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journal homepage: www.elsevier.com/locate/revpalboAn Early Cretaceous zamiaceous cycad of South West Gondwana: *Restrepophyllum* nov. gen. from Patagonia, ArgentinaMauro G. Passalia^{a,*}, Georgina Del Fueyo^b, Sergio Archangelsky^b^a Instituto de Investigaciones en Biodiversidad y Medioambiente, CONICET-UNCo, S.C. de Bariloche, Argentina^b Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', CONICET. Buenos Aires, Argentina

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ABSTRACT

The record of Cycadales in Patagonia begins in the Triassic and extends up to the Oligocene. In this region the group is highly diversified and includes several taxa represented by trunks, leaves and pollen cones. A new cycadalean genus and species, *Restrepophyllum chiguoides*, from the Aptian Anfiteatro de Ticó Formation, Santa Cruz province, Argentina, is described here. The fossil is a leaf compression with well-preserved cuticle. Its morphology, anatomy and ultrastructure are studied by means of light and electron microscopy. The leaf is lanceolate, serrate, and possesses a prominent midvein and decurrent laterals showing an open, simple or dichotomous venation. The leaf is hypostomatic, and the abaxial cuticle is thinner than the adaxial one. The stomata are irregularly distributed and indistinctly oriented between veins. They are monocyclic to imperfectly dicyclic (haplocheilic); the suprastomatal aperture is raised over the epidermis and the guard cells are sunken. Scattered trichomes and crystalliferous idioblasts are also present. The cuticle is composed of three layers: the outer and inner layers are lamellate, while the middle one is granulate. This new cycad leaf is compared with similar fossil leaves from Gondwana and Europe/North America, and also with similar extant cycad leaves. Based on the general morphology and the main characters of the cuticle, *R. chiguoides* is assigned to the family Zamiaceae; moreover it is more closely related to the living *Zamia* (*Chigua*) *restrepoi* (D. Stevenson) Lindstrom than to any other member of the Cycadales. Paleophytogeographic evidence suggests a South American origin of *Zamia/Chigua* and a further migration to northern latitudes. This new type of leaf also suggests the putative existence of a *Chigua* clade that may be traced back to the Early Cretaceous when two cycadalean families, Zamiaceae and Stangeriaceae, were already well-established in Patagonia.

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1. Introduction

The Cycadales represent an ancient lineage of plants that once flourished and diversified, thus successfully attaining a worldwide distribution. The fossil record of this group begins in the Carboniferous and reaches its acme during the Mesozoic, when the three recognized extant families, Cycadaceae, Zamiaceae and Stangeriaceae – among other extinct cycads – appear to have already originated (Taylor et al., 2009). Cycads are restricted today to tropical and subtropical climates of both South and North Hemispheres and have widely disjunct distribution (Stevenson 1990, 1992).

Within Southwestern Gondwana, Antarctica and Patagonia yield a remarkable richness of macrofossil remains mostly assigned to the Zamiaceae. Hermsen et al. (2006, 2007, 2009) studied permineralized material from the Triassic of Antarctica: stems of *Antarcticycas*, leaves of *Yelchophyllum* and pollen cones of *Delemaya* co-occurring in the

same beds. They presented a reconstruction of a whole-plant that looks like a small *Zamia* Linnaeus. *Cetricycas* Conrill, a permineralized stem assigned to the subfamily Encephalartoideae of the Zamiaceae, has been found in the Late Cretaceous of the Antarctic Peninsula (Conrill, 2000). Impression of *Nilssonsonia* Brongniart and *Pseudoctenis* Seward leaf remains attributed to the extinct family Nilssonsoniaceae have also been described from the late Jurassic/early Cretaceous of Antarctica by Gee (1989).

In Patagonia, the oldest cycadalean remains occur in the Triassic and they persist up to the Oligocene. Fossils are represented by both vegetative (stems and leaves) and reproductive organs (pollen cones). The oldest known cycad in Argentina is the silicified stem of *Michelilloa* Archangelsky and Brett from the Upper Triassic Ischigualasto Formation that was related to the extant genus *Dioon* Lindley of the Zamiaceae based on the structure of the leaf gap and long filamentous hairs found in the stem epidermis (Archangelsky and Brett, 1963). Other petrified stems were found in Patagonia in the Upper Cretaceous Allen Formation: *Brunoa* Artabe, Zamuner and Stevenson, *Worsdellia* Artabe, Zamuner and Stevenson and *Chamberlainia* Artabe, Zamuner and Stevenson. *Brunoa* and *Worsdellia* were

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assigned to the Tribe Diooeae and *Chamberlania* to Tribe Encephalartae of the Encephalartoideae (Artabe et al., 2004, 2005). Moreover, two petrified stems i.e. *Bororoa* Petriella (related to the extant *Macrozamia* Miquel of the Encephalartae) and *Menucoa* Petriella (related to the Cycadaceae but also to the Zamiaceae–Encephalartae) were described from the Paleogene of Patagonia (Petriella, 1969, 1972).

Pollen cones of three *Androstrobus* Schimper species (*Androstrobus munku*, *Androstrobus patagonicus* and *Androstrobus rayen*) found in the Aptian Anfiteatro de Ticó Formation of Santa Cruz province, have been described with *in situ* pollen grains which show an affinity to either the Zamiaceae or Cycadaceae (Archangelsky and Villar de Seoane, 2004).

Cycadalean fossil leaf remains from Patagonia are mostly based on impressions. They are more abundant and diverse than stems and pollen cones and have an uninterrupted record that begins in the Triassic (Artabe, 1985) and continues throughout the Jurassic (Artabe et al., 1991), and Cretaceous (Archangelsky, 1997) to their last known occurrence in the Oligocene (Berry, 1938).

However, other fossil leaves have been assigned to the Cycadales based on their distinctive cuticular features (stomata and epidermal cells). They were recovered in the early Cretaceous sediments of the Baqueró Group in Patagonia. The genera *Mesosingeria* Archangelsky, *Mesodescolea* Archangelsky and *Sueria* Menéndez, are considered to be endemic to Patagonia (Archangelsky, 2003). *Mesodescolea plicata* Archangelsky was found to be related to the extant *Stangeria* Moore (Artabe and Archangelsky, 1971) while *Mesosingeria parva* Villar de Seoane may be related to *Encephalartos* Lehmann (Villar de Seoane, 1997) and *Sueria rectinervis* Menéndez to *Zamia* and *Ceratozamia* Brongniart (Artabe, 1994). One particular locality, Bajo Grande in Santa Cruz province, yielded several cutinized leaf remains of cycadaleans: *Almargemia incrassata* and *Ticoa lamellata* (Archangelsky, 1966), *Pseudoctenis dentata* and *Pseudoctenis crassa* (Archangelsky and Baldoni, 1972), *Sueria elegans* and *Mesosingeria parva* (Villar de Seoane, 1997) and *Mesosingeria oblonga* (Villar de Seoane, 2005). It is interesting to note that the three *Androstrobus* species occur at the same locality (Archangelsky and Villar de Seoane, 2004).

In this paper we describe a new cycadalean genus based on a leaf compression recovered from the Anfiteatro de Ticó Formation at the Bajo Grande locality. The morphology, anatomy and ultrastructure of the leaflet are described using light and electron (scanning and transmission) microscopy. The general morphology and cuticle structure suggest that the leaflet can be assigned to the family Zamiaceae, and that is probably closely related to extant *Zamia* (*Chigua*) *restrepoi* (Stevenson) Lindstrom.

Restrepophyllum further underlines the variety that Cycadales attained in the Ticó Flora (i.e., all assemblages that are found in the Anfiteatro de Ticó Formation at several localities, including Bajo Grande) and demonstrates once more the relevance of this group in Patagonian plant communities during the early Cretaceous.

2. Material and methods

The fossil consists of a single incomplete leaflet compression (apical tip and base missing) with cuticle preserved. The specimen was collected by M. Llorens and G. Cladera at the Estancia Bajo Grande locality in Santa Cruz province, Argentina, during a field trip in summer 2002 (see location map and stratigraphic section in Cladera et al., 2007). The fossil came from sediments belonging to the early Late Aptian Anfiteatro de Ticó Formation, the basal unit of the Baqueró Group (Cladera et al., 2002).

The leaflet cuticle was removed from the matrix and oxidized in 40% nitric acid during 5–10 min, followed by 5% ammonium hydroxide during 2 min. Also, a leaflet fragment, counterpart of BAPb 12872b, was macerated in 20% hydrochloric acid followed by 70% hydrofluoric acid yielding several cuticle fragments. Some cuticles showed carbonized

residues that were removed with 50% sodium hypochlorite. A middle fragment of a dried herbarium leaflet of *Zamia* (*Chigua*) *restrepoi* (Stevenson) Lindstrom was cut into small sections, less than 3 mm², with both adaxial and abaxial epidermis and rehydrated. To examine the epidermis of inner surfaces, some of these sections were gently macerated, for less than 45 min, in 20% chromium trioxide solution following Alvin and Boulter (1974). Cleared leaflets of *Zamia* (*Chigua*) *restrepoi* (Stevenson) were also obtained for study.

For light microscopy (LM) observation, fossil cuticles and epidermis of *Zamia* (*Chigua*) *restrepoi* were stained with safranin, mounted in glycerine jelly and observed with a Leitz Diaplan and Zeiss Axioscope 2 microscopes. Light micrographs were taken with a Leica DFC 280 and a Nikon Coolpix 990. For scanning electron microscopy (SEM), fossil cuticles were mounted on exposed film and extant epidermis on double-sided adhesive tape, both attached to stubs and coated with gold. Observations were made under a SEM Jeol-T 100 at 15.1 kV at La Plata Natural History Museum. For transmission electron microscopy (TEM), selected fragments of *Restrepophyllum chiguoides* cuticle and of *Zamia* (*Chigua*) *restrepoi* epidermis that were previously fixed in glutaraldehyde were both stained with 2% osmium tetroxide for 2 h at room temperature. The material was then rinsed in distilled water and dehydrated in an alcohol series, infiltrated with Spurr resin, placed in moulds and dried in vacuum at 70 °C. Finally, ultrathin sections (ca. 800 Å thick) were made with a diamond knife using a Sorval automatic, mounted in single hole grids coated with Formvar and stained with lead citrate (1') and uranyl acetate (10'). Observations were made with a Jeol JEM 100C at 85.0 kV at the Electronic Microscopy Laboratory of CICV-INTA Castelar.

