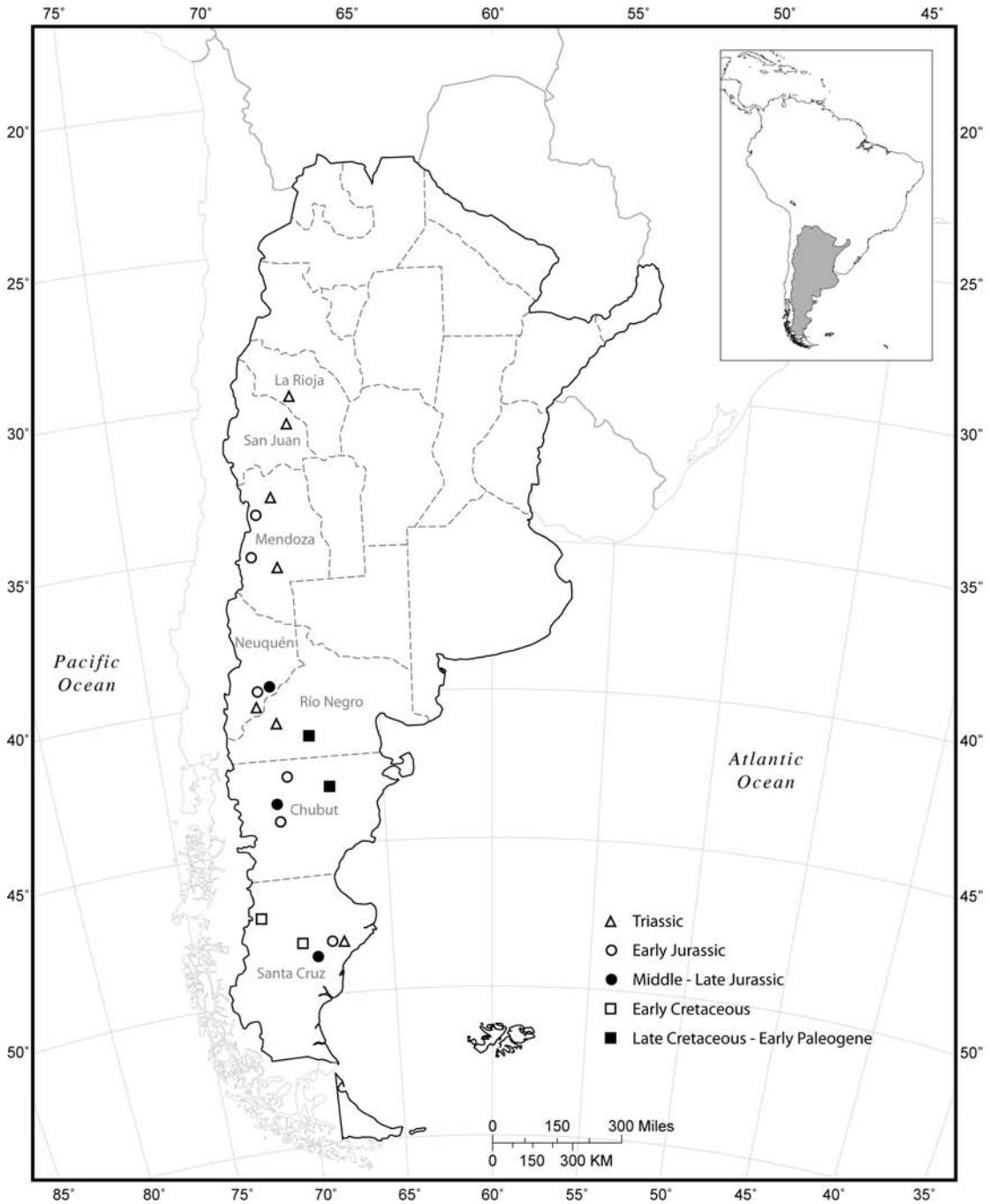


Fig. 9.1. Geographic and stratigraphic distribution of the cycadophyte record in Argentina.

REVIEW OF THE CYCADS AND BENNETTITALEANS FROM THE MESOZOIC OF ARGENTINA

9

N. Rubén Cúneo, Ignacio Escapa, Liliana Villar de Seoane, Analía Artabe, and Silvia Gnaedinger

Cycads and bennettitaleans from Argentina are thoroughly reviewed in light of their fossil record and recent findings from a geographic and stratigraphic perspective. The history of these groups is traced from their first appearance in the Triassic to the last record of cycads in the early Paleogene. Selected cycadophyte taxa have been particularly useful for interpreting their phylogenetic context and possible relationships with modern representatives. Biochronostratigraphic and paleoecological aspects are also considered that suggest that the biogeographic distribution of the cycadophytes was much farther poleward than previously thought, owing to greenhouse conditions prevailing during their time of occurrence in southern South America.

Introduction

Bennettitaleans and cycads are separate groups of seed plants that can be traced as far back as the Triassic for the bennettitaleans (Taylor et al. 2009) and probably even farther into the Late Paleozoic for the cycads (Mamay 1969; Hermsen et al. 2006). In Argentina, where living cycads are absent, both groups can definitely be recognized as early as the Triassic, throughout the Mesozoic, and into the early Paleogene. This record consists mostly of compressions and/or impressions, and, less commonly, permineralizations and mummifications. As elsewhere in the world, it is clear that these plant groups in South America were much more diverse in the past, particularly during the Jurassic and Cretaceous. As a result of the effect of greenhouse conditions during the Mesozoic and early Cenozoic, they had a large biogeographic range that extended toward the poles in both hemispheres, a distribution that strongly contrasts with the more limited range of the cycads in the tropics and subtropics today. This is the case for South America, especially Patagonia, which was located at middle to high latitudes during the late Mesozoic.

Although bennettitaleans (also known as cycadeoids) and cycads are currently considered a paraphyletic group of seed plants (Rothwell and Serbet 1994), they are commonly lumped in a systematically informal group called the cycadophytes in the paleobotanical literature (Taylor et al. 2009). We will continue to use this practical name when referring to the two groups here.

In this chapter, we offer an up-to-date review of these two groups of gymnosperms in Argentina, from the Triassic to the early Paleogene. Besides this survey of the complete fossil cycadophyte record, implications will be discussed regarding their phylogenetic significance, past distribution and diversity, and subsequent biostratigraphical importance. We will also examine their ecological niche in the Mesozoic plant communities as well as the paleoclimatological conditions that governed their presence in southern South America.

