA nov. gen.	*Canals*	*Present*	*Absent*	*Absent*	*Present*	*Abundant*	*Absent*	?	*Present*

Worsdellia, *Neochamberlainia* and *Wintucycas* have some characters in common from *Zamuneria* such as, wide pith, medullary vascular system, and polyxylic centrifugal vascular system. However they are distinguishable by the presence of the centripetal vascular system. Furthermore, *Worsdellia* and *Neochamberlainia* have cortical steles.

Two cycad stems, *Bororoa* and *Menucoa*, are described from the lower Cenozoic of Argentinean Patagonia. The genus *Bororoa* is distinguished from the new taxa by the presence of cone domes, and *Menucoa* has a centripetal vascular system (Petriella, 1969, 1972; Artabe and Stevenson, 1999).

The comparisons among the extant and fossil cycads support the uniqueness of the specimen described here, allowing us to erect a new taxon of cycad: *Zamuneria amyla* gen et sp. nov. The comparison with *Zamuneria* and fossil cycad taxa appears in Table 2. Identification key to all known fossil cycad stems is provided in Table 3.

5.2. Idioblasts: ecological and systematic significance

Zamuneria amyla has well-developed parenchymatous tissues with a marked number of specialized idioblasts. According to Vovides (1991) and Vovides et al. (1993) the term "idioblast" may be applied to a different type of cell, from those parenchymatous ones with specialized contents like tannin or oil, to sclerenchymatous cells, idioblastic sclereids, or trichoblasts. The idioblasts can be classified into three major categories: secretory, tracheoid, and sclerenchymatous (Metcalfe and Chalk, 1979).

The presence of idioblasts in living Cycadales has been noted sometimes (Greguss, 1968). They are scattered throughout the stem, especially in the pith, phloem, rays, the cortex and the sporophyll tissues of the strobili.

The identity of the substances contained in the idioblasts, as well as their functions are not well known, but at least some are thought to have protective functions. According to Norstog and

Table 2
Comparisons among fossil genera stems of Cycadales (characters shared by those of *Zamuneria* are in italics).

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

Table 3
Taxonomical key for fossil cycadalean stems.

1.1.	Monoxilic stems	**2**
1.2.	Polyxylic stems	**7**
2.1.	Medullary bundles absent	**3**
2.2	Medullary bundles present	**6**
3.1	Growth rings present	**4**
3.2	Growth rings absent	**5**
4.1	Small medulla	***Vladiloxylon*** Lutz, Crisafulli et Herbst
4.2	Wide medulla	***Lyssoxylon*** Gould
5.1	With canals and cavities	***Antarcticycas*** Smoot, Taylor et Delevoryas emend. Hermsen et al.
5.2	With canals	***Michelilloa*** Archangelsky et Brett
6.1	Mucilage canals present	***Charmorgia*** Ash
6.2	Mucilage canals absent	***Centricycas*** Cantrill
7.1	Centripetal vascular system absent	**8**
7.2	Centripetal vascular system present	**11**
8.1	With canals	**9**
8.2	With cavities	**10**
9.1	Cone domes present	***Bororoa*** Petriella
9.2	Cone domes absent	***Zamuneria*** Martínez, Iglesias et Artabe
10.1	Cone domes present	***Brunoa*** Artabe, Zamuner et Stevenson
10.2	Cone domes absent	***Sanchucycas*** Nishida, Nishida et Tanaka
11.1	Centrifugal vascular system absent	**12**
11.2	Centrifugal vascular system present	**13**
12.1	Medullary bundles absent	***Fascisvarioxylon*** Jain
12.2	Medullary bundles present	***Lioxylon*** Zhang, Wang, Saiki, Li et Zheng
13.1	Growth rings present	***Sinocycadoxylon*** Zhang, Yang, Fu, Zheng et Wang
13.2	Growth rings absent	**14**
14.1	Cortical steles absent	**15**
14.2	Cortical steles present	**16**
15.1	Cataphylls in vegetative axes present	***Menucoa*** Petriella
15.2	Cataphylls in vegetative axes absent	***Wintucycas*** Martínez, Artabe et Bodnar
16.1	Small medulla and thick cortex	***Neochamberlainia*** Artabe, Zamuner et Stevenson
16.2	Wide medulla and thin cortex	***Worsdellia*** Artabe, Zamuner et Stevenson