The fossil specimen, microscope slides and samples for SEM and TEM are deposited in the paleobotanical collection of the Museo Argentino de Ciencias Naturales Bernardino Rivadavia under the prefixes BAPb, BAPb Pm, BAPb MEB and BAPb MET. The extant studied material are deposited as BAPb Pm 585–587, BAPb MEB 336, 337, and BAPb MET 230–232. Number of samples observed as well as resin blocks and copper grids made are as follow: for BA PB Pm 563, 570, 571, 575, 576, 580, 585, 586 and 587 one sample each; for BA PB Pm 564, 565, 569, 573, 574, 577, 578 and 579 two samples each; for BA PB Pm 562, 572 and 581 three samples each; for BA PB MEB 339 one sample; for BA PB MEB 336 and 337 two samples each; for BA PB MEB 335 and 338 three samples each; for BA PB MEB five samples; for resin block BA PB TEM 230, 35 samples and 15 copper grids; for resin block BA PB TEM 231, 25 samples and 12 copper grids; for resin block BA PB TEM 232, 5 samples and 4 copper grids; for resin block BA PB TEM 233, 5 samples and 4 copper grids and for resin block BA PB TEM 234, 25 samples and 12 copper grids.

The terminology for the cuticular membranes description follows Holloway (1982).

3. Systematic descriptions

Order Cycadales Pfitzer
Family Zamiaceae Reichenbach
Restrepophyllum nov. gen.

Type species: *Restrepophyllum chiguoides* nov. sp.

Etymology: the generic epithet refers to the close similarity of this leaflet with the living species *Zamia* (*Chigua*) *restrepoi*, which was dedicated to the Colombian botanists Padre Sergio Restrepo Jaramillo. *Diagnosis*: Leaf (leaflet?) papyraceous, narrow, lanceolate with serrate margins and simple, regularly spaced teeth. Open venation with a prominent midvein and decurrent laterals at acute angles, reaching margins, simple or dichotomous. Leaf hypostomatic. Abaxial cuticle thin with isodiametric to elongate epidermal cells between veins and strongly elongate cells on veins. Stomata present between veins, irregularly distributed and indistinctly oriented, mostly

monocyclic to imperfectly dicyclic (haplocheilic). Suprastomatal aperture raised over epidermal surface. Guard cells sunken in epistomatal chamber. Adaxial cuticle thicker with elongate epidermal cells.

Comments: *Restrepophyllum* is referred here to the cycads because of its close resemblance to leaflets of extant genus *Zamia* (*Chigua*) *restrepoi* (family Zamiaceae, Stevenson, 1990) now restricted to Colombia, with which it also shares epidermal similarities, especially in the structure of stomata. Leaflets of *Zamia* (*Chigua*) *restrepoi* are similar in shape to those of other extant cycads such as *Zamia* spp. and *Bowenia* Hooker ex Hooker (i.e. *Bowenia serrulata* (Bull) Chamberlain)

but differ in having a midvein. Other cycads (*Cycas* and *Stangeria*) also possess leaflets with a midvein, but however differ from *Chigua* in their venation patterns (Stevenson et al., 1996).

Restrepophyllum chiguoides nov. sp.

Plates I, II and IV. Fig. 1

Holotype: BAPb 12872; BAPb Pm 562–565, 569–581; BAPb MEB 334, 335, 338, 339; BAPb MET 233–234 (all these preparations named as BAPb Pm, BAPb MEB and BAPb MET belong to the single specimen BAPb 12872).

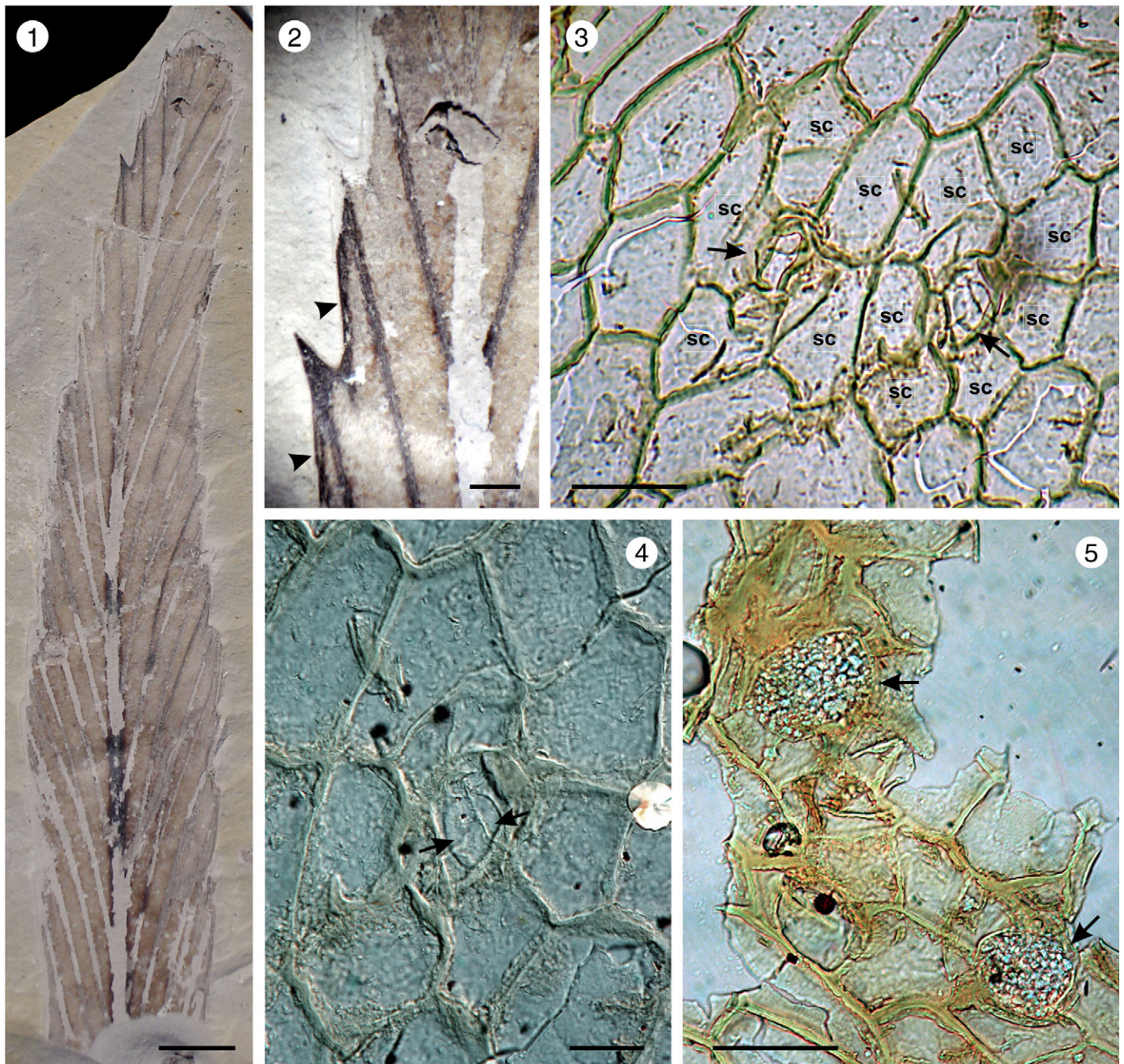


Plate I. *Restrepophyllum chiguoides* nov. gen. et sp. Figs. 3–5 were taken with a transmitted-light microscope. Figs. 1–2, BAPb 12872 holotype. Figs. 3–4, BAPbPm 563 holotype. Fig. 5, BAPbPm 564 holotype.

1. General aspect of leaflet. Scale bar = 0,5 cm.
2. Detail of dentate margin. Obscure line along the margin is produced by the compression border where the cuticle is thicker (arrowheads). Scale bar = 0,1 cm.
3. Detail of two neighbor stomata with subsidiary cells (sc) in contact. Arrows indicate the stomatal pore. Scale bar = 50 μ m.
4. Detail of stomata showed in figure 3. Arrows indicate the guard cells. Scale bar = 20 μ m.
5. Detail of crystalliferous idioblasts (arrows). Scale bar = 50 μ m.

Repository: Museo Argentino de Ciencias. Naturales 'Bernardino Rivadavia', División Paleobotánica.

Type locality: Estancia Bajo Grande, Santa Cruz province, Argentina.

Stratigraphic horizon: Bajo Grande Section, upper plant horizon, Baqueró Group, Anfiteatro de Ticó Formation, Aptian.

Etymology: The species epithet refers to the close similarity with the living species *Zamia* (*Chigua*) *restrepoi*.

Diagnosis: Leaflet papyraceous, narrow, lanceolate, slightly falcate, elongate, with a length/width ratio not less than 5:1. Margins serrate with simple regularly spaced teeth. Teeth straight to slightly flexuous at base, gently concave to straight apically, with an acute apex and rounded sinus. Venation open with a prominent midvein that gradually diminishes in width towards apex. Lateral veins decurrent at an acute angle, straight to slightly curved, parallel and reaching margins without anastomosing. At margins, up to two veins per centimeter are present. Veins may remain simple before reaching margins, or they may dichotomize once at an acute angle halfway between midvein and margin. Cuticle thin, bearing stomata on epidermis on one side of the leaf (hypostomatic), presumably abaxially. Epidermal cells between veins isodiametric to elongate, with few scattered hairs. Anticlinal walls thin, straight to slightly sinuous, occasionally pitted. Periclinal walls smooth. Epidermal cells on veins rectangular, elongate, forming parallel bands. Stomata irregularly distributed and indistinctly oriented, rarely with subsidiary cells in contact. Stomatal apparatus with circular to slightly oval outline, mostly monocyclic to imperfectly dicyclic (haplocheilic) with 5–8 subsidiary cells. Suprastomatal aperture circular to oval, typically raised over epidermal surface. Guard cells sunken in an epistomatal chamber, thickened around aperture.