Triassic

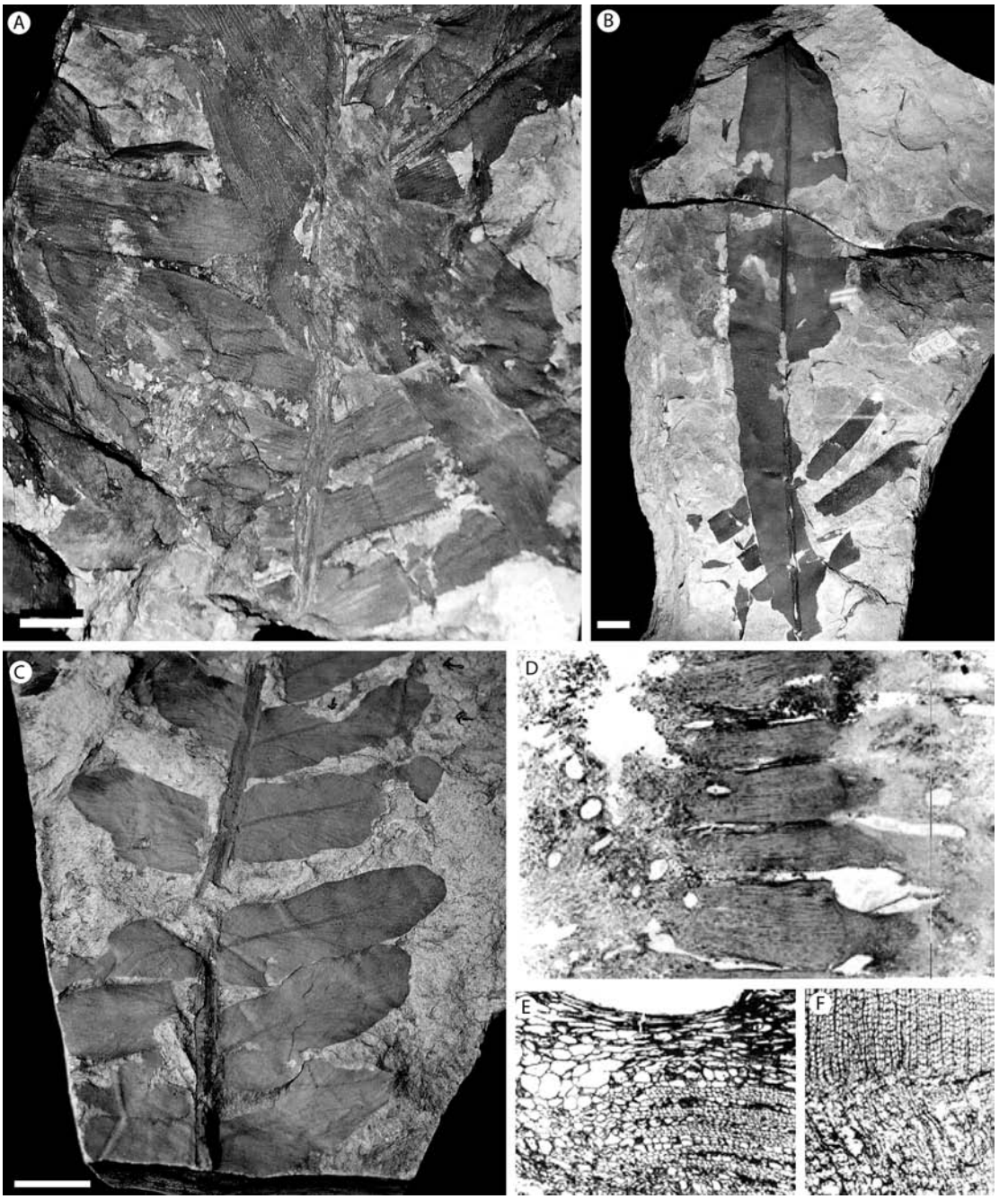
Triassic floras in Argentina are mainly recorded from the western Cuyo region (Uspallata, Sorocayense, and Rincón Blanco Groups) and the Patagonian region (Tronquimalal Group and Vera/Paso Flores Formations in northern Patagonia, and the El Tranquilo Group in southern Patagonia) (Fig. 9.1). These floras characterize a Southwest Gondwana phytogeographic province (Artabe et al. 2003). Here, Triassic deposits are interpreted as fluvial and lacustrine sedimentary facies with a highly diverse vegetation dominated by ferns and corystosperms, but including cycads and bennettitaleans that amount to approximately 25% of the species diversity (Artabe et al. 2007). This represents a pattern that apparently extended to most of the Western Gondwana supercontinent (Anderson and Anderson 1989).

Because the preservational mode of the Triassic cycadophytes in Argentina is comprised almost exclusively of leaf compressions and impressions, with the exception of one permineralized trunk (see below), their true botanical affinities are uncertain. As a result, the use of form genera, such as *Nilssonia* Brongniart, *Pseudoctenis* Seward, and *Ctenis* Lindley et Hutton for cycads, or *Anomozamites* Schimper and *Pterophyllum* Brongniart for bennettitaleans, is common (Artabe and Stevenson 1999; Artabe et al. 2001; Leppe and Moisan 2003). As a result of a lack of sufficient diagnostic characters, Gnaedinger (1999) and Herbst and Troncoso (2000) have suggested a more informal inclusion of these taxa into the "Cycadopsida."

The genus *Pseudoctenis* (Fig. 9.2A) is morphologically the most variable taxon, with approximately 15 species (Artabe et al. 2007), while *Ctenis* and *Nilssonia* have each two species. *Taeniopteris* Brongniart (Fig. 9.2B) is another form genus that occurs profusely in Triassic floras of Argentina as impressions of at least 15 morphospecies described as "Cycadophyta incertae sedis" (Artabe et al. 2007) or "Pteridophylla incertae sedis" (Gnaedinger and Herbst 1998, 2004).

The genus *Kurtziana* Frenguelli (Fig. 9.2C), known from Late Triassic beds in Argentina, Chile, South Africa, and Australia, is a bipinnate frond of possible cycadophyte affinity (Artabe et al. 1991; Spalletti et al. 1999), although Herbst and Gnaedinger (2002) have suggest a possible pteridosperm origin. *Yabeiella* Oishi is another form genus of cycadophytes, with five species in Argentina.

Fig. 9.2. Triassic cycadophytes from Argentina. (A) *Pseudoctenis spatulata* Du Toit. (B) *Taeniopteris vittata* Brongt. (C) *Kurtziana*



brandmayri Frenguelli. (D) *Michelilloa waltonii* Archangelsky et Brett; magnification, 10×. (E, F) *Michelilloa waltonii* Archangelsky et Brett, magnification, 20×. Scale bars (A–C) = 1 cm.

Possible bennettitaleans are only represented by the leaf impressions *Pterophyllum*, with four species, and *Anomozamites*, with two species (Bonetti 1968, 1972; Artabe et al. 2007).

Finally, it is interesting to note the occurrence of permineralized cycad trunks in the Triassic of northwestern Argentina. *Michelilloa waltonii* Archangelsky et Brett (1963) is a slender stem (up to 10 cm in diameter)

without persistent foliar bases or a well-developed periderm (Fig. 9.2D, E, F). It has a wide pith, a monoxylic vascular cylinder divided by leaf gaps into wedges, and a parenchymatous cortex. The genus also has masses of long filamentous hairs on its leaf bases, which is considered a typical cycad feature.

Jurassic

Jurassic cycadophytes in Argentina are apparently represented by only bennettitaleans because true cycads have remained unrecognized or have been doubtfully recorded. Compressions and impressions of reproductive and vegetative organs tentatively assigned to the bennettitaleans have been recovered mostly from Patagonia (Fig. 9.1). Interestingly, there is a great difference in diversity between the Early and the Middle–Late Jurassic record. In the former, the bennettitaleans have a relatively broad geographic distribution, whereas in Middle–Late Jurassic floras, they are highly reduced in both abundance and diversity.

Early Jurassic floras in Patagonia occur in terrestrial or shoreline sedimentary deposits. Here, the most commonly found plant organ is the leaf genus *Otozamites* Braun in Münster, with approximately 10 species, which led Herbst (1968) and Arrondo and Petriella (1980) to call them the classical representatives of Liassic floras in Argentina. In this regard, the following taxa were recognized by Herbst (1966a) from the Piedra Pintada Formation in northwest Patagonia: *O. ameghinoi* Kurtz, *O. barthianus* Kurtz, *O. bunburyanus* var. *major* Kurtz (Fig. 9.3A), *O. simonatoi* Orlando, and two species of *Ptilophyllum* Morris, *P. cutchense* Morris and *P. acutifolium* Morris.