Fawcett (1989) some of the toxins that characterize cycads could be included in the idioblasts. Developmental, morphological and cytochemical studies indicate that idioblasts may contain specific toxins possibly related to defences against predators (Norstog and Fawcett, 1989; Vovides et al., 1993. For example, all cycad genera except *Stangeria* have scattered idioblasts within the leaflet interior or on the epidermis, and probably conferring the cycad foliage a measure of immunity to grazing (Vovides, 1991). Also, some species of *Zamia*, *Dioon* and *Ceratozamia* (Cycadales: Zamiaceae) are hosts by aposematic butterflies of the genus *Eumaeus* Hübner (Lepidoptera). It has been found that some species of this genus sequester substances like cycasin, and then use it as a defence against predators (Castillo-Guevara and Rico-Gray, 2003).

Most of the living gymnosperms are anemophilous; but, many cycads are entomophilous (insect pollinated) (Vovides, 1991; Mound and Terry, 2001; Terry, 2001; Schneider et al., 2002; Proches and Johnson, 2009). Therefore, interactions with herbivorous insects and/or co-symbionts, the presence of idioblasts, and the predominance of starch in cycad tissues, could form part of a complex pollination syndrome (Norstog and Fawcett, 1989; Vovides et al., 1993). In this context, the abundance of idioblasts and starch in the stems also could have some correspondence with those in the cones, and consequently with pollination syndrome.

On the other hand, some types of idioblasts in cones could be taxonomically informative (Vovides et al., 1993), and in this sense, Greguss (1968) describes the absence of secretory idioblasts and the presence of crystals with oxalate of calcium in the rays of *Macrozamia*.

The presence of idioblasts or secretory structures in stems is also known in several other fossil taxa related to cycads, like Pteridosperms such as *Lyginopteris* and *Medullosa* (Steinmann, 1944; Tomescu et al., 2001; Dunn et al., 2003). Even early fossil cycads like *Antarcticycas*, *Michelilloa*, *Charmorgia* and *Lyssoxylon* have secretory idioblasts in their stems (Archangelsky and Brett, 1963; Gould, 1971; Smoot et al., 1985; Ash, 2001.). Therefore, it seems that the presence and functions of idioblasts could be plesiomorphic, common to a group including early Pteridosperms, and other taxa close to Cycadales.

Then, the occurrence of secretory idioblasts together with many possible starch cells in the stem of *Zamuneria amyla* could be correlated as a mechanism of defence against herbivores avoiding their starch consumption. Nonetheless, tunnels and galleries bored by animal activity into different tissues of stem clearly demonstrate that the mechanism was not effective against all invaders, especially insect larvae. Alternatively, idioblasts present in the stem also be related to those of the cones and the pollination syndrome.

5.3. Climate and diversity of cycads in the Cretaceous of Patagonia: the palaeoecological context

The associated leaf macroflora and wood ring analyses from the Mata Amarilla Formation indicate humid and warm temperate climate with a pronounced seasonality caused by different rainfall patterns (Varela et al., 2015). The paedogenic features, such as mottles, slickensides, nodules and iron/manganese oxide concretions, also support warm temperate climates (Varela et al., 2012b). These climatic conditions can be included in the Warm Temperate Belt in the Cretaceous greenhouse period for the middle latitudes in South America as suggested by Iglesias et al. (2011).

The palaeosol where *Zamuneria* grew corresponds to vertic Alfisol with moderate to well drained conditions (Varela et al., 2012b), according to the requirements of a well-drained soil for development of some extant cycads (Whitelock, 2002).

The good preservation of the cycad stem is related to the taphonomic conditions promoted by a rapid burial in a fluvial deposit. This sedimentation type (aggradation of the fluvial system) is associated with high sediment supply/accommodation space conditions (Varela et al., 2015).

Zamuneria together with other taxa such as *Almargemia* Florin, *Androstrobus* Schimper, *Mesodescolea* (Archangelsky) *emend.* Archangelsky et Petriella, *Mesosingeria* Archangelsky, *Pseudoctenis* Seward, *Restrepophyllum* Passalía, Del Fueyo et Archangelsky, *Ticoa* Archangelsky, and *Sueria* Menéndez *emend.* Baldoni depict the diversity of Cycadales in the Cretaceous of South Patagonia (Archangelsky, 1963; Archangelsky and Petriella, 1971; Villar de Seoane, 1997, 2005; Artabe and Stevenson, 1999; Archangelsky and Villar de Seoane, 2004; Cúneo et al., 2010; Passalía et al., 2010).