Description: Only one fragmentary leaf (leaflet?) lacking its base and a brief apical sector has been found (Plate I, 1–2; Fig. 1). The leaf appears to be papyraceous; it is narrow and lanceolate, slightly falcate, 6.8 cm long (incomplete) and 1.3 cm of maximum width (length–width ratio no less than 5:1). The leaf margin is serrate. The teeth are simple, with acute apical tips and they are regularly spaced (1.8 teeth per cm). Basal sides of teeth are straight to slightly flexuous, while their apical sides are straight to gently concave. The open venation shows a prominent midvein, 0.8 mm wide at base, which gradually diminishes towards the apex. Lateral veins are decurrent, at 10°–20° angles, straight to slightly curved, parallel, without anastomoses, and reach the margin with angles up to 30°. At the margins there are about 3 veins per cm, each up to 0.3 mm thick. Veins may be simple reaching the apical tips of teeth, or they may dichotomize once at an acute angle halfway between midrib and margin. In this case the apical branch persists to the apical tip of tooth while the lower may reach the base of the same tooth or the apex of a neighboring tooth. Therefore, each tooth may receive one or two vascular bundles. The leaf margin exhibits a typical compression border where the cuticle is thicker (Plate I, 2). Except for a small fragment, only one cuticle type was recovered from the leaf compression and the surrounding matrix. This material shows signs of severe degradation with many holes with very thin and corroded periclinal cell walls and translucent anticlinal cell walls (Plate II, 2, 11–13). The epidermal cells between veins are

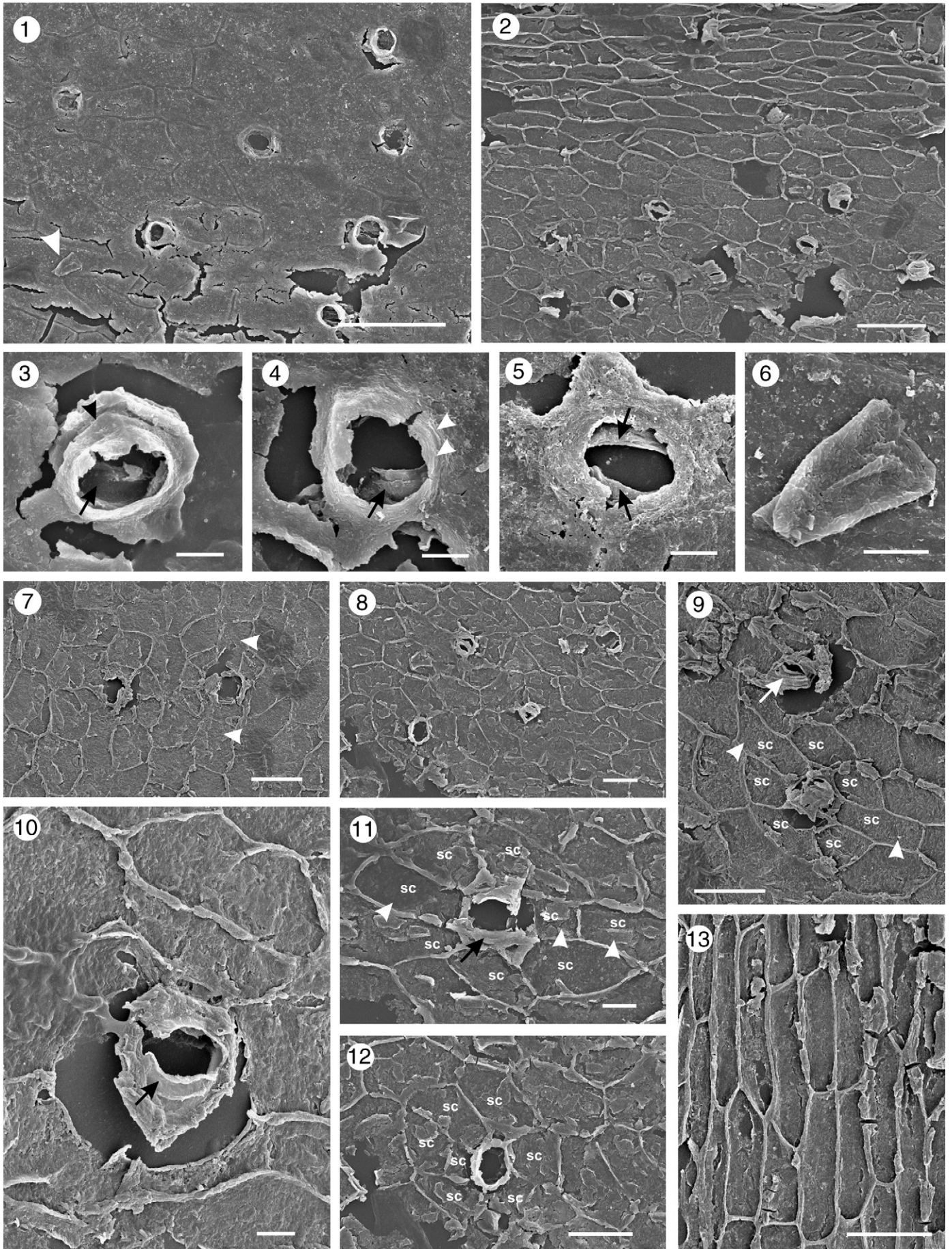
isodiametric to elongate, tetragonal to polygonal, with a maximal length of about 75 µm (Plate II, 2, 7–9). Anticlinal walls are about 5 µm thick, straight to slightly sinuous, occasionally pitted (Plate II, 7–10). Periclinal walls have a smooth surface. Few scattered hairs are presents (Plate II, 1, 6). Idioblast containing probably crystals is sporadically present among epidermal cells (Plate I, 5). Epidermal cells on veins are clearly differentiated and forming long parallel bands; the cells are rectangular, thin and typically elongate, up to 75–100 µm long × 15–20 µm wide (Plate II, 13). They show no stomata, hairs or papillae. Common epidermal cells gradually become elongate when approaching the bands of long cells that characterize the veins (Plate II, 2). The stomata are seen as distinct structures that are clearly visible in the cuticle, and often they are partly broken away from the surrounding epidermal cells, leaving large empty spaces. They are irregularly distributed and indistinctly oriented, 24 per mm², and sporadically have subsidiary cells in contact (Plate I, 3; Plate II, 9). The stomatal apparatus is circular to slightly oval in outline; it is mostly monocyclic to imperfectly dicyclic (haplocheilic), with 5–8 subsidiary cells in external cycle. Subsidiary cells are not strictly differentiated into polar or lateral and rather similar in appearance to the common epidermal cells (Plate I, 3–4; Plate II, 7–12). However, some stomatal apparatus show elongate subsidiary cells in polar position (Plate II, 7, 9, 11). The suprastomatal aperture is circular to oval, 20–35 µm, and raised over the epidermal surface, forming a characteristic solid ring as a bell-like structure that protects the spherical and slightly sunken epistomatal chamber (Plate II, 3–5). This elevated structure shows characteristic thin concentric rings (Plate II, 4). Guard cells are often seen partially preserved and sunken in the epistomatal chamber; they are elongate and thickened around the aperture (Plate II, 10–12). A small fragment of a second (presumably adaxial) cuticle was found adhered to the first section of cuticle; it shows no stomata and only elongate rectangular cells.

With TEM, epidermal cells in transverse section show periclinal walls of variable thickness according to their disposition along the leaflets; marginal cells are thicker than those of the blade (Plate IV, 1–3). In the teeth, the adaxial cuticle has an average thickness of 3.5 µm (3–4.6 µm) while the abaxial one have an average thickness of 1 µm (0.8–1.6 µm) (Plate IV, 1–2). In the leaflet blade, both upper and lower cuticles also show different thickness, the former with an average of 1 µm (0.6–1.2 µm) and the latter 0.6 µm (0.5–0.7 µm) (Plate IV, 3). Due to compression and poor preservation, in some areas of the blade, the adaxial and abaxial cuticles both measure 0.5 µm thick, while in other regions they are 0.8 µm thick. Carbonized mesophyll is preserved between the two blade cuticles (Plate IV, 3).

At ultrastructural level the cuticle on the leaf margin has a better preservation than the lamina. Periclinal walls in teeth have two layers of the cuticular membrane and the remains of what is assumed, the cell wall. The outer layer, the cuticle proper or sublayer A1 in the sense of Archangelsky et al (1986), is lamellate of 0.06 µm thick in the adaxial cuticle and 0.02 µm thick in the abaxial cuticle, with up to 4 lamellae that run almost parallel to the surface (Plate IV, 5–6). Remains of extracuticular material probably belonged to epicuticular waxes may occur on the external surface as an amorphous more

Plate II. *Restrepophyllum chiguoides* nov. gen. et sp., scanning electron micrographs of leaflet abaxial cuticle. Figs. 1, 3, 4, 6, BAPb MEB 334 holotype. Figs. 2, 8, 11, 12, BAPb MEB 335 holotype. Figs. 5, 7, 9, 10, 13, BAPb MEB 339 holotype.

- Outer view of cuticle showing, isodiametric epidermal cells and stomata randomly disposed. Arrowhead indicates a trichome. Scale bar = 100 µm.
- Inner view of cuticle, showing the transition zone of epidermal cells, longer and narrower on the veins (top), to isodiametric-polygonal in the stomatiferous area (bottom). Scale bar = 100 µm.
- 5. Outer views of stomata showing circular to oval suprastomatal apertures raising over the epidermal surface. Note thin concentric cuticular rings (arrowheads) and remains of guard cells (arrows). Scale bar = 10 µm.
- Outer view of cuticle, showing a detail of the trichome appointed in Fig. 1. Note distal part broken. Scale bar = 10 µm.
- 12. Inner views of stomata illustrating the variability in the number and disposition of the subsidiary cells (sc). Note the elongate polar subsidiary cells (arrowheads) in figures 7, 9 and 11 (in the last one the polar subsidiary cell of the right is transversally divided). Arrows in figures 9–11 show remains of guard cells. 7–9, 12, scale bar = 50 µm. 10, scale bar = 10 µm. 11, scale bar = 20 µm.
- Inner view of cuticle, showing elongate epidermal cells on the veins. Note the deep anticlinal walls more or less damaged. Scale bar = 50 µm.



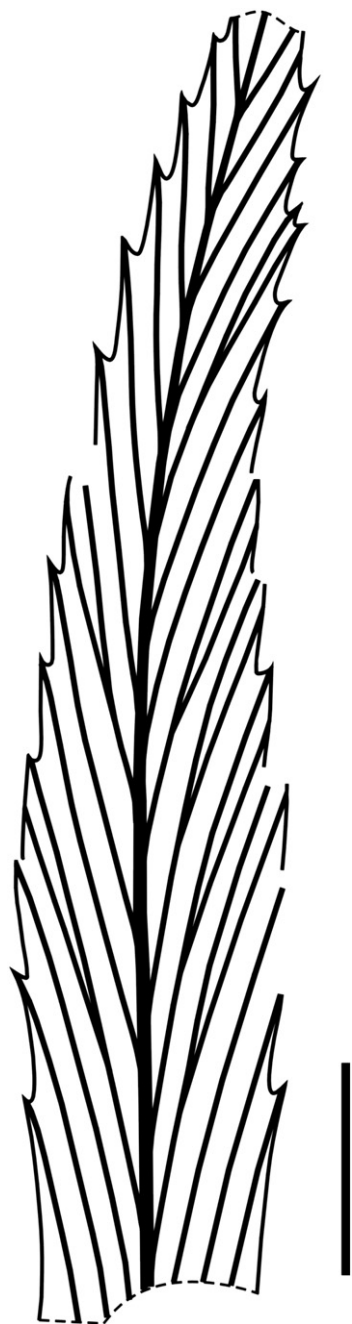


Fig. 1. *Restrepophyllum chiguoides* nov. gen. et sp., line drawing of general aspect of leaflet. BAPb 12872 holotype. Scale bar = 1 cm.

electron dense layer up to $0.04\ \mu\text{m}$ thick (Plate IV, 4). Beneath the cuticle proper there is only a cuticular layer or layer B in the sense of Archangelsky et al (1986), that is $3\ \mu\text{m}$ thick in the adaxial cuticle and $0.8\ \mu\text{m}$ thick in the abaxial cuticle, which is compact and mostly granular showing less electron dense areas, probably because of cuticle degradation (Plate IV, 5). Between the cuticle proper and the granular cuticular layer there are translucent and opaque fibrils that are only observed in certain areas of the cuticle (Plate IV, 6). The innermost layer, attributed to remnants of the cell wall, is $0.04\ \mu\text{m}$ thick in the adaxial cuticle and $0.02\ \mu\text{m}$ thick in the abaxial cuticle; it is mainly electron-lucent and is formed by 3 to 4 parallel lamellae, which in some areas appear to be highly disorganized (Plate IV, 4, 7).

