AMEGHINIANA - 2013 - Tomo 50 (2): 257 – 264 ISSN 0002-7014

NOTA PALEONTOLÓGICA

ON THE PRESENCE OF THE CYCAD *PSEUDOCTENIS DENTATA* ARCHANGELSKY AND BALDONI IN THE PUNTA DEL BARCO FORMATION (LATE APTIAN), SANTA CRUZ PROVINCE, ARGENTINA

MAURO G. PASSALIA

Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA - CONICET), Universidad Nacional del Comahue, Quintral 1250, R8400FRF, San Carlos de Bariloche, Argentina. passaliam@gmail.com

Keywords. *Pseudoctenis*. Cycads. Baqueró Group. Aptian. Cretaceous

The genus *Pseudoctenis* is known mostly from Mesozoic strata, although the oldest record, *Pseudoctenis samchokense* (Kawasaki) Pott *et al.* (2010), was recently described from Permo–Carboniferous strata of China. The earliest Mesozoic cycad foliage unequivocally assigned to the genus *Pseudoctenis* belong to Carnian (Upper Triassic) deposits of both, Southern and Northern Hemisphere (Anderson and Anderson, 1989; Pott *et al.*, 2007a). Several Mesozoic foliage records have been referred to this genus, but most do not yield cuticle and thus, allocation remain inconclusive (*i.e.*, Bonetti, 1968; Artabe, 1986).

In southern South America, more than 20 species referred to *Pseudoctenis* have been recorded from Upper Triassic to Lower Cretaceous deposits (*i.e.*, Artabe and Stevenson, 1999; Leppe and Moisan, 2003). However, only three identified from the Baqueró Group, have their cuticle preserved. One of them, *Pseudoctenis dentata* Archangelsky and Baldoni, 1972, from the Anfiteatro de Ticó Formation (basal unit of the Baqueró Group) is here identified on the basis of well-preserved material collected in the same group; but in its upper unit (Punta del Barco Formation). This record extends the presence of this taxon in the Cretaceous flora of Patagonia and reinforces the importance of the epidermal features in paleotaxonomical assignments of fossil plants.

GEOLOGICAL SETTING, MATERIAL AND METHODS

The fossil specimen consists of a single incomplete leaf compression with preserved cuticle, and its counterpart. It was obtained from an organogenic lens at the southern flank of the Meseta Baqueró, Santa Cruz province (Argentina). The fossil bearing deposits are interpreted are as fluvial floodplain (Limarino *et al.*, 2012) from the upper part of the Punta del Barco Formation, recently dated as late Aptian (114.67± 0.18 Ma, Césari *et al.*, 2011). The plant assemblage of this level also includes fronds of *Korallipteris* sp. cf. *K. argentinica* (Berry *emend*. Herbst) Vera and Passalia, *Gleichenites sanmartinii* Halle, charcoalified gleicheniacean rhizomes and rachides, and the fern-like genus *Sphenopteris* together with the gymnosperm leaves *Araucaria* sp., and *Brachyphyllum* spp. It also includes *in situ* petrified trunks of *Brachyoxylon* sp. cf. *B. boureaui* Serra and *Agathoxylon* sp. (Limarino *et al.*, 2012; Vera and Césari, 2012). Palynological assemblages have been recovered highlighting the presence of lycophytes, ferns (represented by several families), conifers, an uncertain cycadophyte and primitive angiosperms (Limarino *et al.*, 2012).

The cuticle was removed from the matrix of the leaflets and oxidized in 40% nitric acid for 5–10 minutes, followed by 5% ammonium hydroxide for 2 minutes.

For light-microscope (LM) observation, fossil cuticles of *Pseudoctenis* were mounted in glycerine jelly and observed with a Nikon E200 microscope. Micrographs were taken with a Nikon digital DS-Fi1 camera. For the scanning electron microscope (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 Philips XL30 TMP microscope at

the Electronic Microscopy Service of the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina) and a Philips SEM 515 at the Centro Atómico Bariloche (Bariloche, Argentina).

SYSTEMATIC PALEONTOLOGY

Order Cycadales Pers. *ex* Bercht. and J. Presl, 1820

Genus ***Pseudoctenis*** Seward, 1911 *emend*. Harris, 1964

Type species. *Pseudoctenis eathiensis* (Richards) Seward, 1911 *(= Zamites eathiensis Richards, 1834);* original designation. Upper Jurassic, Scotland.

Pseudoctenis dentata Archangelsky and Baldoni, 1972

Figures 1–3

Studied material. MPM PB 3200 (and its counterpart). All the cuticle preparations for light microscope and SEM (MPM PB 3200/ 1–MPM PB 3200/ 22) belong to the same specimen.

Geographic origin. Southern flank of Meseta Baqueró, Santa Cruz province, Argentina.

Stratigraphic origin. Punta del Barco Formation (Baqueró Group), late Aptian (114.67± 0.18 Ma; Césari *et al.*, 2011). Stratigraphic level 12 (depositional sequence 3) of Limarino *et al.* (2012).

Description. The fossil sample consists of only one fragmentary leaf (and its counterpart), lacking its base and apex (Fig. 1). The leaf portion is pinnate, up to 6 cm long. The leaflets are opposite, inserted laterally to the rachis at 55–65º. The rachis is straight, 1 mm wide and longitudinally striated (Fig. 1.3). Leaflets are elongated, up to 2 cm long and 0.4–0.5 cm wide (length/–width ratio no less than 4:1). The base is slightly expanded both cata- and anadromically and apices are not preserved. Adjacent leaflets are 1.5–2 mm apart from each other. The veins (5–6) enter each leaflet and run parallel and occasionally bifurcating once close to the base, without any anastomoses, straight to the apices (Fig. 1.2).