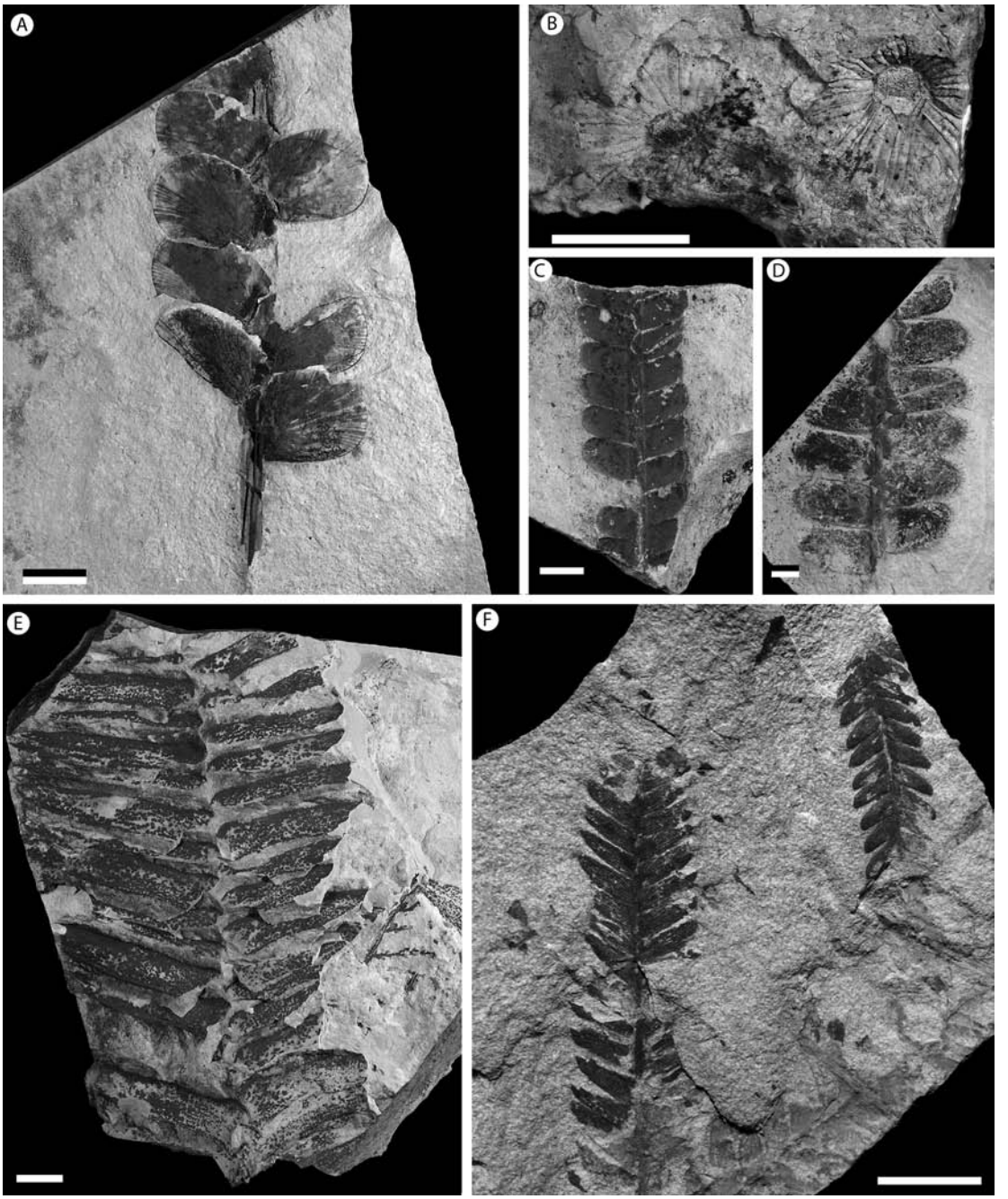
The bennettitalean seed cone *Williamsonia* cf. *gigas* (Bonetti 1964; Herbst and Anzotegui 1968) (Fig. 9.3B) was reported from the Early Jurassic Taquetrén locality in Chubut Province.

From the Nestares Formation in northwestern Patagonia, Arrondo and Petriella (1980) reported *O. albosaxatilis* Herbst, *O. ameghinoi*, *O. bechei* Brongniart, and *O. hislopii* (Oldham) Feist. A similar flora was recovered outside Patagonia from the El Freno Formation in Mendoza, which also included *Taeniopteris* sp., *Ptilophyllum acutifolium*, *Kurtziana brandmayri* Frenguelli, and *Williamsonia* sp. (Spalletti et al. 2007). From the nearby Los Patos Formation, Herbst (1980) described *Otozamites volkheimeri* Herbst.

The genus *Alicurana* Herbst et Gnaedinger (which formerly included some species of *Kurtziana;* Artabe et al. 1991) from the Early Jurassic Nestares Formation in northwestern Patagonia is a bipinnate frond with preserved epidermis that suggests a possible cycadalean affinity (Artabe et al. 1991; Herbst and Gnaedinger 2002).

From the Pampa de Agnia Formation in the central Patagonian Chubut province, Herbst (1966b) described *Otozamites albosaxatilis* (Fig. 9.3C), *O. hislopii*, *O.* cf. *oldhamii*, *O. chubutensis* Herbst (Fig. 9.3D), and *O. sueroi* Herbst. He noted the presence of *O. albosaxatilis* in the Roca Blanca Formation in southern Patagonia as well (Herbst 1965).

Fig. 9.3. Early Jurassic cycadophytes from Argentina. (A) *Otozamites*



Bonetti (1964) reported *Zamites* cf. *gigas* (Fig. 9.3E) and *Otozamites sanctae-crucis* (Feruglio) Archangelsky from the Early Jurassic Taquetrén flora. Herbst and Anzotegui (1968) suggested that the latter species should be assigned to *Zamites pusillus* Halle (Fig. 9.3F).

By the Middle–Late Jurassic, cycadophytes had nearly vanished from Argentina. The only genus noted from this time period is the bennettitalean form genus *Otozamites*, as represented by *O. sanctae-crucis* and

cf. *bunburyanus* De Zigno. (B) *Williamsonia* cf. *gigas* Lindley et Hutton (Carr.). (C) *O.* cf. *albosaxatilis* Herbst. (D) *Otozamites* cf. *chubutensis* Herbst. (E) *Zamites* cf. *gigas* Lindley et Hutton. (F) *Zamites pusillus* Halle. Scale bars = 1 cm.

Fig. 9.4. Early Cretaceous cycads from Argentina. (A) *Mesodescolea* cf. *obtusa* Archangelsky. Scale bar = 1 cm. (B) Cuticle of *Mesosingeria parva* Villar de Seoane. Scale bar = 50 µm. (C) *Pseudoctenis ornata* Archangelsky, Andreis, Archangelsky et Artabe. Scale bar = 1 cm. (D) *Ticoa lamellata* Archangelsky. Scale bar = 1 cm. (E) Stoma of *Ticoa lanceolata* Villar de Seoane. Scale bar = 20 µm. (F) Cuticle of *Ticoa lanceolata* Villar de Seoane. Scale bar = 50 µm.

Otozamites sp. (Baldoni 1977) from the Middle–Late Jurassic La Matilde Formation in southern Patagonia. Conversely, the species *O. traversoi* Baldoni, *O. linearis* Halle, *O. sanctae-crucis*, and *O. simonatoi* Orlando were reported from northwestern Patagonia (Baldoni 1978, 1981).

The genus *Ptilophyllum*, mentioned earlier in this chapter in association with Late Jurassic floras in Patagonia, probably does not truly occur here. *Ptilophyllum antarcticum* (Seward) Halle was reported from the Lago Argentino locality, thought to be of Late Jurassic age (Bonetti 1974). However, because the age of this flora was based on its close resemblance to the Hope Bay flora from Antarctica (Gee 1989), whose age has recently been reassigned to either the Early Jurassic (Rees and Cleal 2004) or the Middle Jurassic (Hunter 2005), the real presence of the genus in Late Jurassic floras of Argentina is therefore questionable.

In summary, it is definitely clear that, for some reason, the cycadophytes experienced a marked retraction in their range, diversity, and abundance during the Middle–Late Jurassic in Argentina. A good example is the genus *Otozamites*. Nonetheless, the group was able to recover during the Early Cretaceous.