Periclinal walls in the leaflet blade have, in both adaxial and abaxial cuticles, only the granular layer preserved (Plate IV, 3). In

certain inner regions, this layer shows fibrils in a somewhat reticulate disposition.

4. Discussion and comparisons

Although the single specimen described in this paper lacks a fragment of the base and their apical tip, it shows enough diagnostic characters in its elongate shape and epidermal structure to allow comparison with extant and fossil leaves.

4.1. Comparison with the living *Zamia* (*Chigua*) *restrepoi*

Leaflets with a midvein are present in some extant cycad genera: *Cycas* Linnaeus (Cycadaceae) and *Stangeria* (Stangeriaceae), as well as in the extant *Zamia* (*Chigua*) *restrepoi* (Zamiaceae). *Cycas* differs from *Restrepophyllum* in possessing only one vein in each leaflet. *Stangeria* has dichotomous lateral veins, but they depart at a near right angle (Lindstrom, 2009), whereas in *Restrepophyllum* the veins depart at a quite acute angle. The leaflet of *Zamia* (*Chigua*) are morphologically closest to the fossil specimen in that they have a similar physiognomy (elongated and serrate laminae) and venation pattern (a prominent midrib and decurrent lateral veins, arising at low angles and dichotomized). Additionally, *Restrepophyllum* is more similar to *Zamia* (*Chigua*) *restrepoi* (Plate III) than to *Zamia* (*Chigua*) *bernalii* (Mickle et al., 2008). Table 1 shows the comparison of main characters found in *Restrepophyllum chiguoides* and *Zamia* (*Chigua*) *restrepoi*.

The leaflet adaxial epidermal cells of *Zamia* (*Chigua*) *restrepoi* in transverse section are about $4\ \mu\text{m}$ thick while those of the abaxial epidermis are $2\ \mu\text{m}$ thick (Plate V, 1–2 respectively). Ultrastructurally, both epidermal cells have similar organization, composed of a four layered cuticular membrane and the cell wall. The former outermost layer is the homogeneous cuticular proper which has up to 7 slightly less electron dense lamellae that become more compact towards the surface and slightly discernible towards the next inner layer (Plate V, 5). The cuticle proper is thicker in the adaxial epidermis, $1.1\ \mu\text{m}$, against the $0.3\ \mu\text{m}$ thick abaxial epidermis (Plate V, 1–2). Beneath the cuticle proper, there is the reticulate layer that is $1\ \mu\text{m}$ thick in the adaxial epidermis and $0.5\ \mu\text{m}$ thick in the abaxial epidermis. The lumina or lacunae are loose and larger in the contact with the cuticle proper becoming more compact and smaller to hardly distinguishable towards the third layer (Plate V, 4). This layer appears granulate and is the thickest of the cuticular membrane, $1.7\ \mu\text{m}$ thick in the adaxial epidermis and $1.1\ \mu\text{m}$ thick in the abaxial epidermis. (Plate V, 1–3). Within this layer, two distinct sublayers are seen; the outer, thinner and more electron dense is $0.6\ \mu\text{m}$ thick adaxially and $0.5\ \mu\text{m}$ thick abaxially. The inner is thicker, slightly fibrilous and less electron dense, $1.1\ \mu\text{m}$ thick and $0.6\ \mu\text{m}$ thick in the adaxial and abaxial epidermis, respectively (Plate V, 1–2). The cell wall is the less electron dense layer and is lamellate being $0.2\ \mu\text{m}$ thick in the adaxial epidermis and $0.1\ \mu\text{m}$ thick in the abaxial epidermis (Plate V, 1–3). Up to 6 parallel and compactly disposed lamellae are separated by thinner and darker channels (Plate V, 3).

When comparing cuticular membranes in transverse section of *Restrepophyllum chiguoides* with those of *Zamia* (*Chigua*) *restrepoi*, both show to be almost alike. They have thicker adaxial than abaxial epidermis ($3.5\ \mu\text{m}$ and $4\ \mu\text{m}$ thick in the fossil and extant, respectively) versus $1\ \mu\text{m}$ and $2\ \mu\text{m}$ thick in the fossil and extant, respectively). Ultrastructurally, the membranes of these two genera resemble one another in the lamellate cuticle proper and cell walls. Both also have a granulate cuticular layer, although in *Z. (Chigua) restrepoi* there are two granulate sublayers. The most striking difference is that in the living taxon there is a reticulate layer that is not recognized in *R. chiguoides*. According to Holloway (1982), the cuticle of *Z. (Chigua) restrepoi* corresponds to the structural type 2 where the outer slightly lamellate region gradually merges with the inner mainly reticulate region. In this regard and probably due to poor preservation

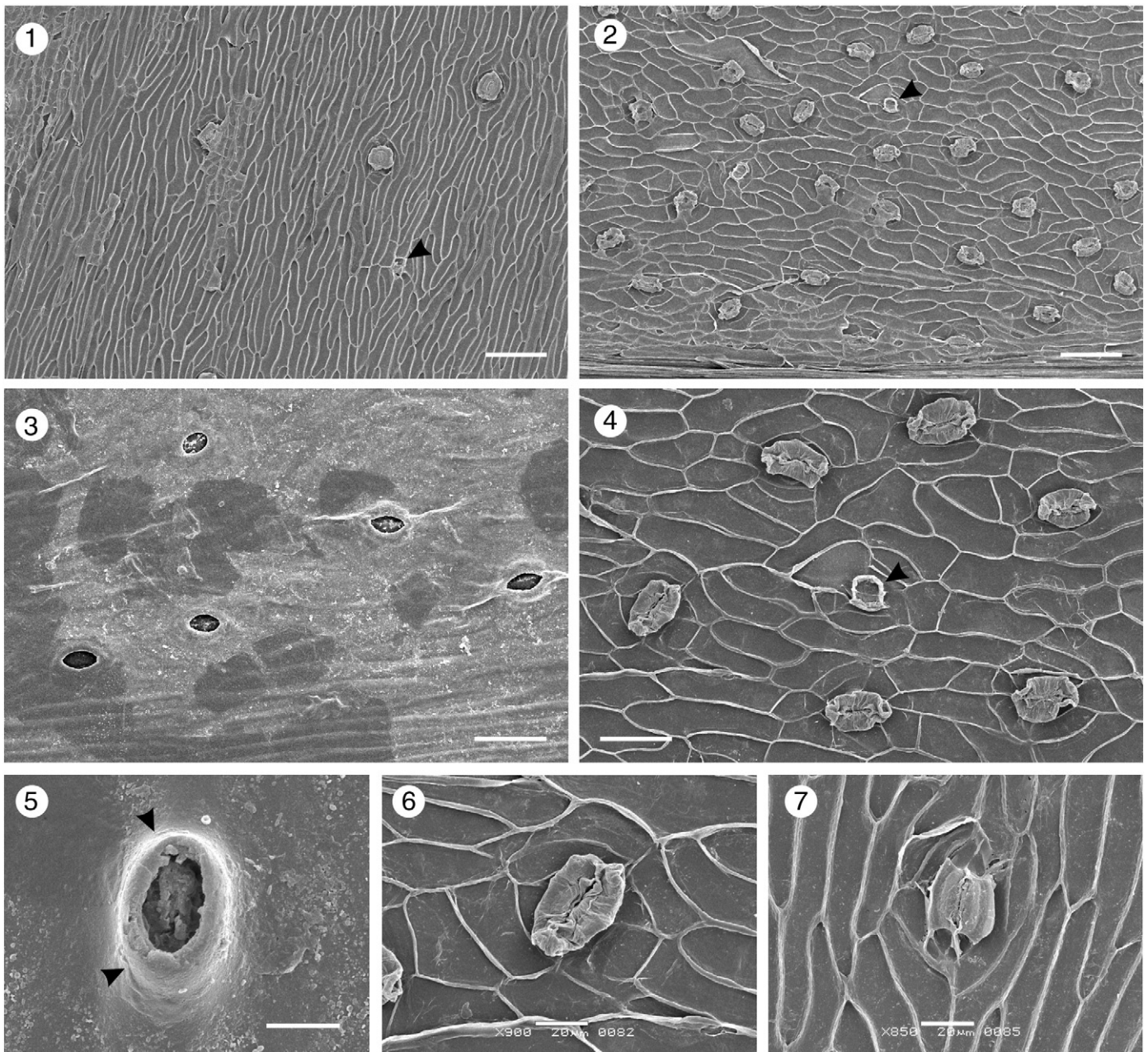


Plate III. *Zamia (Chigua) restrepoi*, scanning electron micrographs of leaflet cuticle. Figs. 1, 4, 5, 7, BAPb MEB 337. Figs. 2–3, 6, BAPb MEB 336.

1. Inner view of adaxial cuticle, showing elongate epidermal cells and a few stomata. Arrowhead indicate a trichome base. Scale bar = 100 μm .
2. Inner view of abaxial cuticle, showing moderately elongate epidermal cells and a lot of stomata randomly distributed and indistinctly oriented. Arrowhead indicate a probable trichome base. Scale bar = 100 μm .
- 3–4. Abaxial cuticle, showing the disposition and orientation of stomata. Scale bar = 50 μm . 3. Outer view of cuticle, showing a smooth surface. 4. Inner view of cuticle, showing the guard cells to each stomata and the probable trichome base appointed in figure 2 (arrowhead).
5. Outer view of adaxial cuticle, showing a stomata with their oval supra-stomatal aperture raised over the epidermal surface. Note thin concentric rings bordering the supra-stomatal aperture (arrowheads). Scale bar = 10 μm .
6. Inner view of abaxial cuticle, showing a detail of stomata. Scale bar = 20 μm .
7. Inner view of adaxial cuticle, showing a detail of stomata. Scale bar = 20 μm .

R. chiguoides does not fit in any of the six types defined by this author. Interesting to note is that other extant cycad, *Stangeria paradoxa* T. Moore, shares with *R. chiguoides* and *Z. (Chigua) restrepoi* the lamellate cell wall, although the cuticular membrane is amorphous and reticulate (Artabe and Archangelsky, 1971).

It is clear that *Restrepophyllum* is more related to the living *Zamia (Chigua) restrepoi* than to any other member of the order. This supports the assignment of *Restrepophyllum* to the family Zamiaceae of the order Cycadales. If this is indeed the case, we posit that the

Patagonian fossil represents a leaflet of a pinnate large leaf. This is also congruent with the geographic distribution of both taxa, exclusive to South America.

4.2. Comparison with fossil cycadalean leaves

Similar leaf types found in Mesozoic strata in several regions have been referred to cycads. Our comparisons will be referred to material

that was described with preserved cuticle from two major paleogeographic regions, Gondwana and Europe/North America.