Ab- and adaxial cuticles were obtained (Fig. 2–3); stomata were more abundant in one of them (the assumed abaxial cuticle). Although scarce, the presence of stomata in the adaxial cuticle indicates that the leaf is amphistomatic. Both cuticles between 1–1.5 m (abaxial) and 2–2.5 m (adaxial) thick. Trichome bases or papillae were not observed in any cuticle.

The adaxial cuticle (Fig. 2.8–9, 3.7–8) exhibit epidermal cells with variable shape and size, from isodiametric (oval to polygonal; *c*. 50 m in diameter) to elongate (up to 50 m long). Although epidermal cells are distributed arbitrarily, elongate cells appear arranged in short rows in some cases. Epidermal cells are uniform with respect to the thickness of both the periclinal and anticlinal walls. The periclinal walls are smooth whereas the anticlinal walls are strongly sinuous. The amplitude of the sinuosity is 8–10 m. The anticlinal wall is relatively thin, although with slight thickenings mainly on the bends. The epidermal cells show a more and less rounded pit in the concave side of each bend of the anticlinal walls (Fig. 3.8). Only a few stomata have been observed in a single fragment of cuticle from the adaxial side (Fig. 2.8).

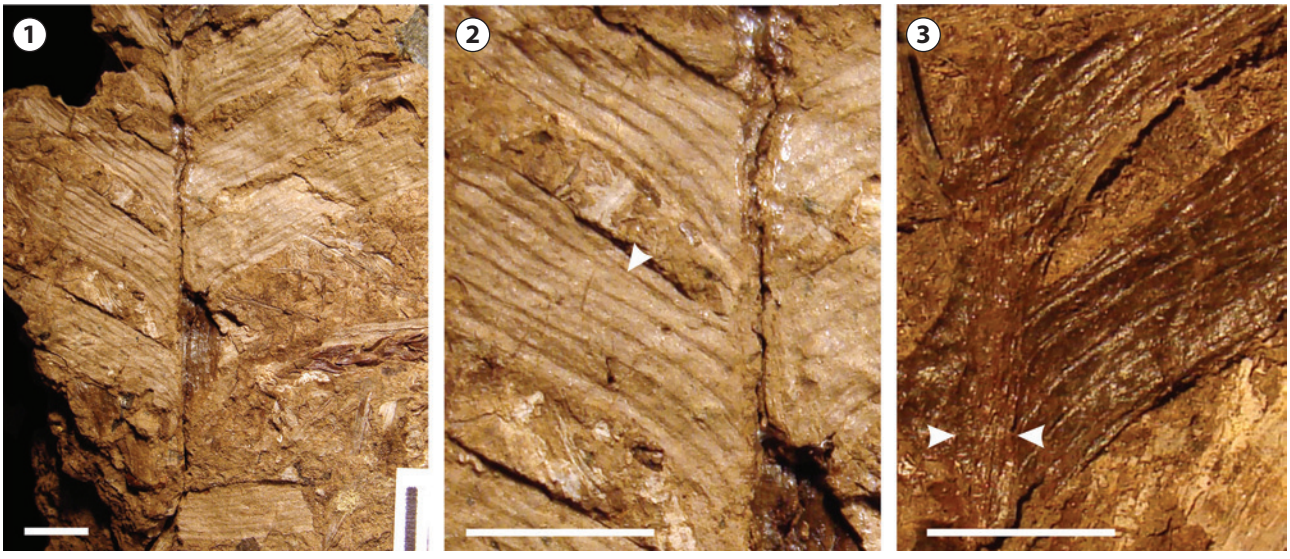


Figure 1. ***Pseudoctenis dentata*** Archangelsky and Baldoni (MPM PB 3200). **1,** general view. Scale bar = 0.5 cm; **2,** detail of 1. Arrowhead indicates the point of bifurcation of a vein. Scale bar = 0.5 cm; **3,** detail of the counterpart figured in 2 but with the cuticle preserved. The rachis is comprised between arrowheads. Scale bar = 0.5 cm.

The stomata are longitudinally elongate and oriented parallel to the vein courses. Subsidiary cells are apparently differentiated in lateral and polar cells.

The abaxial cuticle (Fig. 2.1–7, 3.1–6) comprises stomatal areas between the veins. Their surface show parallel longitudinal cutin ridges (Fig. 2.1–2, 3.1). There are ridges longs and conspicuously concentrated in zones (Fig. 2.2) as well as scattered short ridges. No other ornamentation is visible on periclinal walls. All epidermal cell walls in the abaxial cuticle have a relatively uniform thickness, like in the adaxial ones. Epidermal cells over the leaflet margin and veins are mostly elongate and have anticlinal walls markedly undulate (upper part of Fig. 2.3 and Fig. 2.7) comparable to the adaxial cuticle. Epidermal cells between veins are variable in shape and size and their anticlinal walls are less strongly sinuous. Cells are mostly isodiametric and have three or more ill-defined flanges, and their sizes are similar to those cells from the adaxial side. Somewhat elongate cells are also present, with their major axis indistinctly oriented. Although less conspicuous than in the adaxial cuticle, epidermal cells on the abaxial side apparently have similar pits too (Fig. 3.4).