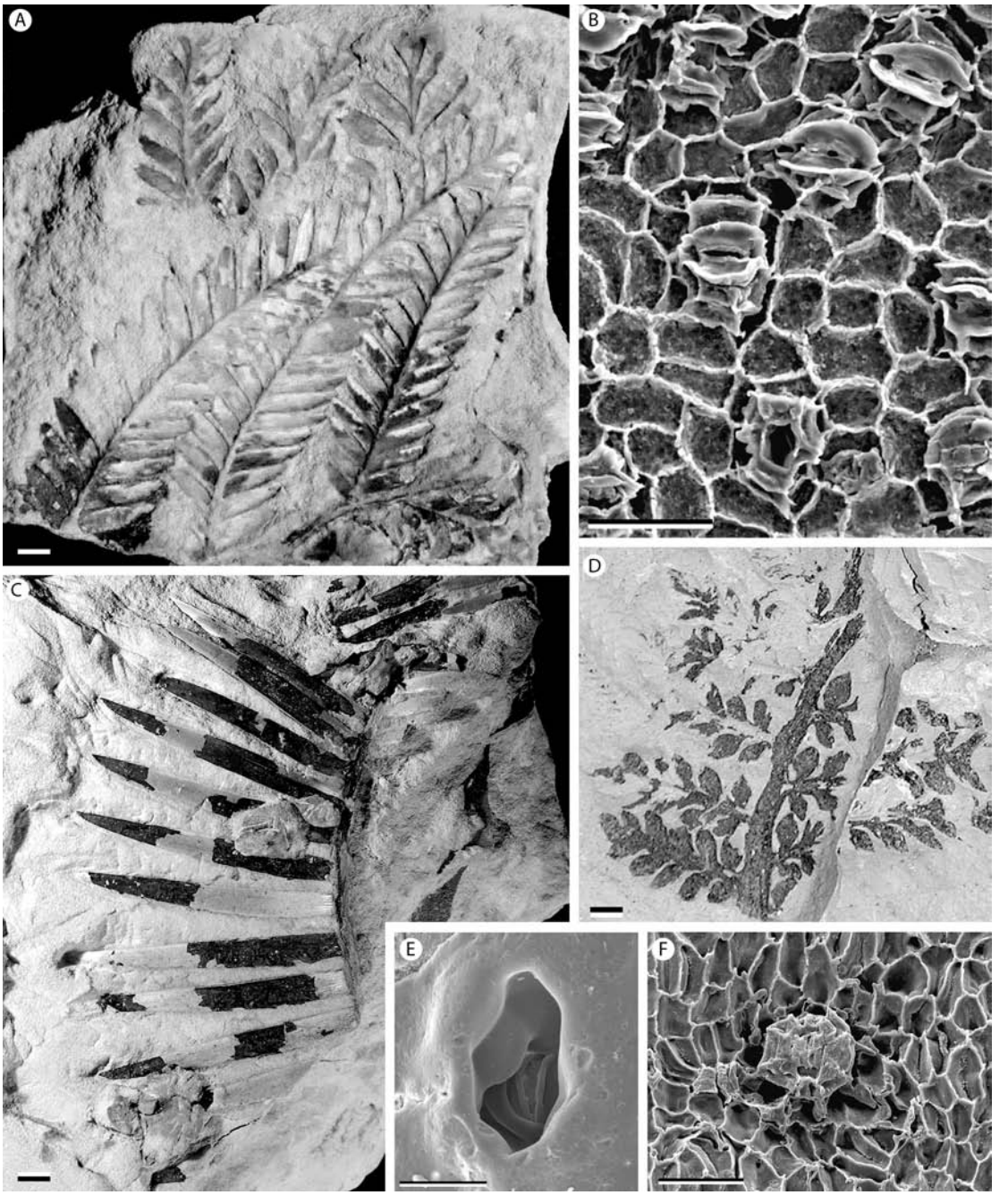
Cretaceous

Cretaceous cycads and bennettitaleans from Argentina are known only from Patagonia (Fig. 9.1). Two different floras can be envisaged: an Early Cretaceous flora in southern Patagonia, and a Late Cretaceous flora in northern Patagonia. These two floras have completely different preservational modes, as compressions with cuticle and impressions occur in the former and permineralizations in the latter.

Early Cretaceous Cycads and Bennettitaleans in Southern Patagonia

Both groups of cycadophytes have been consistently recovered from the Central Deseado Massif intracratonic basin and the marginal Austral/Magellanean basin (Fig. 9.1). The main record comes from the Barremian–Aptian Baqueró Group, which probably preserves the richest Early Cretaceous flora in the Southern Hemisphere. Cycads and bennettitaleans, along with conifers, represent the most diverse and abundant plant groups in these sediments. In many cases, even mummified cuticles and epidermal features have been found.

Cycads in the Baqueró Group have been assigned to five genera of pinnate leaves (Figs. 9.4, 9.5), i.e., *Almargemia* Florin, *Mesodescolea* Archangelsky (Fig. 9.4A), *Mesosingeria* Archangelsky (Fig. 9.4B), *Pseudoctenis* (Fig. 9.4C), and *Ticoa* Archangelsky (Fig. 9.4D), as well as to two genera with lanceolate and entire laminae, *Nilssonia* and *Sueria* Menéndez. These leaf genera share xeric traits such as trichomes on both leaf surfaces, sunken stomata protected by large or small episotomatal chambers (Fig. 9.4E), and thick cuticular membranes. Similar features are also observed in the microsporophyll cuticles of the cycad



pollen organ species *Androstrobus* Schimper (Archangelsky and Villar de Seoane 2004).

Pseudoctenis and *Ticoa* have the most ornamented epidermis, with *P. crassa* Archangelsky et Baldoni bearing the most varied types of trichomes. *Mesosingeria oblonga* Villar de Seoane has the deepest stomata, with epistomatal chambers up to 18 µm. *Almargemia incrassata* Archangelsky has monocyclic to imperfectly dicyclic abaxial stomata and sparse

Fig. 9.5. Early Cretaceous cycads and bennettitaleans from Argentina. (A) *Pseudoctenis giganteus* Archangelsky and *Ptilophyllum* sp. Scale bar = 10 cm. (B) *Williamsonia bulbiformis* Menéndez. Scale bar = 1 cm. (C) *Cycadolepis oblonga* Menéndez. Scale bar = 1 cm. (D) Stoma of *Otozamites ornatus* Villar de Seoane. Scale bar = 10 µm. (E) Cuticle of *O. ornatus.* Scale bar = 1 mm.

papillae on both leaf surfaces (Archangelsky 1966), while *Mesodescolea plicata* Archangelsky has monocyclic stomata and trichome bases on its abaxial epidermis (Archangelsky 1963a).

The endemic genus *Mesosingeria* contains seven species: *M. coriacea* Archangelsky, *M. herbstii* Archangelsky, *M. mucronata* Archangelsky, *M. obtusa* Archangelsky, *M. striata* Archangelsky, *M. parva* Villar de Seoane, and *M. oblonga* Villar de Seoane (Archangelsky 1963b; Villar de Seoane 1997, 2005). They differentiate from one another by their cuticular characters.

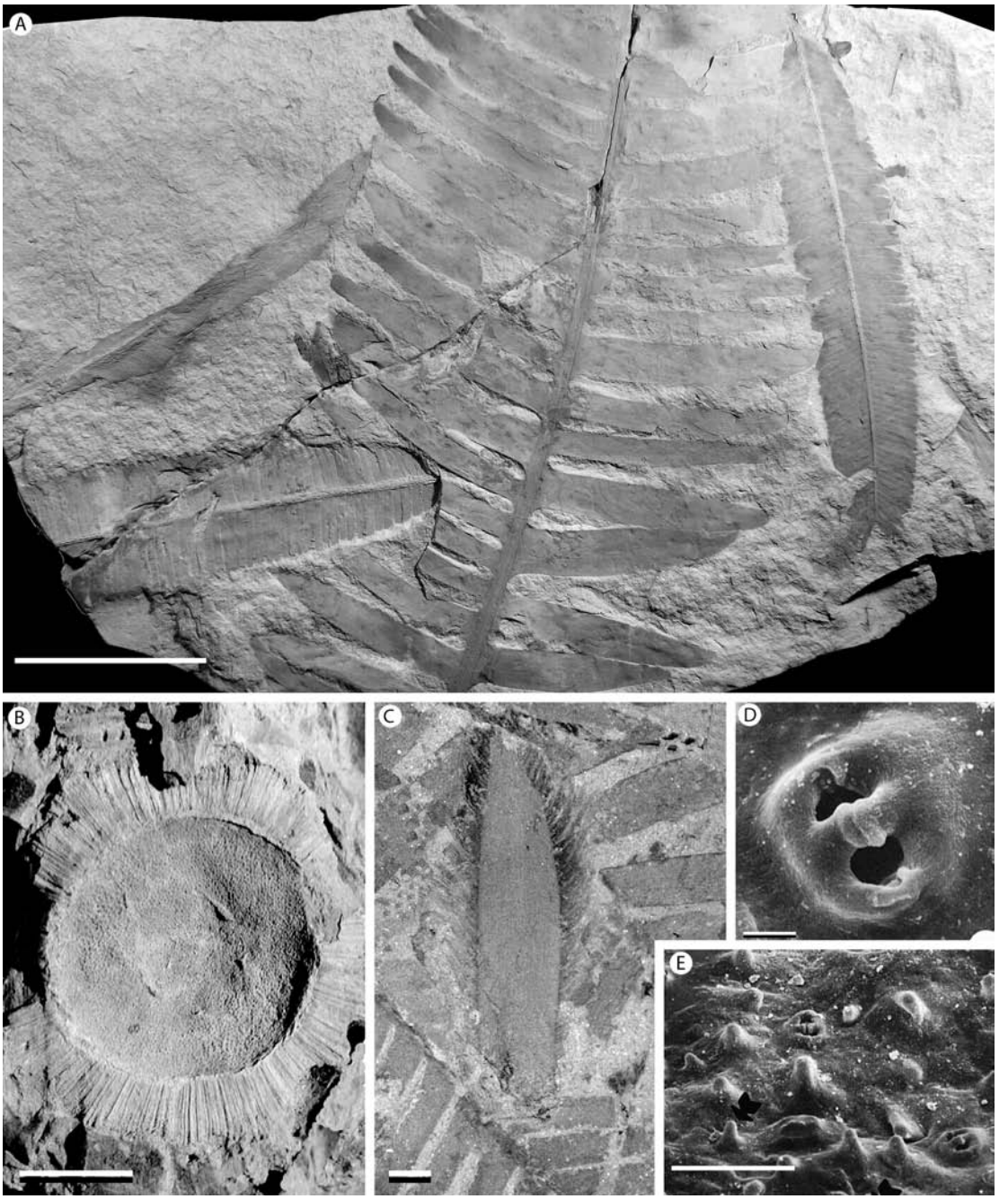
Mesodescolea is a leaf genus that compares with the living cycad *Stangeria* T. Moore in its cuticular features (Artabe and Archangelsky 1992)