4.2.1. Similar leaves from Gondwana

The vast Gondwana continent has yielded some Mesozoic leaves that are comparable to *Restrepophyllum*. Patagonia is probably the region in which the largest variety of cycads with cuticles have been described and studied with light and electronic microscopy.

Sueria Menéndez emend. Baldoni is a genus with taeniopteroid physiognomy and a cuticle with haplocheilic stomata. Two Patagonian species are known, *S. rectinervis* Menéndez emend. Artabe (1994) and *S. elegans* Villar de Seoane (1997), the last one is recorded from the same formation as *Restrepophyllum* (Anfiteatro de Ticó Formation, Baqueró Group). However, there is no generic diagnosis that unifies characters of both species. Differences in external morphology and cuticular structure, distinguishes *Restrepophyllum* from *Sueria* that has anticlinal walls with perforations (at least in *S. rectinervis*) which give the cell wall a sinuous aspect; the subsidiary cells of *S. rectinervis* also have a cutine thickening that projects over the guard cells (subsidiary cell corona) (Artabe, 1994). *Sueria elegans* has thinner and degraded cuticular membranes that measure 2.5 µm thick and consist of a thin homogeneous cuticle proper up to 0.25 µm thick, and beneath, a dense compact upper cuticular layer of 0.75 µm thickness, and a lower spongy cuticular layer of 1.5 µm thickness.

Other cycad leaves known from the Baqueró Group include *Mesodescolea plicata* Archangelsky (Stangeriaceae), as well as several species belonging to genera of unknown family affinity: *Mesosingeria* Archangelsky (7 spp), *Pseudoctenis* Seward (4 spp), *Ticoa* Archangelsky (4 spp) and *Almargemia* Florin (1 sp). Although *Restrepophyllum chiguoides* shares a few cuticular features in common with these cycad species, it is distinguishable by its taeniopteroid gross morphology. Other differences are found at the cuticle ultrastructural level of the cuticle. *Ticoa harrisii* Archangelsky shows a thicker cuticle proper of 1.5–2.5 µm thickness that consists of two sublayers (an outer lamellate sublayer and an inner homogeneous sublayer), as well as a thinner cuticular layer that is 0.3–0.5 µm thick and spongy (Archangelsky et al., 1986). Villar de Seoane (2005) described the ultrastructure of epidermal cells in *Ticoa lanceolata* Villar de Seoane which differs in having a thicker compact cuticle proper of 1 µm thickness and a thicker cuticular layer of 5 µm thickness that consists of an upper granular layer and an inner alveolate–lamellate layer. In *Mesodescolea plicata* the cuticular membrane is thicker, measuring 5–8 µm thick, and is characterized by a homogeneous granulate layer divided into two sublayers that are distinctly electron-dense (Artabe and Archangelsky, 1971). Periclinal walls of *Mesosingeria parva* Villar de Seoane are up to 12 µm thick and consist of an homogeneous 0.5 µm thick cuticle proper, and two cuticular layers, an upper compact layer of 3.5 µm thickness, and a lower alveolate layer of 7.0 µm thickness, while remnants of the cell wall are observed as a 1.5 µm thick compact layer (Villar de Seoane, 1997). *M. oblonga* Villar de Seoane (2005), also shows a 15 µm thick cuticular membranes with a compact 1.5 µm thick cuticle proper, and an outer granulate 4 µm thick cuticular layer, as well as an inner alveolate 9.5 µm thick cuticular layer.

The microsporophyll epidermis of the three *Androstrobus* species (*Androstrobus munku*, *Androstrobus patagonicus* and *Androstrobus rayen*) that also occur at the does not share any morphological feature with *R. chiguoides*. Although ultrastructurally all of these epidermis have an innermost granulate layer, the striking difference are found within the outermost layer. That of *Androstrobus* spp. shows two lamellate sublayers, the upper one with thin, compact and parallel lamellae; and the inner one with irregular somehow widely anastomosed to reticulate lamellae (Archangelsky and Villar de Seoane, 2004). In this respect, the inner sublayer of *Androstrobus patagonicus* having a coarser lamellation resembles the outer lamellate layer of *R. chiguoides*. However, until more material is found, the relationship among the leaflet of *R. chiguoides* and pollen cones of three *Androstrobus* species all occurring at the same fossiliferous locality, will remain unknown.

A few TEM studies of fossil cycadalean cuticles from other sites are known. *Pseudoctenis ornata* Archangelsky et al. (1995), from the Aptian Punta del Barco Formation, Baqueró Group, has an adaxial epidermis thicker than the abaxial one, as has been observed in *Restrepophyllum chiguoides*. However, in *P. ornata* both epidermis are thicker, measuring 8.5 µm thick adaxially and up to 6 µm thick abaxially. Here the upper cuticle consists of an outer lamellate layer and an inner granulate layer, which slightly resemble both epidermis of *R. chiguoides*. On the other hand, the lower cuticle of *P. ornata* differs in having an outer homogeneous layer, externally lamellate, and an inner lamellate–granulate layer (Archangelsky et al., 1995). Leaflets of *Kurtziana brandmayri* Frenguelli from the Jurassic Nestares Formation, Neuquén province, have thicker periclinal walls, from 3.3 µm up to 6.3 µm in thickness, while the cuticular membrane has an upper homogeneous layer and a lower lamellate–reticulate layer (Artabe et al., 1991).

If only shape and venation pattern are considered, the Bajo Grande specimen described in this paper would fit well in the morphogenus *Phyllopteroides* (Medwell) emend. Cantrill and Webb. This genus was described by Medwell (1954) for Lower Cretaceous foliage of Victoria (Australia) to correct a former problem of nomenclature (see Cantrill and Webb, 1987 for details). *Phyllopteroides*, as presently defined, includes pinnate leaves (or fronds) with leaflets (or pinnae) having a prominent midrib and non-anastomosing lateral veins arising at acute angles, arch, and divide dichotomously once or twice. The leaflets of *Phyllopteroides* greatly vary in their shape, size, vein density and margins that may be entire, lobate, crenate, serrate or dentate. The presence of a cuticle has been certified in a few cases (Douglas, 1969; Cantrill and Webb, 1987), although they lack enough characters to ascertain taxonomic affiliation.

The genus *Phyllopteroides* includes six species of leaves or isolated leaflets from the Cretaceous of Australia (Neocomian–Cenomanian): *P. dentata* (Medwell) Cantrill and Webb (1987), *P. lanceolata* (Walkom) Medwell (1954), *P. serrata* Cantrill and Webb (1987), *P. laevis* Cantrill and Webb (1987), *P. macclymontae* McLoughlin et al. (1995) and *P. westralensis* McLoughlin (1996). A single species was also described from the Cretaceous (late Albian) of Antarctica: *P. antarctica* Cantrill and Nagalingum (2005). Other specimens that have been also included in *Phyllopteroides* come from the Lower

Plate IV. *Restrepophyllum chiguoides*, transmission electron microscope micrographs of leaflet cuticle in transverse section. Figs. 1, 2, 4–7. BAPb MET 233 holotype. Fig. 3. BAPb MET 234 holotype.

- 1, 2. Cuticular membrane (CM) of marginal cells. Arrows indicate remains of extracuticular material Scale bar = 1 µm. 1. Thicker adaxial CM. 2. Thinner abaxial CM.
3. CM of blade cells. Note thin lower epidermis and thicker upper epidermis. Carbonized mesophyll is observed between them (arrows). Dark crystals are uranyl acetate precipitate (arrowheads). Scale bar = 200 nm.
4. Abaxial granulate cuticular layer (GCL) and lamellate innermost layer (arrowheads). Remains of extracuticular material occur as the outer amorphous electron dense irregular layer (arrows). Scale bar = 200 nm.
5. Adaxial CM showing lamellate cuticle proper (CP) and granular cuticular layer (GCL). Less electron dense areas indicate cuticle degradation (arrows). Scale bar = 200 nm.
6. Adaxial CM showing a detail of lamellate cuticle proper (CP). Note fibrillous material (arrows) between de cuticle proper (CP) and the granular cuticular layer (GCL). Scale bar = 100 nm.
7. Adaxial CM showing a detail of lamellate most inner layer (arrows). Scale bar = 200 nm.

Cretaceous of India (Banerji, 1992, 1996), the Aptian of Antarctica (Falcon-Lang and Cantrill, 2002; Parica et al., 2007), and the late Albian–Cenomanian of New Zealand (Parrish et al., 1998) and Patagonia (Passalia, 2007).

Restrepophyllum chiguoides is most similar to the Australian specimens described by Cantrill and Webb (1987) as *Phyllopteroides dentata*. This species is distinguishable from the other species of *Phyllopteroides*, in having longer leaflets with the highest length–