Stomata in the abaxial cuticle are irregularly distributed in the zones comprised between veins and indistinctly oriented. Adjacent stomata often have subsidiary cells in contact, or else they share a common subsidiary cell (Fig. 3.4). The stomatal apparatus is mostly monocyclic (presumably haplocheilic), with usually 5–7 subsidiary cells not differentiated into polar or lateral cells. A lesser sinuosity is possible a remarkable feature of the subsidiary anticlinal cell walls. In spite of them, cells are rather similar —in shape and size— to the surrounding epidermal cells from which they are not easily discernible. An elevated circular structure, about 40 m in diameter, is visible on the outer surface above each stomata (Fig. 3.1–2). This elevated structure is occasionally connected to ridges arranged either in a polar position (Fig. 3.2) as well as radially (Fig. 2.5). The guard cells are 30–40 m long and less than 10 µm wide. They have a central zone that is somewhat sunken with respect to the poles, and show ventral longitudinal thickenings (Fig. 2.6, 3.6) covered by fine radial striations (lamellae) produced by cutin or probably lignine deposits (Fig. 3.6).

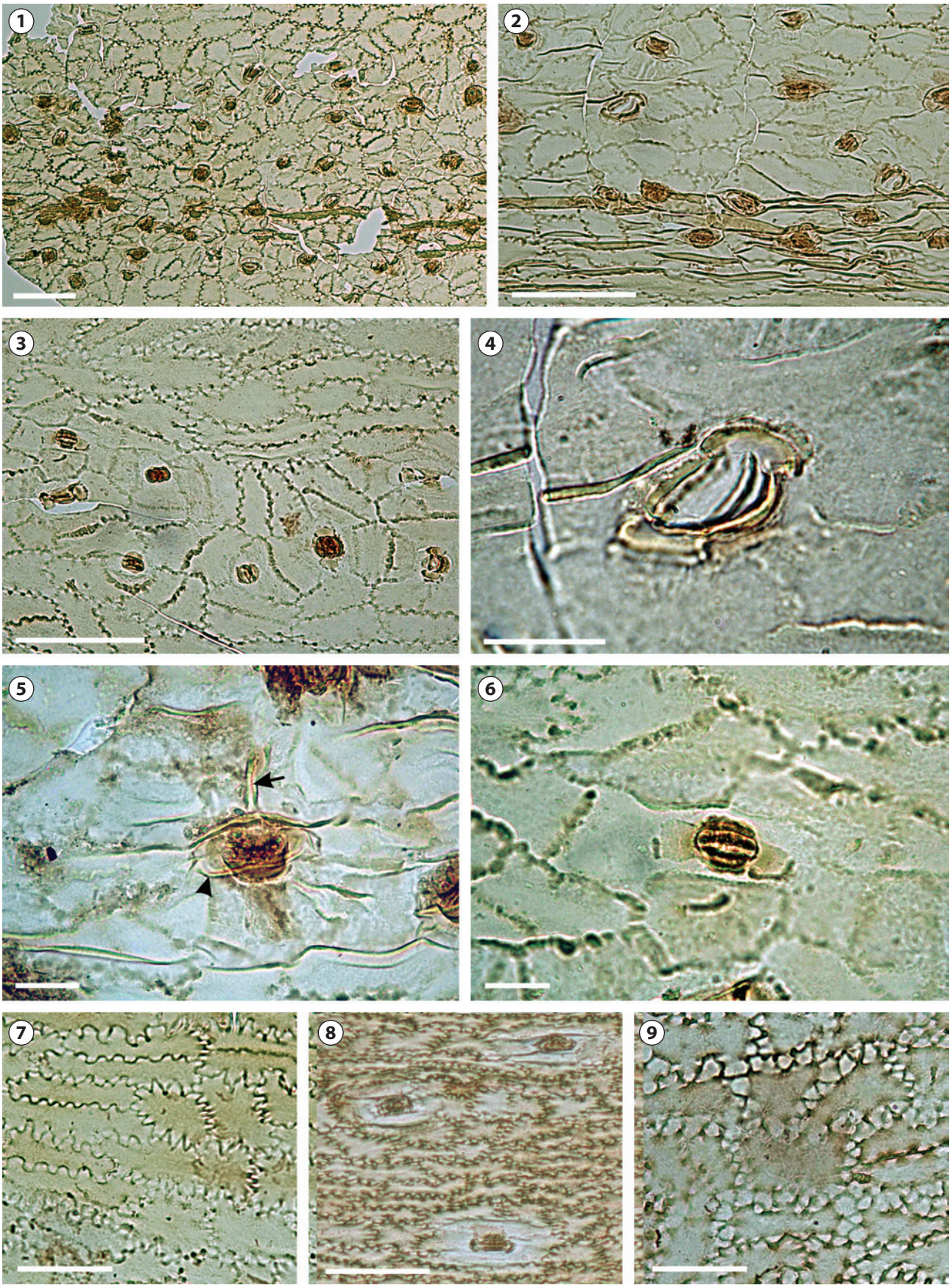
DISCUSSION

Among the fossil cycadophyte leaf-genera, the specimen described here fits in the genus *Pseudoctenis* (Seward) Harris (1932, 1964) based on the following macromorphological and epidermal features: simply pinnate leaf; narrow, elongate leaflets with entire margin, laterally inserted to the rachis; parallel veins, simple or forked, not anastomosing; haplocheilic stomata, (or at least with multiple subsidiary cells). The latest feature distinguishes *Pseudoctenis* from the bennettitalean genus *Pterophyllum* Brongniart, which has a similar leaf physiognomy, but displays syndetocheilic stomata. *Ctenis* (Lindley and Hutton) Harris, a genus similar to *Pseudoctenis*, is differentiated by its frequent anastomosing veins (Harris, 1964).