Pseudoctenis is another common genus of pinnate leaves with three species defined by their epidermal features: *P. crassa*, *P. dentata* Archangelsky et Baldoni (Archangelsky and Baldoni 1972; Artabe 1994), and *P. ornata* A. Archangelsky, Andreis, S. Archangelsky et Artabe (Fig. 9.4C) (Archangelsky et al. 1995). *Pseudoctenis giganteus* A. Archangelsky (Fig. 9.5A) has been assigned to impressions of huge leaves (Archangelsky 1997), while *P. ensiformis* Halle is known from the Kachaike Formation (Longobucco et al. 1985).

Ticoa is another endemic genus with at least five species that are principally distinguished by cuticular characters, such as stomata distribution and density, and trichome types (Fig. 9.4E, F). *Ticoa harrisii* Archangelsky, *T. magnipinnulata* Archangelsky, *T. lamellata* Archangelsky, and *T. lanceolata* Archangelsky were described from the lower Baqueró Group (Archangelsky 1963a, 1966, 1976; Villar de Seoane 2005), while *T. magallanica* Archangelsky is known from the Springhill Formation, Austral basin.

Entire leaves of *Nilssonia and Sueria* were also described from the Baqueró Group. *Nilssonia clarkii* Berry is a large, coriaceous leaf (Berry 1924). *Sueria rectinervis* Menéndez has a cuticle with hairs and fewer adaxial stomata but more abundant abaxial ones (Menéndez 1965; Artabe 1994), while *Sueria elegans* Villar de Seoane has some hairs and abundant abaxial stomata (Villar de Seoane 1997). According to Hermsen et al. (2007), the presence of perforated external cells and accessory cell coronas in *Sueria* is unique to the Cycadales.

Ultrastructural studies of the cuticle of five of the seven genera of cycad leaves from the Early Cretaceous Baqueró flora show that the cutinized layer is the thickest part of the epidermal wall (Villar de Seoane 2005). This cuticle is divided into an outer layer without cellulose and an inner layer with cellulose and pectinaceous microchannels. Transmission electronic microscopic studies have shown the following similarities: *Mesodescolea*, *Mesosingeria*, and *Ticoa* have a granulate outer layer, whereas in *Pseudoctenis* it is lamellate and in *Sueria* compact. *Mesosingeria*, *Sueria*, and *Ticoa* have an alveolate inner layer, whereas it is granulate in *Mesodescolea* and *Pseudoctenis*. Interestingly, the layers differ in thickness, with *Sueria elegans* having the thinnest cuticular membrane (2.5 µm) and *Mesosingeria oblonga* the thickest (13.5 µm).



Three different species of *Androstrobus* (cycad microsporophylls with in situ pollen grains) were described from the Anfiteatro de Ticó Formation of the Lower Baqueró Group (Archangelsky and Villar de Seoane 2004). These microsporophylls are rhomboidal and distally truncate, with a thick cuticle in which the typical (actinocytic) stomatal apparatus are embedded. Microsporangia bear pollen masses stuck to their internal walls. *Androstrobus munku* Archangelsky et Villar de Seoane

has monocolpate pollen, which is ellipsoidal to fusiform in polar view, 39 µm long and 28 µm wide, and possesses a smooth to scabrate exine. *Androstrobus patagonicus* Archangelsky et Villar de Seoane has monocolpate pollen grains, which are 34 µm long and 28 µm wide, are circular to subcircular in polar view, and have a smooth exine with a basal laminated layer, an alveolate ectexine, and abundant orbicules. *Androstrobus rayen* Archangelsky et Villar de Seoane has monocolpate pollen, which is ellipsoidal to circular in outline in polar view, 25 µm long and 20 µm wide, and has a scabrate exine, an alveolate–tectate ectexine, and abundant orbicules.

Bennettitaleans in the Early Cretaceous of Argentina are represented by five leaf genera (*Dictyozamites* Medlicott et Blanford, *Otozamites*, *Pterophyllum*, *Ptilophyllum* [Fig. 9.5A], and *Zamites* Brongniart), one genus of scale leaves (*Cycadolepis* Saporta), and one genus of seed cones (*Williamsonia* Carruthers, Fig. 9.5B, C), all of which are recorded from both the Baqueró Group, and the Springhill and Kachaike formations.

There is a large variety of leaf species within each genus that are mostly differentiated from one another by the size of their pinnae, the different protection structures associated with their sunken stomata, and the trichome and papillae types present on their abaxial epidermis (Fig. 9.5D, E). They have in common a falcate shape to their pinnae and paracytic stomata on the leaf epidermis.

Dictyozamites is the only genus with reticulate venation. On the basis of cuticular features, four species were described: *D. areolatus* Archangelsky et Baldoni, *D. crassinervis* Menéndez, *D. latifolius* Menéndez, and *D. minusculus* Menéndez (Archangelsky and Baldoni 1972; Menéndez 1966).

Otozamites is the most diverse leaf genus with seven species: *O. archangelskyi* Baldoni et Taylor (1983), *O. grandis* Menéndez, *O. patagonicus* Villar de Seoane (1995), *O. parvus* Villar de Seoane (2001), *O. parviauriculata* Menéndez (1966), *O. ornatus* Villar de Seoane (1999), and *O. waltonii* Archangelsky et Baldoni (1972). *Pterophyllum* is only represented by two species, *P. trichomatosum* (Archangelsky and Baldoni 1972) and *Pterophyllum* sp. (Menéndez 1966).

Ptilophyllum is represented by two impressions—*Ptilophyllum antarcticum* and *P. hislopii* (Oldham) Seward (Menéndez 1966) (Fig. 9.5A)—and four compressions—*P. longipinnatum* Menéndez (1966), *P. valvatum* Villar de Seoane (1995), *P. angustus* Baldoni et Taylor (1983), *P. ghiense* Baldoni (1977), and *P. acutifolium* (cf. Passalia 2007). *Zamites*, on the other hand, is another genus scarcely represented with only two species: *Z. decurrens* Menéndez (1966) and *Z. grandis* Archangelsky et Baldoni (1972).

Reproductive structures have been referred to two species of *Williamsonia*, *W. bulbiformis* Menéndez (Fig. 9.5B) and *W. umbonata* Menéndez (1966), and several species of *Cycadolepis* (Menéndez 1966; Baldoni 1974) (Fig. 9.5C).

Ultrastructurally, a cuticle proper, an outer layer, and an inner layer with microchannels or pathways form the external epidermal wall of bennettitalean organs, except the receptacle of *Williamsonia*. On this basis, three different groups of taxa can be delineated. The first group contains *Dictyozamites*, *Otozamites*, and *Zamites* with an outer lamellate layer, and an inner reticulate layer only in the case of *Dictyozamites*. The second contains *Otozamites* and *Zamites* with an inner alveolate layer. The third contains *Ptilophyllum* and *Pterophyllum* with an inner lamellate–reticulate layer, the former having an outer alveolate layer and the latter an outer reticulate one. The receptacle of *Williamsonia* has a cuticular membrane with a fibrous aspect, while its bracts have an outer reticulate layer and an inner lamellate layer, which is similar to *Cycadolepis* (Villar de Seoane 2003).