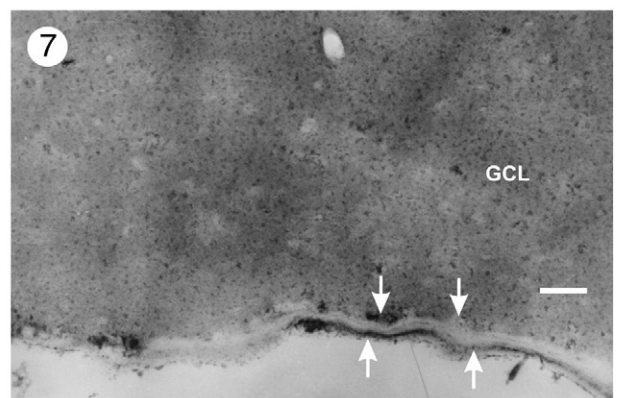
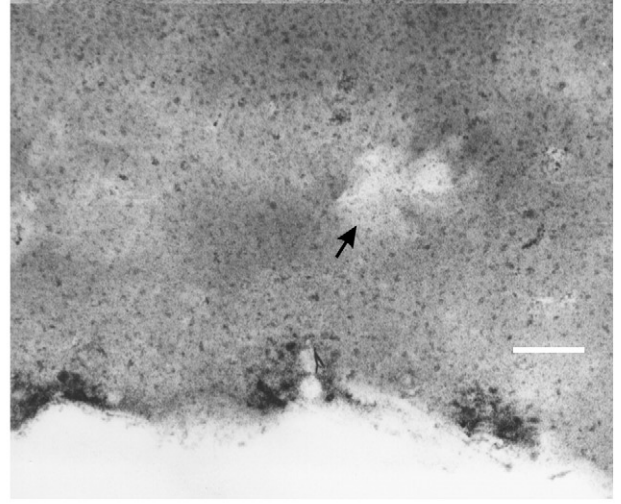
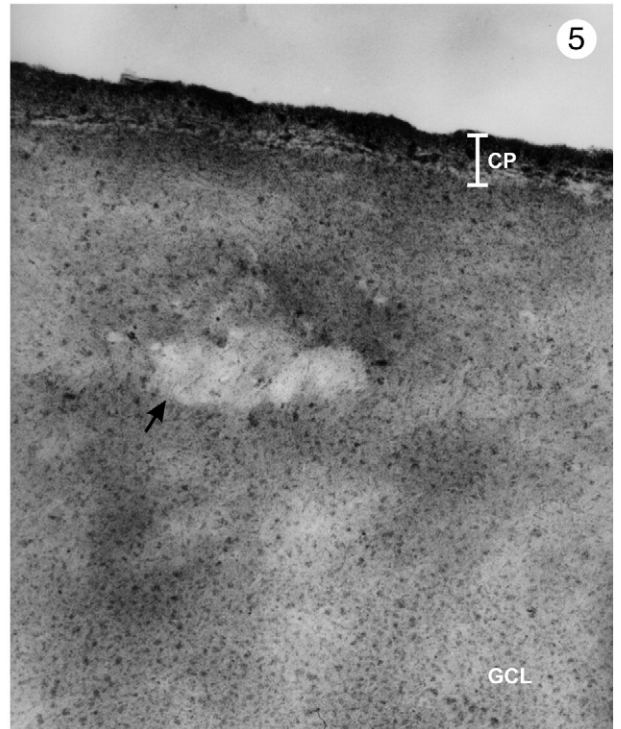
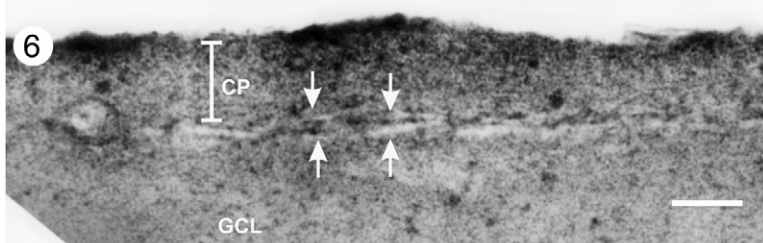
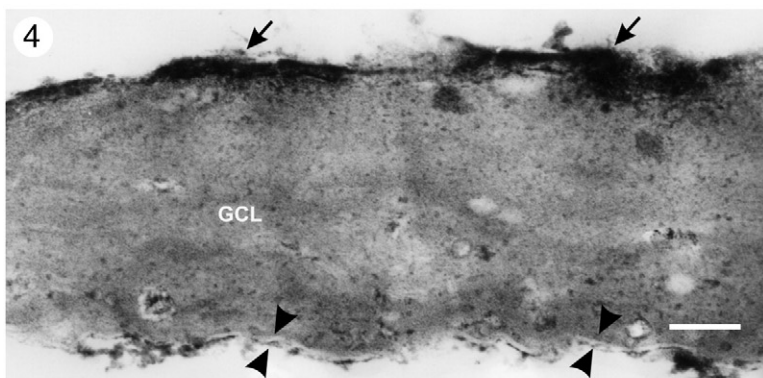
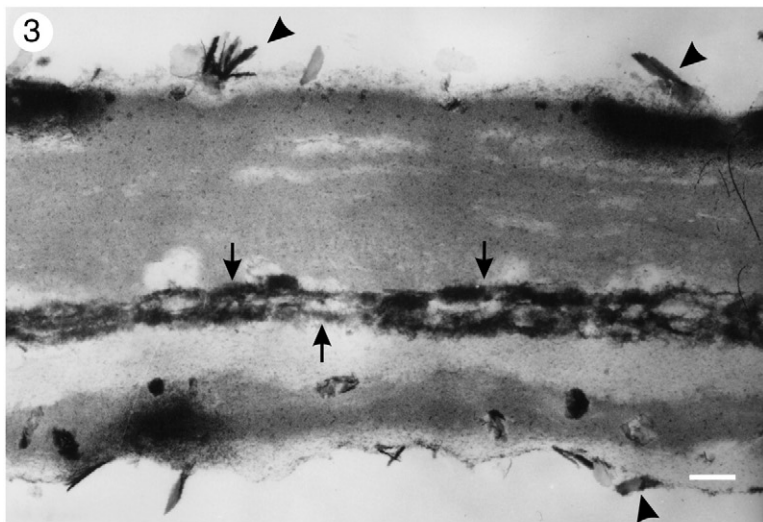
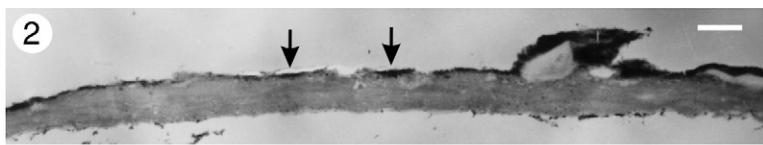
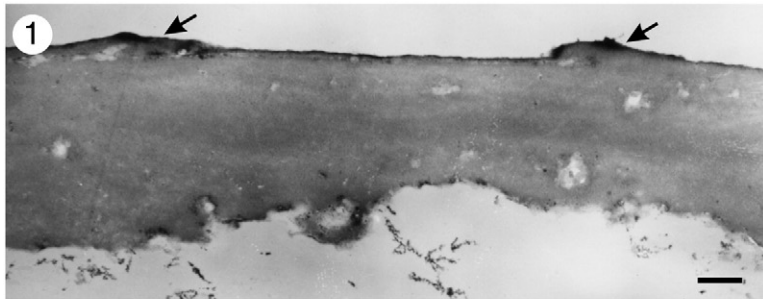


Table 1
Comparison between the fossil *Restrepophyllum chiguoides* and the extant *Zamia (Chigua) restrepoi*.

	<i>Restrepophyllum chiguoides</i>	<i>Zamia (Chigua) restrepoi</i>
Leaflet form	Lanceolate to slightly falcate	Lanceolate to lanceolate-ovate
Leaflet size	6.8 cm long (incomplete) and 1.3 cm wide	15–25 cm long and 3–5 cm wide
Leaflet margin	Regularly toothed, the base?	Irregularly toothed, the base entire
Venation	Open	Open
Midvein	Prominent	Prominent
Number and angle of secondary veins	More than 14 pairs, decurrent, 10–20°, alternate, simple or dichotomic	About 10–12 pairs, decurrent, 2–30°, alternate, mostly simple
Termination of secondary veins	Most terminate in teeth and a few in the margin	Most terminate in widely spaced teeth
Type of leaflet	Hypostomatic	Amphistomatic
Adaxial epidermis	Thicker up to 3.5 µm thick	Thicker up to 4 µm thick
Abaxial epidermis	Thinner up to 1 µm thick	Thinner up to 2 µm thick
Anticlinal walls	Straight to slightly sinuous	Slightly curvuous
Epidermal cells	Rectangular-elongate to isodiametric with acute ends	Rectangular-elongate with rounded ends
Stomatal disposition	Randomly distributed and indistinctly oriented	Randomly or evenly distributed and indistinctly oriented
Stomatal apparatus outline	Circular to slightly oval	Circular and elliptic, mostly circular
Stomatal frequency	24 per mm ²	45 per mm ²
Stomatal type	Mostly monocyclic to imperfectly dicyclic	Monocyclic
Subsidiary cells	5–8 overarching the stomatal pore	4–5 overarching the stomatal pore
Idioblast	Crystalliferous	With dark contents
Trichomes	Scattered	Abundant
Periclinal walls	3-layered: Lamellate cuticle proper Granulate cuticular layer Lamellate cell wall	5-layered: Lamellate cuticle proper Reticulate cuticular layer Outer granulate cuticular sublayer Inner granulate cuticular sublayer Lamellate cell wall

width ratio (nearly 4–6:1 to 8:1, measured on specimens figured by [Cantrill and Webb, 1987](#), as Figs. 7.A, 7.B and 7.D and by [Douglas, 1969](#), as Figs. 73–75). This feature is an attribute observed in *Restrepophyllum chiguoides*, which has a length–width ratio not less than 5:1. However, the Patagonian specimens can be differentiated from *P. dentata*, as well as from all the other species of *Phyllopteroides*, by having more sparsely spaced lateral veins (approximately 1.5 veins per 5 mm compared to 5–8 veins in *P. dentata* and not less than 6 to 20 veins in the other *Phyllopteroides* species). Other differences include teeth density (lower in *R. chiguoides*), the number of dichotomies of the lateral veins (maximum 1 in *R. chiguoides* compared to 1 or 2 in *P. dentata*) and the number of veins per tooth (1–2 in *R. chiguoides* compared to approximately 4 in *P. dentata*).