The genus *Pseudoctenis* (Seward) Harris was erected by Seward (1911), who identified *Zamites eathiensis* Richards from the Upper Jurassic of Scotland as the type species, but he gave no valid diagnosis. Later, Harris (1932, 1964) described the cuticle of three *Pseudoctenis* species from the Jurassic of Yorkshire and provided a good diagnosis for the genus that includes both macromorphological and epidermal characters. However, the cuticle of the type species (*P. eathiensis*) remains unknown to date, rendering to *Pseudoctenis* a technically problematic genus (Pott *et al.*, 2007a). Despite this, the emended diagnosis of Harris has been broadly accepted as the morphological delimitation of *Pseudoctenis* from other cycadophyte genera (*i.e.*, Kustatscher and van Konijnenburg-van Cittert, 2007; Pott *et al.*, 2010).

In addition to the features previously mentioned, the generic diagnosis of *Pseudoctenis* by Harris (1964, p. 70–71) includes "(anticlinal) cell walls straight or nearly straight". However, *Pseudoctenis dentata* has epidermal cells with undulated anticlinal walls, which is the only feature not shared with the generic diagnosis. The nature of the anticlinal cell wall has often been used in the fossil record to distinguish between Bennettitales (typically sinuous) and the Cycadales (straight to slightly curved). However, this character is less reliable than previously thought: sinuous cell walls are present in both extant (*i.e.*, *Stangeria eriopus* (Kunze) Baillon, *Cycas micholitzii* Dyer, *Macrozamia* spp.; Pant and Nautiyal, 1963; Dower *et al.*, 2004) and fossil cycads (*i.e.*, *Pseudoctenis cornelli* Pott *et al.*, 2007a) whereas, in contrast, straight walls occur in many, usually early, bennettitalean species (*e.g.*, in the genera *Pterophyllum* or *Anomozamites*; Harris, 1932: 107; Pott *et al.*, 2007b; Pott and McLoughlin, 2009).

Among the several species of *Pseudoctenis* described from southern South America, only three have preserved cuticles, all of which were recorded from the Baqueró Group: *Pseudoctenis dentata* and *P. crassa* from the Anfiteatro de Ticó Formation (Archangelsky and Baldoni, 1972), and *P. ornata* from the Punta del Barco Formation (A. Archangelsky *et al.*, 1995). A fourth species (*i.e.*, *P. giganteus* A. Archangelsky,


1
2
3
4
5
6
7
8
9

1997), distinguished by its notorious giant size, was defined from the Anfiteatro de Ticó Formation, but is preserved as impressions only. *Pseudoctenis crassa*, based on isolated leaflets only, is characterized by epidermal cells with clearly non-undulate anticlinal walls, although they might be not strictly straight either. Moreover, this species presents abundant hair bases and longitudinally oriented stomata forming short rows (Archangelsky and Baldoni, 1972). The leaf physiognomy of *Pseudoctenis ornata* is rather similar to that of the specimen described here, but it differs definitively by its cuticular features (*i.e.*, epidermal cells with straight anticlinal cell walls and papillae protecting the stomatal pores; Archangelsky *et al.*, 1995).