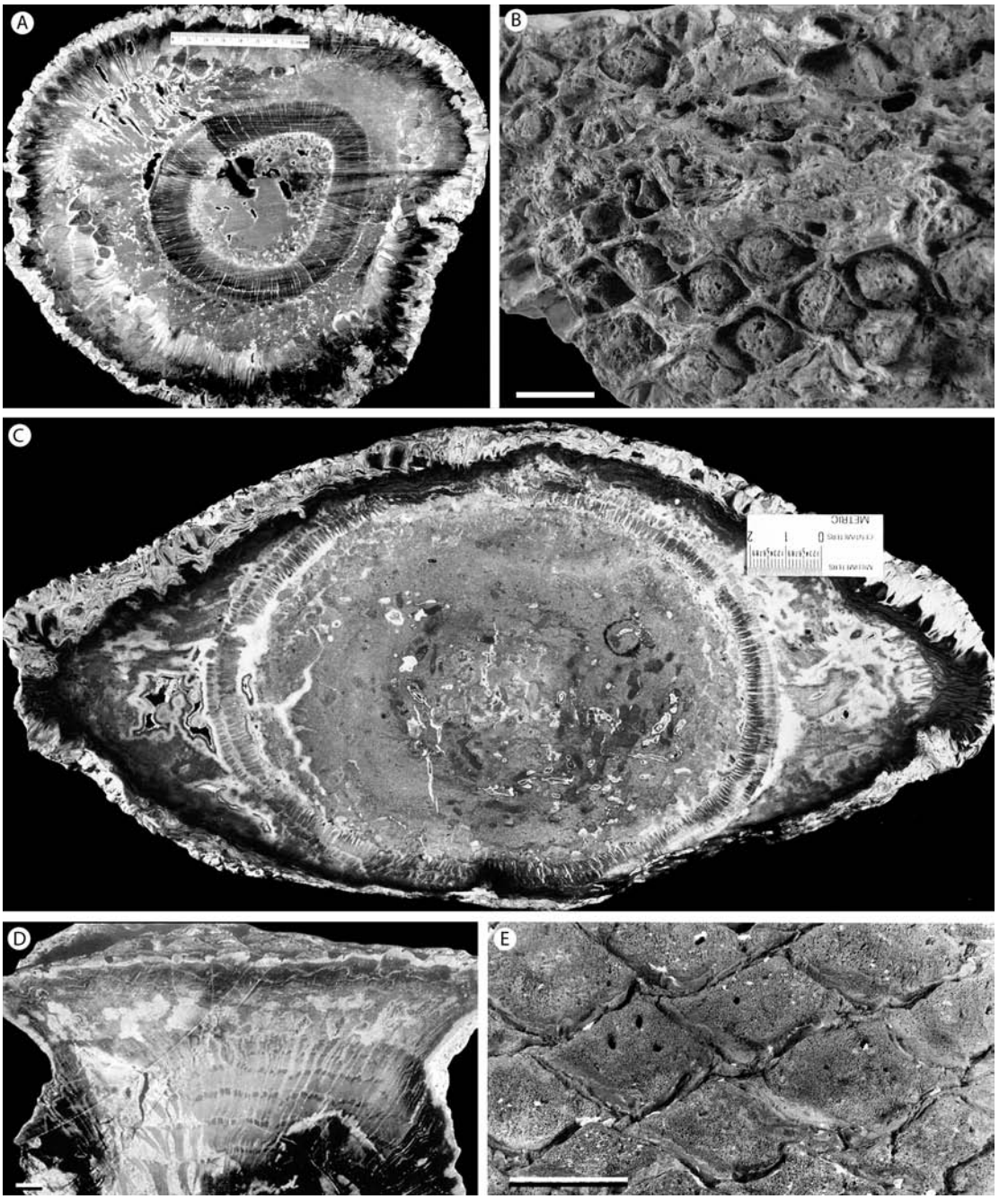
The Late Cretaceous to Earliest Paleogene Record

During this time span, cycads are the only cycadophytes in Argentina and are represented by 5 of the 14 genera of permineralized cycad stems known worldwide at this time. They are *Chamberlainia* Artabe, Zamuner et Stevenson, *Worsdellia* Artabe, Zamuner et Stevenson, and *Brunoa* Artabe, Zamuner et Stevenson from the Late Cretaceous (Artabe et al. 2004, 2005), *Bororoa* Petriella (1972, 1978) from the latest Cretaceous (?)–Paleocene, and *Menucoa* Petriella (1969) from the Paleocene, all recovered from northern Patagonia (Allen and Bororo Formations) (Artabe et al. 2004, 2005).

Chamberlainia pteridospermoidea Artabe, Zamuner et Stevenson (Fig. 9.6A, B) is another multilacunar polyxylic (centripetal/centrifugal) stem, which is covered by persistent rhomboidal foliar bases and smaller cataphylls in cycles. The central parenchymatous pith contains idioblasts, mucilage canals, and arcs of medullary vascular bundles. It has a vascular system with three rings of centrifugal secondary xylem and phloem, endarch or mesarch primary xylem, and centripetal secondary bundles. The parenchymatous cortex possesses extrafascicular concentric bundles. A few bulbils are present along the stem.

Worsdellia bonettii Artabe, Zamuner et Stevenson (Fig. 9.6C) is also a multilacunar polyxylic stem covered by alternating cycles of cataphylls and persistent rhomboidal bases of small dimensions. The parenchymatous pith is wide and contains mucilage canals and peripheral medullary bundles. It has a manoxylic vascular cylinder with two concentric rings of centrifugal secondary xylem and phloem and centripetal vascular bundles (inverted) with respect to the inner ring. The leaf traces run irregularly and produce a girdling configuration, while the parenchymatous cortex has extrafascicular concentric bundles.

Brunoa santarrosensis Artabe, Zamuner et Stevenson (Fig. 9.6D, E) is a multilacunar polyxylic stem covered by cataphylls and persistent rhomboidal foliar bases in alternating cycles. It has mucilage cavities in



its parenchymatous cortex and medullary vascular bundles that form rings related to cone domes. The wood parenchyma in *B. santarrosensis* is scanty outside cortical steles. The leaf traces run irregularly and produce a girdling configuration. Its vascular cylinder is composed of six rings of collateral vascular bundles with phloem toward the outside and divided into fanlike sectors by multiseriate, parenchymatous rays.

Bororoa (Fig. 9.7A–C) was originally established by Petriella (1972), who described two species, *B. anzulovichii* and *B. andreisii*. The generic concept of *Bororoa* refers to a polyxylic stem with a persistent armor of leaf bases. The parenchymatous pith has medullary vascular bundles forming rings related to cone domes and mucilage channels. Wide primary rays divide these vascular rings. The tracheids of its secondary xylem have alternate, multiseriate, and areolate pittings. The parenchymatous cortex is differentiated into an inner zone with leaf traces running obliquely and an outer zone with girdling traces. *Bororoa anzulovichii* differs from *B. andreisii* in its larger stem diameter, the presence of stone cells in the pith, uniseriate secondary rays, and a cortex without periderm layers. *B. anzulovichii* also has leaf bases lacking periderm layers and but containing hypodermic fibers.

The monospecific genus *Menucoa* (*M. cazaui* Petriella) was erected by Petriella (1969) for polyxylic stems with a persistent armor of leaf bases (Fig. 9.7D). The parenchymatous pith in this stem has collateral bundles and mucilage channels, while wide primary rays divide vascular rings. The parenchymatous cortex has mucilage ducts and collateral traces running obliquely in the inner zone and showing girdling in the outer one. The leaf bases in this genus have several collateral bundles arranged in no apparent order.

Fig. 9.6. Late Cretaceous cycads from Argentina. (A, B) *Chamberlainia pteridospermoidea* Artabe, Zamuner et Stevenson. (c) *Worsdellia bonettii* Artabe, Zamuner et Stevenson. (D, E) *Brunoa santarrosensis* Artabe, Zamuner et Stevenson. Scale bars (A) = 8 cm, (B, D, E) = 1 cm, (C) = 2 cm.

Discussion

Taxonomic and Phylogenetic Considerations

Cycads and bennettitaleans, as well as pteridosperms, have traditionally been placed into the informal taxon of the "cycadophytes" (Taylor et al. 2009), which clearly represents a paraphyletic group within the spermatophyte clade (Crane 1985; Doyle and Donoghue 1992; Rothwell and Serbet 1994). However, the phylogenetic position of each group is not well defined, especially that of the fossil order Bennettitales.