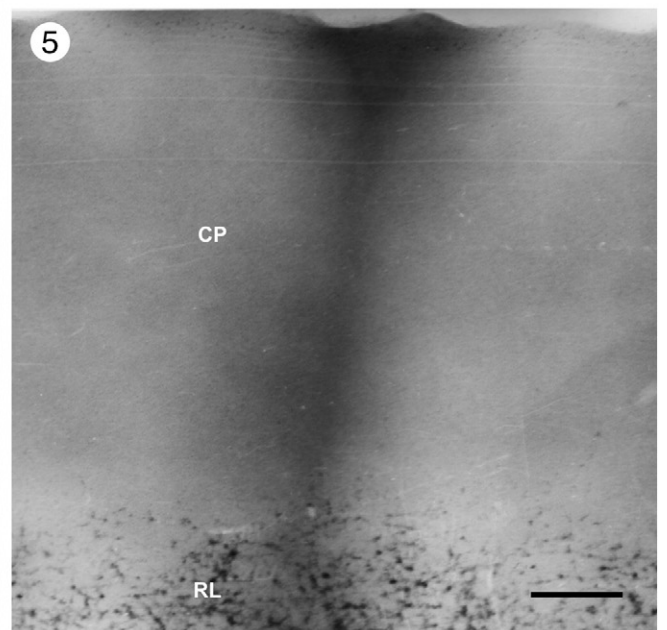
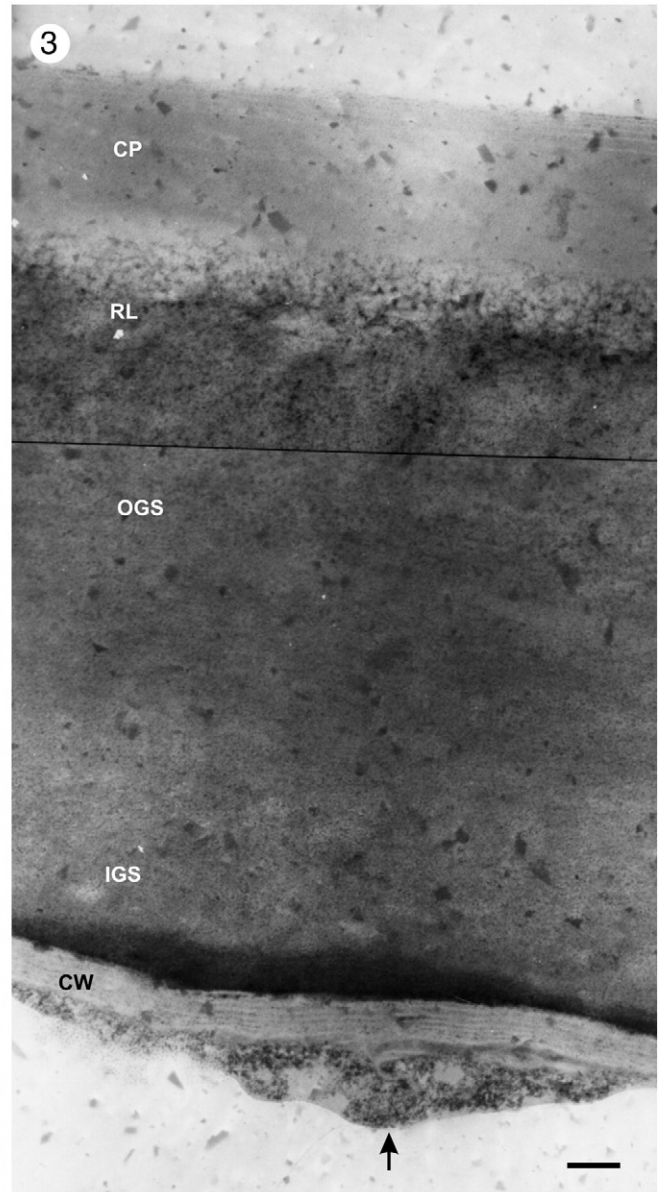
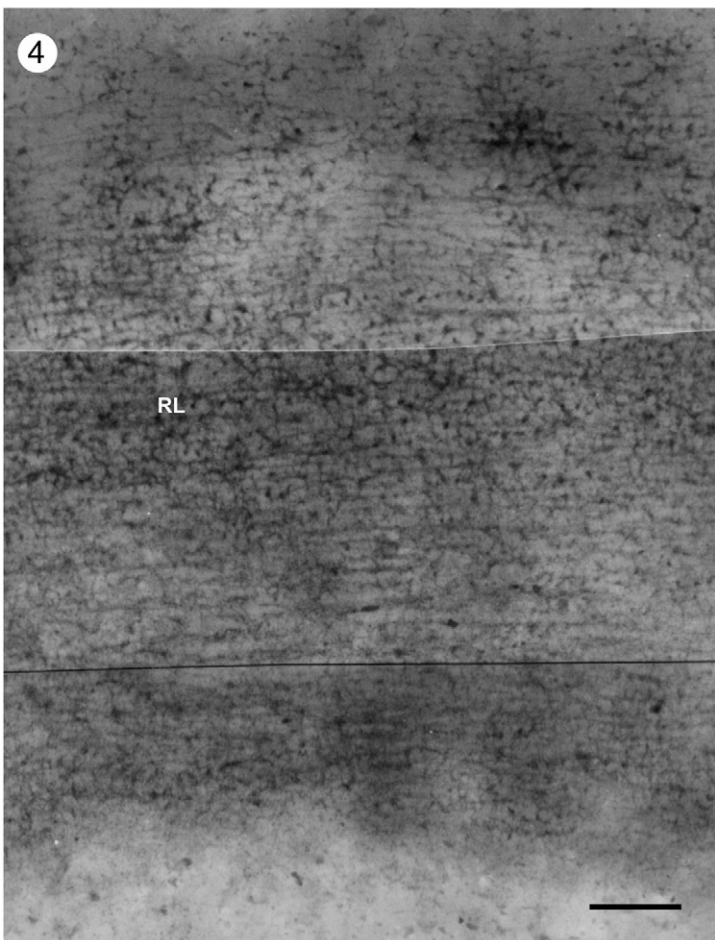
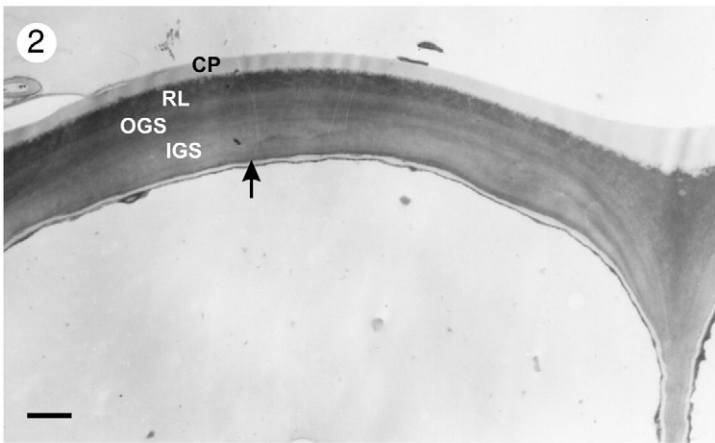
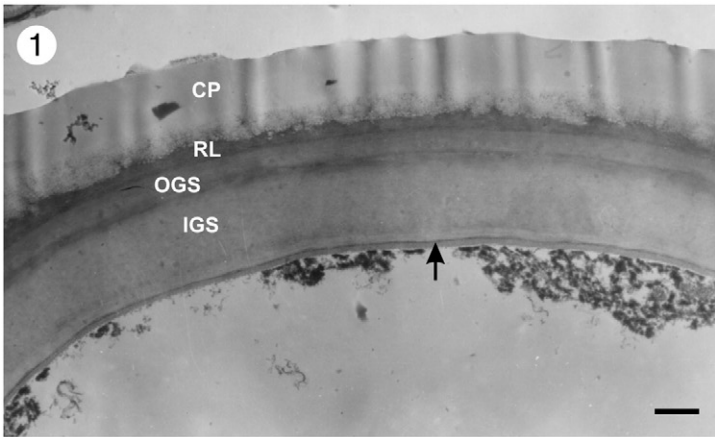
Microscopic features were included by [Medwell \(1954\)](#) in her original diagnosis of *Phyllopteroides*. Later, [Douglas \(1969\)](#) proposed deleting the cuticular details mentioned by Medwell from the generic diagnosis because he considered them misinterpreted. This proposal was supported by [Cantrill and Webb \(1987\)](#) who expanded the *Phyllopteroides* diagnosis, by adding more precise details of the venation, but excluding cuticular features. However, [Douglas \(1969\)](#) and [Cantrill and Webb \(1987\)](#) were able to recover small fragments of cuticle from *Phyllopteroides dentata*. Douglas' description states that the cuticle is very thin, with indistinguishable interveinal area cells while cells on veins are rectangular, small, with finely sinuous anticlinal walls. Additionally, both set of authors mention the presence of projections on the cuticle surface forming elongated elliptical bodies that resemble stomata. These bodies are restricted to certain leaves and they were interpreted as fertile organs ([Douglas,](#)

[1969](#)) or as some type of fungi ([Cantrill and Webb, 1987](#)). The scarce cuticular details of *P. dentata* hinder any comparison with *Restrepophyllum*: the elliptical bodies present in *P. dentata*, are absent in the cuticle of *Restrepophyllum*. The well-preserved cuticular structure of the Patagonian specimens allows the recognition of a new genus that is clearly related to the cycads and that may be compared with extant taxa (in this respect we partly follow [Harris, 1932](#)). [Cantrill and Webb \(1987\)](#) suggested an osmundaceous (pteridophyte) alliance of *Phyllopteroides*, based on the co-occurrence, in Albian strata of Australia, of *P. dentata* foliage and *Cacumen expansa* [Cantrill and Webb](#), a fertile organ bearing spores of *Osmundacidites mollis* ([Cookson and Dettmann](#)) [Douglas \(Cantrill and Webb, 1987\)](#). In this regard *Restrepophyllum chiguoides* though possessing *Phyllopteroides*-like physiognomy, has an affinity with the cycads, suggesting at the same time that eventually not all specimens previously referred to *Phyllopteroides* are necessary pteridophytes, and they might well be related to cycadophytes.

Morrissia dentata [Bose and Banerji \(1981\)](#), from the Jurassic–Lower Cretaceous of India is a species somewhat comparable to *Restrepophyllum chiguoides*. It consists of pinnate leaves carrying elongated leaflets, with serrate margin, a prominent midrib and numerous lateral veins arising at an angle of 35–45°, simple or forked (mostly once) ([Bose and Banerji, 1981](#)). No cuticular details are known. *R. chiguoides* differs from the Indian species in having more widely spaced lateral vein that arising from the midvein at lower angles. Teeth with acute tips and rounded sinuses are features shared by both species; however in *R. chiguoides* the teeth are more widely spaced and are vascularized by a lower number of veins.

Plate V. *Zamia (Chigua) restrepoi* transmission electron microscope micrographs of leaflet epidermis in transverse section. All photographs belong to BAPb MET 230.

- Cuticular membrane (CM) showing the cuticle proper (CP), the reticulate layer (RL), the outer granulate sublayer (OGS) and the inner granulate sublayer (IGS). Arrow indicates the cell wall. Scale bar = 1 µm. 1. Thicker adaxial CM. 2. Thinner abaxial CM.
- Detail of abaxial four layered CM. Note lamellate cell wall (CW). Arrow shows remains of cellular contents. Dark crystals are TEM film developer precipitate. Scale bar = 100 nm.
- Detail of reticulate layer (RL). Scale bar = 200 nm.
- Detail of lamellate cuticle proper (CP) and part of the reticulate layer (RL). Scale bar = 200 nm.



Glandulataenia, a taeniopteroid leaf from the Triassic of India, has a cuticle with distinctive rows of gland-like bodies on the areas between veins (Pant, 1990), a feature not present in *Restrepophyllum*.

4.2.2. Similar leaves from Europe/North America

Eostangeria Barthel is an extinct cycad genus with three species (*E. saxonica*, *E. ruzinciana* and *E. pseudopteris*) from the Cenozoic of Europe and Western North America (Kvaček and Manchester, 1999; Uzunova et al., 2001). This genus includes elongate simple leaflets with a midrib, simple or dichotomized lateral veins, and serrate margin. The epidermal characters of *Eostangeria* include moderately sunken cycadalean stomata somewhat irregularly oriented, darker subsidiary cells, and elongate common cells in adaxial epidermis that are occasionally intermixed with shorter cells (Kvaček and Manchester, 1999). *Eostangeria* is comparable to extant South African cycad *Stangeria* T. Moore in its external physiognomy, but more closely to the Zamiaceae (i.e. *Zamia*) in epidermal structure (Kvaček and Manchester, 1999). In gross morphology, *Restrepophyllum* somewhat resembles to *Eostangeria*; however, it is mostly distinguished by the lateral veins emerging at very low angles and by the presence of regularly spaced teeth of uniform size. At cuticular level, there are similarities (stomata haplocheilic, sunken, straight walled epidermal cells), although *Eostangeria* has short, dark, stained, intercalated cells on the lower epidermis that are lacking in *Restrepophyllum*. This feature was also mentioned by Kvaček and Manchester (1999) and Uzunova et al. (2001) as a difference between *Eostangeria* and extant *Zamia* (*Chigua*) *restrepoi*.