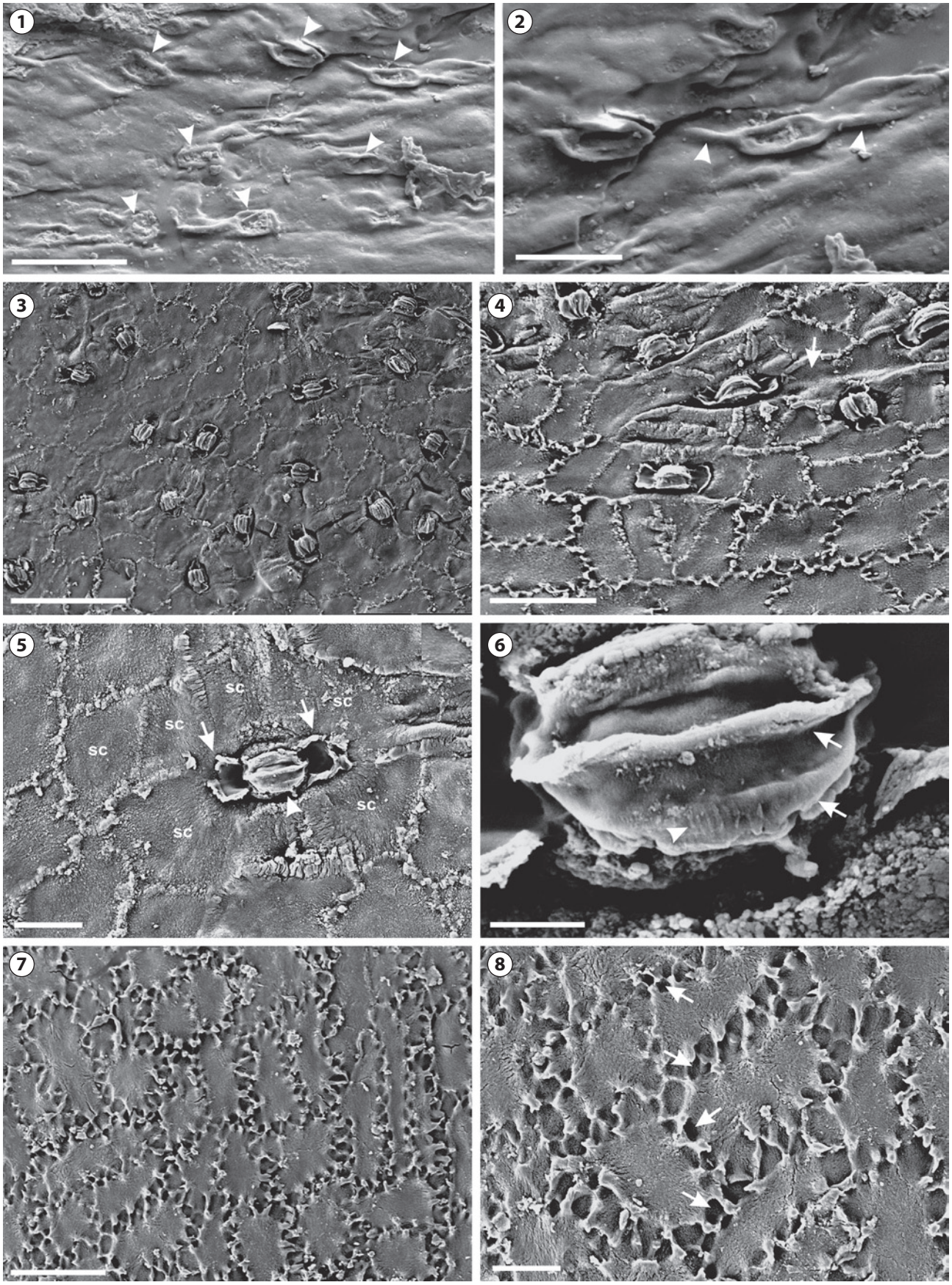
Pseudoctenis dentata was defined by Archangelsky and Baldoni (1972) on the basis of several specimens collected in the Anfiteatro de Ticó Formation at Cerro Bayo, which is also known as Bajo Grande. Its original description was later expanded by epidermal characters (Artabe, 1994) trough observations using scanning electron microscope. Despite of some macromorphological differences, the specimens described here from Meseta Baqueró and those from Cerro Bayo, share substantial similitude at cuticular level allowing them to be considered as conspecific. On the basis of the diagnoses of *Pseudoctenis dentata* (Archangelsky and Baldoni, 1972), the main macromorphological differences with the Meseta Baqueró specimen include a rachis half as thick, and two times wider leaflets in the former. This variation gives the specimens from both localities and unit a different physiognomic appearance. However, the specimen LP 6562 of Cerro Bayo has a slender rachis and leaflets as longer as those of the Meseta Baqueró specimen, being the wide of leaflets the only difference between them. The number of veins on each leaflet is quite similar in the specimens from both localities. In the leaf studied here, two vein bifurcations were observed, a feature not mentioned for the Cerro Bayo specimens. Nevertheless, the venation of several of these specimens is not so clearly preserved and consequently the non-recognition of bifurcated veins does not necessarily imply their absence. Unfortunately, the apices of the leaflets are not preserved in the Meseta Baqueró specimen. *Pseudoctenis dentata* is characterized by very distinct leaflet apices showing small teeth.

Therefore, if macromorphological features generate some doubt about the conspecificity of specimens from both localities, this uncertainty disappear when comparing their virtually indistinguishable cuticles. Leaves are amphistomatic with only a few stomata on the adaxial side. Although Artabe (1994) stated the absence of stomata in the adaxial cuticle, this is a feature mentioned and illustrated in the diagnoses of this species (Archangelsky and Baldoni, 1972). The adaxial stomata of the specimens from Cerro Bayo and Meseta Baqueró are markedly elongate with subsidiary cells differentiated in polar and lateral cells. They also share an abaxial cuticle surface with thickenings producing conspicuous ridges, and the shape of epidermal cells with distinctive undulated anticlinal walls. Since sinuous anticlinal walls are relatively uncommon in fossil cycads, their presence is here considered a relevant character for the specific assignment of the Meseta Baqueró specimens. Among the more than fifteen fossil cycad species with preserved cuticles collected from the Baqueró Group, *Pseudoctenis dentata* and *Sueria rectinervis* Menéndez have epidermal cells with undulate anticlinal cell walls. Considering an important number of *Pseudoctenis* species with preserved cuticle recorded worldwide (see Appendix 1), only one of them (*P. cornelii* Pott, Kerp and Krings) has also undulated anticlinal cell walls. Other features shared between the specimens from Meseta Baqueró and Cerro Bayo include the distribution and orientation of stomata, the presence of striations radiating from the suprastomatal aperture over the subsidiaries, and occlusive cells that are identical in shape, disposition and thickness. Therefore, based on the cuticular features they share they are herein considered conspecific, referring MPM PB 3200 to *Pseudoctenis dentata* Archangelsky and Baldoni, 1972.