Living cycads consist of 10 to 12 genera and almost 300 species that have been treated differently in various classification systems (Stevenson 1981, 1990, 1992; Jones 2002). Depending on the author, modern cycads can be grouped into three or five families. The most commonly accepted classification (Stevenson 1992) recognizes the suborder Cycadineae with the family Cycadaceae (*Cycas*), and the suborder Zamiineae with the families Stangeriaceae (*Stangeria*, *Bowenia*) and Zamiaceae (*Dioon*, *Encephalartos*, *Macrozamia*, *Lepidozamia*, *Ceratozamia*, *Microcycas*, *Zamia*, and *Chigua*). The monophyletic character of these families is supported by both morphological (Crane 1988; Stevenson 1990; Brenner et al. 2003; Hermsen et al. 2006) and molecular phylogenetic analyses (Rai et al. 2003). However, among the latter, the monophyly of the Stangeriaceae and Zamiaceae has been questioned (Rai et al. 2003; Chaw et al. 2005).

Cycads show a unique combination of plesiomorphic and apomorphic characters (Brenner et al. 2003) and have been interpreted as the

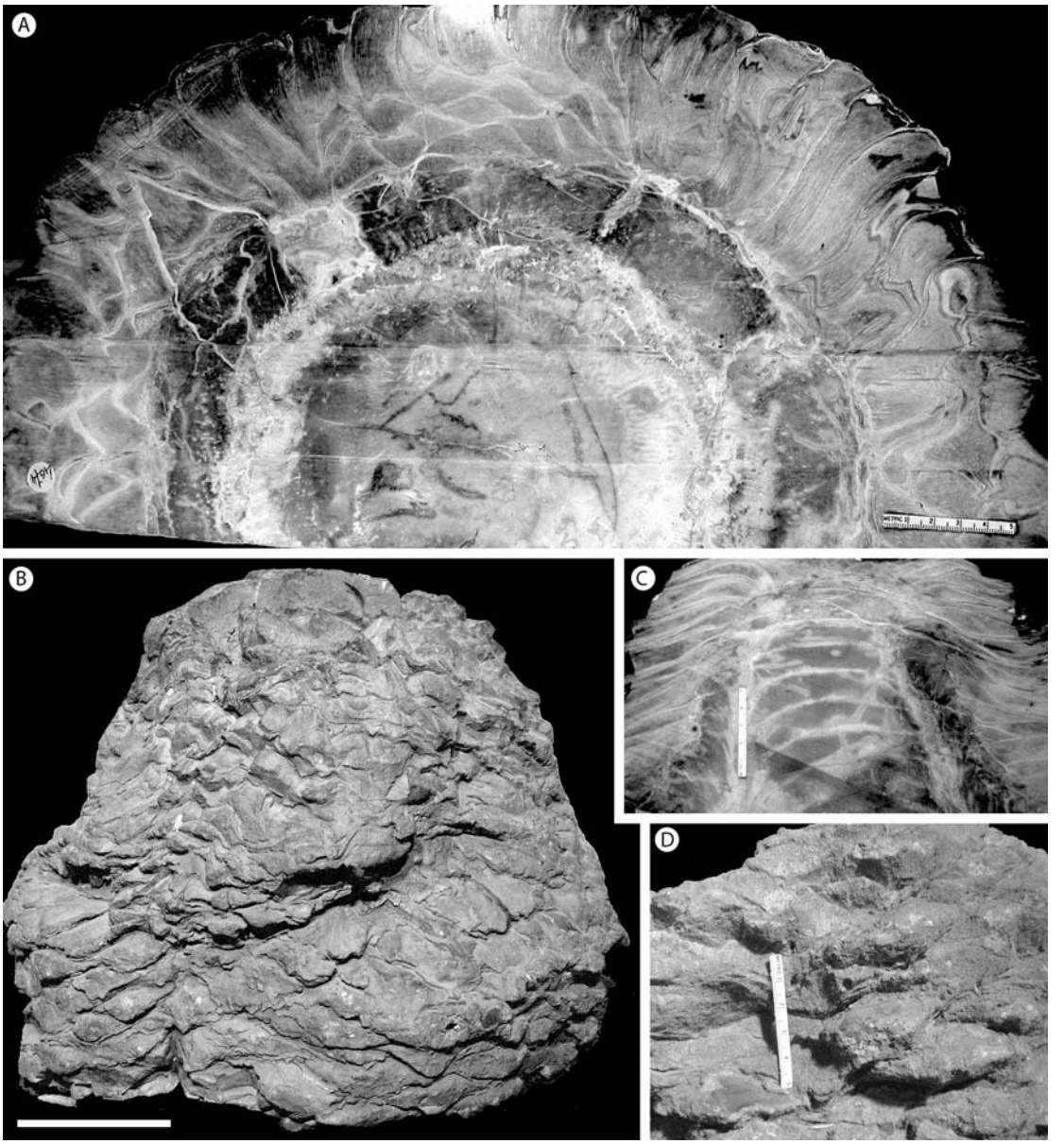


Fig. 9.7. Paleocene cycads from Argentina. (A–C) *Boroa anzulovichii* Petriella. (D) *Menucoa cazaui* Petriella. Scale bars (A, C, D) = 5 cm, (B) = 10 cm.

group basal to the remaining modern gymnosperms (Ginkgoales, Coniferales, and Gnetales). This means they are sister to all living seed plants (Crane 1988; Stevenson 1990; Chaw et al. 2000), or sister to *Ginkgo* (Chaw et al. 1997). However, when fossils—the ancient remains of once-living plants—are included, new relationships must be considered. For instance, it has long been known that the cycads and seed ferns are related to one another (Worsdell 1906; Delevoryas 1955; Stewart and Rothwell 1993), and some studies postulate that Paleozoic medullosas can either be included in the same clade (Crane 1985) or are basal to the cycads (Rothwell and Serbet 1994). Furthermore, Doyle (1996) and Bateman et al. (2006) simply count the cycads as part of a pteridosperm clade.

In order to define phylogenetic relationships among the cycads, several cladistic analyses have been performed with living genera (Stevenson 1990; De Laubenfeld 1999; Chaw et al. 2005) or with both living and fossil genera (Brenner et al. 2003; Hermsen et al. 2006). The latter included morphological and anatomical characters that allowed for the inclusion of fossil morphotaxa of vegetative organs. Taxa such as the stems of *Michelilloa* (Triassic), *Menucoa* (Paleocene), and *Bororoa* (Cretaceous?–Paleocene) and the leaves of *Kurtziana* (Triassic–Early Jurassic), *Mesodescolea*, *Ticoa*, *Ctenis*, *Almargemia*, and *Sueria* (Early Cretaceous) were run in the analyses as representative cycads from Argentina. As a result *Mesodescolea* (formerly assigned to Stangeriaceae; Archangelsky and Petriella 1971), *Sueria*, and *Ctenis* occupy positions clearly basal to the Stangeriaceae. On the other hand, Triassic–Early Jurassic *Kurtziana* (*Alicurana*) and Early Cretaceous *Ticoa* are both basal to a clade that includes all extant Zamiaceae and related fossil genera. This is supported by synapomorphies related to epidermal characters such as wall thickness and occurrences of perforations in the epidermal cell walls. *Almargemia*, in turn, is basal to the extant subfamily Zamiodeae (sensu Stevenson 1992), a position that is supported by cuticular characters as well.

For this study, we have run a new cladistic analysis incorporating the genera *Brunoa*, *Chamberlainia*, and *Worsdellia* that were not included in the original matrixes (Tables 9.1, 9.2). Cladistic analysis of the resulting matrix (69 characters and 35 taxa) was performed by TNT (Goloboff et al. 2009); characters were treated as nonordered following Hermsen et al. (2006). A heuristic search (1000 replicates starting from a random Wagner tree followed by tree bisection and reconnection, or TBR) was conducted under equal weights. A single most parsimonious tree of 155 steps was obtained (Fig. 9.8) without changing the topologies initially obtained by Brenner et al. (2003) and Hermsen et al. (2006).