There are several morphogenera that include elongate leaflets from Permian to Cretaceous, that have a strong midrib and simple or forked, non-anastomosing lateral veins. These genera share a basic taeniopterid gross morphology, but have distinctive cuticle features and therefore may be allied to the Cycadales (i.e. *Doratophyllum* Harris, *Nilssonia* Brongniart, and possibly *Lepingia* Liu and Yao), as well as Bennettitales (*Nilssoniopteris* Nathorst and *Taeniozamites* Harris) or even Pentoxylales (*Nipaniophyllum* Sahn). They all differ from *Restrepophyllum chiguoides* by having entire margin, lateral veins emerging mostly at wide angles, and present at a very high density. At a cuticular level, *Restrepophyllum chiguoides* is comparable only with genera having haplocheilic stomata, and therefore related to Cycadales. The cuticle characters mentioned in the diagnosis of *Doratophyllum* (Harris, 1932) are typical of a 'generalized cycad' and are also consequently observed in *Restrepophyllum chiguoides*. The Patagonian specimen differs in that *Doratophyllum* has frequent short hairs on the veins. The most conspicuous characters that distinguish the genus *Nilssonia* from others similar fossil cycads possibly involve their external morphology (lamina attached to the upper edge of the rachis, entire or transversely dissected blade) rather than cuticular features. In addition, the lateral veins usually depart perpendicularly from the midvein, and the leaf margins are straight and entire. The epidermal characters are quite variable among species of *Nilssonia*, and some are similar to those observed in *Restrepophyllum* (i.e. guard cells sunken in an epistomatal chamber formed by a more or less regular ring of subsidiary cells and epidermal cells with straight to slightly sinuous anticlinal walls). A quite typical *Nilssonia* feature – resin bodies (Harris, 1932) – lacking in *Restrepophyllum*, is also absent in various species of *Nilssonia* (i.e. Kvaček, 1995; Pott et al., 2007). *Nilssonia* is known from Triassic–Cretaceous strata of Argentina, including the Baqueró Group, but only as impressions.

5. Paleoenvironment at Bajo Grande locality

According to Cladera et al (2002), the paleotopography at the Bajo Grande locality where *Restrepophyllum chiguoides* and other plant communities were deposited, is interpreted as fluvial sinuous channels associated to shallow and extensive lakes, while the climate in the area was hot to temperate.

Cuticular membranes of cycadaleans at the Bajo Grande fossiliferous locality are of variable thickness. There are taxa that show thin cuticles such as *Almargemia incrassata* (2 µm thick), *Androstrobus rayen* (2.4 µm thick), *Sueria elegans* (2.5 µm thick) and *Ticoa lamellata* (3 µm thick); others have thicker cuticle, for example *Androstrobus patagonicus* (3.7 µm thick), *Restrepophyllum chiguoides* (3–4.6 µm thick) and *Androstrobus munku* (4.7 µm thick), while still others have the thickest cuticle: *Mesosingeria parva* (12 µm thick) and *M. oblonga* (15 µm thick) (Archangelsky, 1966; Archangelsky and Villar de Seoane, 2004; Villar de Seoane, 1997, 2005). Ultrastructure studies showed that regardless the cuticular membranes thickness, most of them were adapted to low rates of cuticular transpiration because they have an outer lamellate layer and remains of probable epicuticular waxes which both form the main barrier to the diffusion of water and solutes across the cuticles (Baker, 1982; Santier and Chamel, 1998; Evert, 2006). Although this may have been true, there is another factor to which most probably these cuticular membranes may have adapted. There is strong evidence that the vegetation in Patagonia during the Early Cretaceous grew under environmental stressful conditions due to the persistent volcanic activity (Archangelsky et al., 1995; Archangelsky, 2001). A similar interpretation has been recently suggested for the xeromorphic features of *Pseudofrenelopsis parceramosa* (Fontaine) Watson from the early Cretaceous of England and the U.S.A.; these cuticles did not necessarily develop to reduce water loss but most probably to provide a structural protection against the high particulate content in the atmosphere caused by localized volcanism (Haworth and McElwain 2008).

6. Paleophytogeographic implications.

Other cycads have been found in the same Anfiteatro de Ticó Formation where *Restrepophyllum* occurs, notably *Mesodescolea*, that resembles the extant cycad *Stangeria* which is now restricted to SE Africa (Archangelsky and Petriella, 1971; Artabe and Archangelsky, 1971). This Africa–South America distribution was present when both continents were united as a Western Gondwana paleogeographic province and persisted up to the mid-Cretaceous when the shifting apart of the landmasses gave rise to the barrier now represented by the Atlantic Ocean. A similar transatlantic distribution was recently described for a shizaeaceous fern found in mid-Cretaceous Patagonian strata (spores of *Palaeomohria* Archangelsky) and the extant genus *Mohria* Swartz that now grows in SE Africa and Madagascar (Archangelsky, 2009). There is also an araucariaceous conifer with *Cyclisphaera*-type pollen that occurs in the Cretaceous of both South Africa and Patagonia (Del Fueyo and Archangelsky, 2005).

Uzunova et al. (2001) revised all tertiary material of *Eostangeria* found in central Europe (*E. saxonica* Barthel, *E. ruzinciniana* Palamarev, Petkova & Uzunova) and western North America (*E. pseudopteris* Kvaček & Manchester). Morphological and anatomical similarities with the extant genera *Zamia* (*Chigua*) and *Stangeria* suggest close relationships with *Eostangeria*, although some differences seem to support it as an independent taxon (Uzunova et al., 2001). A new subfamily within the Zamiaceae, additional to the Encephalartoideae and Zamioideae was established: the Eostangerioideae Kvaček, Palamarev & Uzunova. The similarities between *Eostangeria* and *Zamia* (*Chigua*) was taken by Uzunova et al. (2001) as an argument to suggest that both taxa may be members of the same lineage. It was suggested that the Neogene species *Eostangeria ruzinciniana* was a descendant of the Paleogene *Eostangeria saxonica*. In addition, the presence of *Zamia* (*Chigua*) in tropical forests of Colombia might be explained by means of a possible migration of *Zamia* (*Chigua*) ancestors from North America to South America during the Late Tertiary (Uzunova et al., 2001).

Restrepophyllum is also similar to *Zamia* (*Chigua*) *restrepoi* in many characters (see Table 1) and being original from South America, may

stand as another possible member of a primitive zamiaceous stock from which *Zamia* (*Chigua*) may have evolved. In this regard, it is significant that the genus *Zamia* (to which both *Chigua* species are now combined, Lindstrom, 2009) is exclusively neotropical and extends southward to Bolivia, near the Argentinean border (Sabato, 1990; Norstog and Nicholls, 1997). Therefore, the hypothesis of *Zamia/Chigua* having originated in South America should be pondered with a new approach by considering the evidence provided here, in which case migration of *Eostangeria* ancestors took place from South to North during the Paleogene, when global climatic conditions were at their climax (Zachos et al., 2001), similarly to those prevailing during the Early Cretaceous and Paleogene in Patagonia.

7. Is there a *Chigua* clade?

The leaf morphology and cuticular anatomy of *Restrepophyllum* are closest to those of extant genus *Chigua* which has been combined with *Zamia* (Lindstrom, 2009). Several characters originally defined for *Chigua* (Stevenson, 1990) are also found in *Zamia* as well as in other cycads. Lindstrom (2009) especially analyzed 5 characters used originally to define *Chigua* of which the character “prominent midvein present, lateral veins longitudinally and dichotomously branched” is particularly significant (Stevenson et al., 1996). This character is absent in *Zamia*, although they occur in *Cycas* (which lacks secondary venation) and *Stangeria* (which has laterals departing at right angle and a different cuticular structure). The presence/absence of a midvein in lanceolate/elongate fossil leaves is a strong taxonomical character used to separate genera.

Molecular data used to combine *Chigua* with *Zamia* suggest that both are genetically close (De Luca et al., 1995; Caputo et al. 1996). Chaw et al. (2005) have also concluded that *Chigua* is paraphyletic with *Zamia*, and both may be members of the same clade. Caputo et al. (2004) in a preliminary phylogenetic analysis of *Zamia*, that included *Zamia* (*Chigua*) *restrepoi*, show that morphological resemblance in this genus does not correspond to the pattern of phylogenetic relationships but it is rather broadly congruent with geographical distribution (a Northamerican and Caribbean clade on one hand and a Central-South American clade on the other). This geographical separation of clades, the large number of species (more than 50) with exclusive distribution in the neotropics, and the lack of field information on most taxa (including a detailed knowledge of phenotypic and genotypic variation), call for more work to be done in order to better understand their differences and relationships. In this regard, we agree with Lindstrom (2009) that the classification of *Zamia* is still incomplete and that at present there is a limited understanding on the geographical distribution and morphological variation of each species.

Restrepophyllum, and co-occurring fertile structures (*Androstrobus* spp.) of a putative fossil zamiaceous cycads add data that could be useful in future phylogenetic studies. In this particular case, the significance of the ‘time factor’, ‘paleogeography’ and the weight of the character ‘midvein present’ – including perhaps some stomatal peculiarities – may have played a role in the evolution of *Zamia* (*Chigua*). If this is the case, maybe a *Chigua* ‘lineage’ could be traced back in time to the early Cretaceous. A similar case involves to the Cretaceous *Mesodescolea*, which comes from the same locality in Patagonia as *Restrepophyllum* and living *Stangeria* in Africa (Chaw et al. 2005). Time and space are factors that have had influence in the dynamics of plant evolution.

8. Conclusions

On the basis of a Cretaceous (Aptian) leaflet compression, a new cycadalean genus and species *Restrepophyllum chiguoides*, has been described from the Anfiteatro de Ticó Formation at the Bajo Grande locality, Patagonia, Argentina.

This new record adds to the list of several fossil cycad taxa, including leaves and pollen cones, that have been described from the same sediments. This underscores the fact that the cycadophytes were a diversified component in the Aptian communities of Patagonia.

Although three cycadalean pollen cones (*Androstrobus* spp.) have been described from the same deposits, at the moment there is no evidences linking *Restrepophyllum* with some of them.

The general morphology and cuticle structure of *Restrepophyllum* share several characters in common with the extant *Zamia* (*Chigua*) *restrepoi* (Stevenson) Lindstrom. This similarity suggests that *Restrepophyllum* can be assigned to the cycad family Zamiaceae.

The likely close relationship between *Restrepophyllum* and living *Zamia* (*Chigua*) *restrepoi* is in consistent with the geographical distribution of both, the extant and fossil taxa, and suggests a possible South American origin of *Zamia/Chigua* and a further migration to northern latitudes.

This new type of leaf also suggests the likely existence of a *Chigua* clade that may be traced back to the Early Cretaceous when two cycadalean families, Zamiaceae and Stangeriaceae, were already well-established in Patagonia.

Because *Restrepophyllum chiguoides* consists of a *Phyllopteroides*-like leaflet, we suggest that some of the specimens previously referred to the Gondwanan morphogenera *Phyllopteroides* may also be related to cycadophytes.

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