CONCLUSIONS

The cycad leaf *Pseudoctenis dentata* has been recognized in floodplain deposits from the Aptian Punta del Barco Formation in Meseta Baqueró. This new record clearly differs from others cycad species of the Baqueró Group, *i.e.*, *P. orna-*

Figure 2. ***Pseudoctenis dentata*** Archangelsky and Baldoni, leaflet cuticle of the specimen MPM PB 3200 observed under transmitted-light microscope; **1,** abaxial cuticle showing a zone between veins with stomata irregularly distributed and indistinctly oriented. (MPM PB 3200/ 13) Scale bar = 100 µm; **2–3,** abaxial cuticle showing the disposition and orientation of stomata. Scale bars = 100 µm; **2,** detail showing parallel longitudinal cutinized ridges (bottom) near to leaflet margin (MPM PB 3200 /1); **3,** transition zone from the stomatiferous area (bottom) to a vein area with epidermal cells longitudinally elongated and anticlinal walls more sinuous (top (MPM PB 3200 /3); **4,** detail of 2 showing a stomata (MPM PB 3200 /1). Scale bar = 20 µm; **5,** outer view of abaxial cuticle showing striations (arrow) radiating from the stomata. Arrowhead indicates the suprastomatal aperture (MPM PB 3200 /1). Scale bar = 20 µm; **6,** inner view of abaxial cuticle showing a detail of stomatal apparatus. Note the longitudinal thickenings (obscure lines) in the central zone of occlusive cells (MPM PB 3200/ 3). Scale bar = 20 µm; **7,** abaxial cuticle showing epidermal cells in a vein zone (MPM PB 3200/ 3). Scale bar = 50 µm; **8,** adaxial cuticle showing scarce stomata (MPM PB 3200/ 21). Scale bar = 100 µm; **9,** detail of adaxial cuticle showing epidermal cells (MPM PB 3200/ 9). Scale bar = 50 µm.


1
2
3
4
5
SC
SC
SC
SC
SC
SC
6
7
8

ta and *P. crassa,* by its cuticular features, and from *P. giganteus* by its size and leaflets shape.

This new specimen extends the record of *Pseudoctenis dentata* from the Anfiteatro de Ticó to the Punta del Barco Formations, thus being present during the time of deposition of most of the Baqueró Group.

The major differences between the new specimen of *Pseudoctenis dentata* and those previously described from Cerro Bayo lie in its macromorphological physiognomy. Contrasting, their cuticles are virtually indistinguishable, remarking the importance of considering the role of cuticle in specific determination of fossil leaves.

ACKNOWLEDGMENTS

Thanks are due to S. Césari and E. Vera for their help in improving this manuscript. A special thanks to the reviewers Josefina Bodnar and Christian Pott for their numerous suggestions and comments. This work was funded by the Consejo Nacional de Ciencia y Tecnología (CONICET) through PIP 0512.

REFERENCES

Anderson, J.M. and Anderson, H.M. 1989. *Palaeoflora of Southern Africa, Molteno Formation (Triassic), Gymnosperms (excluding* Dicroidium*)*. Balkema, Rotterdam, 567 p.

Archangelsky, A. 1997. *Pseudoctenis giganteus*, nueva cycadal de la Formación Baqueró, Cretácico inferior de Argentina. *Ameghiniana* 3: 387–391.

Archangelsky, A., Andreis, R.R., Archangelsky, S. and Artabe, A.E. 1995. Cuticular characters adapted to volcanic stress in a new Cretaceous cycad leaf from Patagonia, Argentina. Considerations on the stratigraphy and depositional history of the Baqueró Formation. *Review of Palaeobotany and Palynology* 89: 213–233.

Archangelsky, S. and Baldoni, A. 1972. Notas sobre las flora fósil de la zona de Ticó, provincia de Santa Cruz. X. Dos nuevas especies de *Pseudoctenis* (Cycadales) *Ameghiniana* 9: 241–257.

Artabe, A.E. 1986. Estudio sistemático de la tagoflora triásica de Los Menucos, provincia de Río Negro, Argentina. Parte II. Cycadophyta, Ginkgophyta y Coniferophyta. *Ameghiniana* 22: 159–180.

Artabe, A.E. 1994. Estudio al microscopio electrónico de barrido (MEB) de dos cicadópsidas fósiles de Argentina. *Pseudoctenis dentata* Archangelsky y Baldoni 1972 y *Sueria rectinervis* Menéndez 1965. *Ameghiniana* 31: 115–124.

Artabe, A.E. and Stevenson, D.W. 1999. Fossil Cycadales of Argentina. *Botanical Review* 65: 219–238.Bonetti, M.I. 1968. Las especies del género *Pseudoctenis* en la flora Triásica de Barreal (San Juan). *Ameghiniana* 5: 433–446.

Césari, S.N., Limarino, C.O., Llorens, M., Passalia, M.G., Perez Loinaze, V.S. and Vera, E.I. 2011. High-precision late Aptian Pb/ U age for the Punta del Barco Formation (Baqueró Group), Santa Cruz Province, Argentina. *Journal of South American Earth Sciences* 31: 426–431.

Dower, B.L., Bateman, R.M. and Stevenson, D.W. 2004. Systematics, ontogeny, and phylogenetic implications of exceptional anatomically preserved cycadophyte leaves from the Middle Jurassic of Bearreraig Bay, Skye, Northwest Scotland. *Botanical Review* 70: 105–120.

Harris, T.M. 1932. The fossil flora of Scoresby Sound, East Greenland. Part 3: Caytoniales and Bennettitales. *Meddelelserom Grønland* 85: 1–133.

Harris, T.M. 1964. The Yorkshire Jurassic Flora. II.—Caytoniales, Cycadales & Pteridosperms. *Trustees of the British Museum (Natural History).* London, 191 p.