In addition, *Zamuneria* has a medullary vascular system (synapomorphy of Encephalarteae), and a centrifugal polyxylic stem, features shared with the extant Encephalarteae. It is important that the tribe Encephalarteae is also monophyletic based on molecular phylogeny (Condamine et al., 2015). If *Zamuneria* is classified in Encephalarteae, it provides the evidence of the tribe as early as the middle Cenomanian. The absence of the centripetal vascular system and the cortical steles in *Zamuneria* could be considered as derived characters in the tribe (Artabe et al., 2005), showing higher morphological diversities in the tribe than in Present. To more clearly evaluate character evolution in the cycadales further combined analysis of entire order should be performed.

This early record of *Zamuneria* gives us some clues about the diversification of the Encephalarteae across the Cretaceous of Patagonia, probably reaching a peak in the Late Cretaceous, as shown by several taxa in Northern Patagonia (e.g. *Neochamberlainia*, *Wintucycas* and *Worsdellia*) (Artabe et al., 2004, 2005; Martínez et al., 2012). These data agree with the occurrence of the temperate to hot climate proposed for that period (Cladera et al., 2002; Barreda and Archangelsky, 2006; Iglesias et al., 2011), similar to the present climate in Africa and Australia, where the extant Encephalarteae occur. The presence of warm to hot climate elements in the megaflora is in accordance with palynofloras and macrofloras recorded from several Cretaceous strata of Austral and Neuquén Basins (Del Fueyo et al., 2007; Archangelsky and Del Fueyo, 2010; Martínez, 2010, 2012; Martínez and Olivo, 2015; Martínez et al., 2016).

The latest record of cycad stems in Argentina comes from Paleogene strata of Patagonia (Petriella, 1972), and cycad fossil leaves were recently described from Eocene strata of Patagonia (Wilf et al., 2016). The extinction of cycads in Patagonia was apparently driven by the post-Paleogene climatic change (warm and humid to cold and dry conditions), and other factors (e.g. unable to migrate to warmer regions) (Martínez et al., 2012; Martínez and Artabe, 2014), as already documented for the fossil fauna of Antarctica, Patagonian primates and reptiles, and other regions of the world (e.g., La Grand Coupure in France). Like other living forms, including vertebrates, insects and plants, cycads endured in Patagonia until the global cooling event at the late Eocene — early Oligocene (Zachos et al., 2001), being part of what Goin et al. (2010) called the 'Patagonian Hinge'.

6. Conclusions

Zamuneria is a new taxon with characters very similar to those of living and fossil Encephalarteae in having manoxylic wood, parenchymatous pith, centrifugal polyxyly and medullary vascular bundles. The centripetal vascular system absent, large amount of parenchyma tissue and idioblasts are remarkable features in this genus, and may be related to some ecological adaptations. This new record suggests an early presence of Encephalarteae in middle Cenomanian.

The process in vegetation dynamics and, consequently, floristic diversity patterns (diversification and extinction of taxa) in Patagonia can be related to the climate change. During most of the Cretaceous, the southern part of South America maintained a warm-temperate climate; a situation that benefited the development of tropical and subtropical taxa (e.g., ferns, cycads, araucarians and palms). The occurrence of several genera of Encephalarteae in the Cretaceous suggests Patagonia as a possible area of early diversification and dispersion across southern continents of Gondwana. Then, the subsequent separation of Gondwana spread the Encephalarteae to other landmasses (South America, Africa and Australia). The other possibility is that the living Encephalarteae were relicts of wider Gondwana distribution.

At present, the genera of Encephalarteae (*Encephalartos*, *Macrozamia* and *Lepidozamia*) are well diversified in Africa and Australia. In contrast, they became extinct in South America, with the last records from Paleogene strata of Patagonia. The extinction of this group in Patagonia was probably influenced by a climatic change (warm and humid to cold and dry conditions), and other factors (e.g., unable to migrate to warmer regions), as one of the victims of the late Eocene global cooling.

The new fossil taxon, *Zamuneria amyla* gen. et sp. nov., found in Patagonia is another example of the composition of the original Gondwanan flora, providing fossil linking of South America with the living genera of Encephalarteae present in Africa (*Encephalartos*) and Australia (*Macrozamia* and *Lepidozamia*). This record

also increases the knowledge of Gondwana Cretaceous floras, and allows us to reconstruct theirs phytogeographical patterns. However, additional studies are needed in several areas of the southern Hemisphere, to help us to better understand the role of cycads in the Mesozoic and Cenozoic ecosystems.

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