Kustatscher, E. and van Konijnenburg-van Cittert, J.H.A. 2007. Taxonomical and palaeogeographic considerations on the seed fern genus Ptilozamites with some comments on *Anomozamites, Dicroidium, Pseudoctenis* and *Ctenozamites*. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 243: 71–100.

Leppe, M. and Moisan, P. 2003. Nuevos registros de Cycadales y Cycadeoidales del Triásico Superior del río Bíobío, Chile. *Revista Chilena de Historia Natural* 76: 475–484.

Limarino, C.O., Passalia, M.G., Llorens, M., Vera, E.I., Perez Loinaze, V. and Césari, S.N. 2012. Depositional environments and floristic associations of Aptian sequences affected by volcanism in Patagonia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 323–325: 22–41.

Pant, D.D. and Nautiyal, D.D. 1963. Cuticle and epidermis of recent Cycadales leaves, sporangia and seeds. *Senckenbergíana Biologica* 44: 257–336.

Pott, C., Kerp, H. and Krings, M. 2007a. *Pseudoctenis cornelii* nov. spec. (cycadalean foliage) from the Carnian (Upper Triassic) of Lunz, Lower Austria. *Annalen des Naturhistorischen Museums Wien* A 109: 1–17.

Pott, C., van Konijnenburg-van Cittert, J.H.A., Kerp, H. and Krings, M. 2007b. Revision of the *Pterophyllum* species (Cycadophytina: Bennettitales) in the Carnian (Late Triassic) flora from Lunz, Lower Austria. *Review of Palaeobotany and Palynology* 147: 3–27.

Pott, C. and McLoughlin, S. 2009. Bennettitalean foliage in the Rhaetian–Bajocian (latest Triassic–Middle Jurassic) floras of Scania, southern Sweden. *Review of Palaeobotany and Palynology* 158: 117–166.

Pott, C., McLoughlin, S. and Lindström, A. 2010. Late Palaeozoic foliage from China displays affinities to Cycadales rather than to Bennettitales necessitating a re-evaluation of the Palaeozoic Pterophyllum species. *Acta Palaeontologica Polonica* 55: 157–168.

Vera, E.I. and Césari, S.N. (2012). Fossil woods (Coniferales) from the Baqueró Group (Aptian), Santa Cruz Province, Argentina. *Anais da Academia Brasileira de Ciências* 84: 617–625.

Seward, A.C. 1911. The Jurassic flora of Sutherland. *Transactions of the Royal Society of Edinburgh* 47: 643–709.

APPENDIX 1.

Pseudoctenis species with preserved cuticle.

Paleozoic

Figure 3. ***Pseudoctenis dentata*** Archangelsky and Baldoni, scanning electron micrographs of leaflets cuticle (MPM PB 3200); **1,** outer view of abaxial cuticle. Arrowheads indicate stomatal pores. Scale bar = 100 µm; **2,** detail of 1 showing the suprastomatal apertures raised over the epidermal surface. Note the folds in polar position (arrowheads). Scale bar = 50 µm; **3,** inner view of abaxial cuticle showing an inter-vein area with stomata irregularly distributed and indistinctly oriented. Scale bar = 100 µm; **4,** inner view of abaxial cuticle showing the sinuous anticlinal cells walls and the variability in the disposition of the subsidiary cells. Note the stomata in the bottom with subsidiary cells differentiated in polar and lateral. Arrow indicates a subsidiary cell shared by two neighbors stomata. Scale bar = 50 µm; **5,** detail of 3 showing a monocyclic (haplocheilic) stomata with subsidiary cells (sc) not differentiated into polar and lateral. Note the different relative position between the polar zones of the guard cells (arrows) and their central sunken zone (arrowhead). Scale bar = 20 µm; **6,** detail of 5 showing the central zone of guard cells with ventral longitudinal thickenings (arrows) covered by fine radiating striations (arrowhead. Scale bar = 5 µm; **7,** inner view of adaxial cuticle showing epidermal cells. Scale bar = 50 µm; **8,** detail of 7. Arrows indicate possible pits on the epidermal cell wall. Scale bar = 20 µm.

P. samchokense (Kawasaki) Pott *et al.*, 2010. Late Paleozoic, China.

Triassic

P. spectabilis Harris, 1932. Lower Lias, Greenland.

P. depressa Harris, 1932. Lower Lias, Greenland.

P. florinii Lundblad, 1950. Rhaeto–Liassic, Sweden.

P. cteniformis (Nathorst) Harris, 1950. Rhaetic, Sweden*

*P. cornelii*** Pott *et al.*, 2007a. Carnian, Austria.

P. chinensis (Hsü) Kustatscher and van Konijnenburg-van Cittert, J.H.A., 2007. Late Triassic, China.

P. stewartii Ash, 2001. Late Carnian, United States.

Jurassic

P. lanei Thomas, 1913 (figured in Harris, 1932 and 1964). Middle Jurassic, England. Also recognized from the Middle–Late Triassic of Kyrgyzstan (Central Asia) with epidermal characters partially preserved (Moisan *et al.*, 2011)

P. locusta Harris, 1964. Middle Jurassic, England

P. oleosa Harris, 1964. Middle Jurassic, England

P. herriesi Harris, 1964. Middle Jurassic, England

P. barulensis Doludenko and Svanidze, 1969. Upper Jurassic, Georgia

P. latus Doludenko and Svanidze, 1969. Upper Jurassic, Georgia

P. creyensis Barale, 1981. Kimmeridgian, France

P. cf. *P. heathiensis* (Richards) Seward in Van der Burgh and van Konijnenburg-van Cittert, 1984. Kimmeridgian, Scotland

Cretaceous

*P. dentata*** Archangelsky and Baldoni, 1972. Aptian, Argentina

P. crassa Archangelsky and Baldoni, 1972. Aptian, Argentina

P. ornata A. Archangelsky *et al.,* 1995. Aptian, Argentina

P. foljambeae Watson and Cusack, 2005. Wealden, England

P. divana Watson and Cusack, 2005. Wealden, England

P. babiensis Kvaček, 2008. Cenomanian, Czech Republic

*see Pott and McLoughlin (2009) about taxonomical status of this species.
** with exception of *P. dentata* and *P. cornelli*, the remaining species have epidermal cells with straight anticlinal walls.

REFERENCES (APPENDIX 1)

Archangelsky, A., Andreis, R.R., Archangelsky, S. and Artabe, A.E. 1995. Cuticular characters adapted to volcanic stress in a new Cretaceous cycad leaf from Patagonia, Argentina. Considerations on the stratigraphy and depositional history of the Baqueró Formation. *Review of Palaeobotany and Palynology* 89: 213–233.

Archangelsky, S. and Baldoni, A. 1972. Notas sobre las flora fósil de la zona de Ticó, provincia de Santa Cruz. X. Dos nuevas especies de *Pseudoctenis* (Cycadales) *Ameghiniana* 9: 241–257.

Ash, S. 2001. New cycadophytes from the Upper Triassic Chinle Formation of the southwestern United States. *Paleobios* 21: 15–28.

Barale, G. 1981. La paléoflore jurassique du Jura Français: étude systematique, aspects stratigraphiques et paléoécologiques. *Documents des Laboratoires de Géologie Lyon* 81: 1–467.

Doludenko, M.P. and Svanidze, C.I. 1969. Pozdnějurskaja flora Gruzii (The Late Jurassic flora of Georgia). *Trudy Geologičeskogo Instituta* 178: 1–116 (in russian).

Harris, T.M. 1932. The fossil flora of Scoresby Sound, East Greenland. Part 3: Caytoniales and Bennettitales. *Meddelelserom Grønland* 85: 1–133.

Harris, T.M. 1950. Notes on the Jurassic Flora of Yorkshire, 46–48. *Annals and Magazine of Natural History*, *Series 12* 3: 1001–1030.

Harris, T.M. 1964. The Yorkshire Jurassic Flora. II.—Caytoniales, Cycadales & Pteridosperms. *Trustees of the British Museum (Natural History).* London, 191 p.

Kustatscher, E. and van Konijnenburg-van Cittert, J.H.A. 2007. Taxonomical and palaeogeographic considerations on the seed fern genus Ptilozamites with some comments on *Anomozamites, Dicroidium, Pseudoctenis* and *Ctenozamites*. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 243: 71–100.

Kvaček, J. 2008. New cycad foliage of *Pseudoctenis babiensis* from the Bohemian Cenomanian. *Acta Musei Nationalis Pragae* 64: 125–131.

Lundblad, A.B. 1950. Studies in the Rhaeto–Liassic floras of Sweden. I. Pteridophyta, Pteridospermae and Cycadophyta from the mining district of NW Scania. *Kungliga Svenska Vetenskapsakademiens Handlingar*, *Fjärde Serien* 1: 1–82.

Moisan, P., Voigt, S., Pott, C., Buchwitz, M., Schneider, J.W. and Kerp, H. 2011. Cycadalean and bennettitalean foliage from the Triassic Madygen Lagerstätte (SW Kyrgyzstan, Central Asia). *Review of Palaeobotany and Palynology* 164: 93–108.

Pott, C., Kerp, H. and Krings, M. 2007a. *Pseudoctenis cornelii* nov. spec. (cycadalean foliage) from the Carnian (Upper Triassic) of Lunz, Lower Austria. *Annalen des Naturhistorischen Museums Wien* A 109: 1–17.

Pott, C. and McLoughlin, S. 2009. Bennettitalean foliage in the Rhaetian–Bajocian (latest Triassic–Middle Jurassic) floras of Scania, southern Sweden. *Review of Palaeobotany and Palynology* 158: 117–166.

Pott, C., McLoughlin, S. and Lindström, A. 2010. Late Palaeozoic foliage from China displays affinities to Cycadales rather than to Bennettitales necessitating a re-evaluation of the Palaeozoic Pterophyllum species. *Acta Palaeontologica Polonica* 55: 157–168.

Richards, J.T. 1884. On Scottish fossil cycadaceous leaves contained in the Hugh Miller Collection. *Proceedings of the Royal Society of Edinburgh* 8: 116–123.

Thomas, H.H. 1913. The fossil flora of the Cleveland District of Yorkshire I, The flora of the Marske Quarry. *The Quarterly Journal of the Geological Society of London* 69: 223–251.

Van der Burgh, J. and van Konijnenburg-van Cittert, J.H.A. 1984. A drifted flora from the Kimmeridgian (Upper Jurassic) of Lothbeg Point, Sutherland, Scotland. *Review of Palaeobotany and Palynology* 43: 359–396.

Watson, J. And Cusack, H.A. 2005. Cycadales of the English Wealden. *Monograph of the Palaeontographical Society*, *London*, 189 p.

doi: 10.5710/AMGH.17.04.2013.575

Recibido: 29 de febrero de 2012

Aceptado: 17 de abril de 2013