As expected from their morphological features, the Triassic genera *Michelilloa* and *Antarcticycas* occur outside the clade, with *Michelilloa* representing the basal form of the clade that includes all extant and fossil cycads. This position is supported by two synapomorphies, the presence of multilacunar nodes and girdling leaf traces, both of which are considered a prerequisite for the order Cycadales (Loconte and Stevenson 1990). On the other hand, *Brunoa*, *Worsdellia*, and *Chamberlainia* sort out into the clade that represents the family Zamiaceae. The last two genera occupy a position basal to the clade exclusively conformed by the extant genera of the Encephalartoideae tribe (*Lepidozamia*, *Macrozamia*, and *Encephalartos*); this position is mainly supported by the presence of cortical steles. On the other hand, *Brunoa* occurs as sister to *Fascisvarioxylon* in a clade placed sister to the group conformed by *Chamberlainia*, *Worsdellia*, and the extant tribe Encephalartoideae. Finally, the Cretaceous–Paleogene genera *Menucoa* and *Bororoa* form a trichotomy together with the clade involving the Encephalartoideae tribe and the fossil genera *Brunoa*, *Chamberlainia*, *Worsdellia*, and *Fascisvarioxylon*. On the basis of their phylogenetic position, all these taxa

Table 9.1. List of Characters and States Used for the Cladistic Analysis

Source. From Hermsen et al. (2006).

Character	State
0 Coralloid roots	0, absent; 1, present
1 Root buds	0, absent; 1, present
2 Primary thickening meristem	0, internal derivatives; 1, external derivatives
3 Cone domes	0, absent; 1, present
4 Medullary bundles	0, absent; 1, present
5 Cortical steles	0, absent; 1, present
6 Secondary polyxyly	0, monoxylic; 1, polyxylic
7 Wood parenchyma	0, abundant; 1, scanty
8 Nodal anatomy	0, unilacunar; 1, multilacunar
9 Axillary buds	0, absent; 1, present
10 Leaf traces	0, radial; 1, girdling
11 Petiole bundle pattern	0, C-shaped; 1, omega; 2, obscure omega
12 Prickles	0, absent; 1, present
13 Petiole spines	0, absent; 1, transitional; 2, abrupt
14 Leaf base	0, vascularized stipules; 1, vestigial stipules; 2, estipulate
15 Ptyxis	0, circinate; 1, noncircinate
16 Pinna ptyxis	0, circinate; 1, adplicate; 2, conduplicate; 3, involute
17 Acroscopic basal callus	0, absent; 1, present
18 Pinna traces	0, two or more; 1, one
19 Trichomes	0, colored; 1, transparent
20 Curved trichomes	0, absent; 1, present
21 Equally branched trichomes	0, absent; 1, present
22 Cataphylls	0, absent; 1, present; 2, irregular
23 Peduncular cataphylls	0, absent; 1, present
24 Sporophyll pubescence	0, present; 1, absent
25 Sporophyll vasculature	0, planar; 1, three-dimensional; 2, *Macrozamia* type
26 Megasporophyll	0, absent; 1, pinnatifid; 2, simple
27 Megasporophyll spines	0, absent; 1, single; 2, two
28 Megasporophyll lobing	0, absent; 1, lateral
29 Megasporophyll shape	0, flat; 1, peltate; 2, adaxially thickened
30 Megasporophyll skirt	0, absent; 1, above; 2, below
31 Ovule position	0, lateral; 1, below; 2, above; 3, terminal
32 Ovule number	0, more than two; 1, two
33 Ovule vasculature	0, simple; 1, medullosan; 2, cycadean
34 Integument vasculature	0, single; 1, double
35 Micropyle	0, distal; 1, proximal
36 Endospermic jacket	0, absent; 1, present
37 Buffer cells	0, absent; 1, present
38 Seed	0, absent; 1, radiospermic; 2, platyspermic
39 Coronula	0, absent; 1, distinct; 2, indistinct
40 Cotyledon bundle	0, collateral; 1, concentric
41 Pollen shape	0, oblong; 1, elliptic
42 Proximal shape	0, convex; 1, concave
43 Pollen exine	0, psilate; 1, fossulate; 2, foveolate
44 Sperm number	0, many; 1, 4–8; 2, 2
45 Leaf bases	0, persistent; 1, ephemeral

Character	State
46 Inverse polyxyly	0, absent; 1, continuous ring; 2, random
47 Mucilage	0, canals; 1, absent; 2, cavities
48 Accessory cell corona	0, absent; 1, present
49 Guard cell corona	0, absent; 1, present
50 Number of accessory cell layers	0, zero; 1, one; 2, two; 3, more than two
51 Overarching accessory cells	0, absent; 1, present
52 Epidermal cells	0, without perforations; 1, with perforations; 2, corners only
53 Anticlinal pegs	0, absent; 1, present
54 Cuticular lamellae	0, absent; 1, present
55 Stomate position	0, hypostomatic; 1, amphistomatic
56 Epidermal cells	0, thin walled; 1, thick and thin walled
57 Lamina position	0, lateral; 1, adaxial
58 Leaves	0, bipinnate; 1, pinnate; 2, simple
59 Terminal pinna	0, all stages; 1, seedlings; 2, absent
60 Pinna attachment	0, decurrent; 1, articulate
61 Midrib	0, *Marattia* type; 1, absent; 2, *Cycas* type; 3, *Chigua* type
62 Veins	0, free; 1, anastomosing
63 Stomates	0, flush; 1, sunken
64 Guard cell orientation	0, irregular; 1, longitudinal
65 Stomatal shape	0, oblong; 1, circular
66 Stomatal type	0, haplocheilic; 1, syndetocheilic
67 Microsporangia	0, absent; 1, free; 2, clustered with some fused; 3, clustered with all fused
68 Pollen wall	0, spongy; 1, alveolar

could be considered as fossil form genera that could pertain to the tribe Encephalartoideae. Even though our cladogram shows a high degree of resolution, the phylogenetic hypotheses show low support values (e.g., all the nodes show Bremmer support values of 1), which suggests that if additional data (characters and taxa) were to be added, they could lead to changes in the postulated relationships.

The extinct bennettitaleans have previously been placed within the "anthophyte" clade (Crane 1985; Doyle and Donoghue 1992; Rothwell and Serbet 1994; Doyle 1996), which also includes flowering plants and the gnetophytes. However, some molecular studies reject the existence of an "anthophyte" clade and postulate that the Gnetales are more closely related to the conifers than to the angiosperms (Chaw et al. 1997). It is clear that relationships among extant seed plants (i.e., *Ginkgo*, conifers, cycads, gnetophytes, and angiosperms) do not yet show a consensus. This could be explained by many reasons, such as the clash between morphological and molecular studies, or the alternative homology hypothesis for certain morphological structures. In addition, extant seed plants represent just a small portion of the complete diversity of this clade, and the inclusion of new fossil information could readily change the relationships among major groups of seed plants (Donoghue et al. 1989).

Table 9.2. Full Coding for *Brunoa, Worsdellia,* and *Chamberlania*

Brunoa
???110111?1???????????1??????????????????????012??????????? ??????????
Worsdellia
???011101?1???????????1??????????????????????010??????????? ??????????
Chamberlainia
???011101?1???????????1??????????????????????010??????????? ??????????

Bennettitaleans are widely accepted as a monophyletic group, which is supported by synapomorphies such as the cutinization of the guard cells, bivalvate synangia, interseminal scales, and numerous ovules (Crane 1985). Although internal relationships within the Bennettitales have not yet been resolved, two families are traditionally recognized, the Williamsoniaceae and the Cycadeoidaceae (see Watson and Sincock 1992; Taylor et al. 2009). However, these families are contradicted in the morphological phylogenetic analysis conducted by Crane (1985), although some pivotal taxa (especially from the Triassic) were not included in Crane's analysis. The current fossil record in Argentina indicates that only the Williamsoniaceae was ever present.

In summary, the internal relationships within the Bennettitales and phylogenetic position of this order within the context of the seed plants remain controversial (see also Crepet and Stevenson 2010; Rothwell and Stockey 2010). Nonetheless, it is clear that a more refined character discussion, the reconstruction of "whole plants," and their inclusion in broader phylogenetic studies could lead to the better understanding of the evolution of this particular group. Unfortunately, the bennettitalean record in Argentina does not contribute much to this matter because only compressions and impressions of reproductive organs have been preserved, and only few of these, such as the diverse bracts of *Cycadolepis*, have retained cuticular characters. Thus, it would be valuable to undertake more detailed study of the structure and ultrastructure of extremely well-preserved cutinized material to gain additional morphological characters useful for a better understanding of the phylogenetic relationships of Argentinian bennettitaleans.

Bio and Chronostratigraphic Aspects

Both cycads and bennettitaleans from Argentina have been used successfully for biostratigraphic and chronostratigraphic purposes. Stipanicic (2002) suggested that Triassic cycadophytes in Argentina include some morphospecies that show variable stratigraphic ranges; some are restricted to the Triassic (in particular Neotriassic species of *Pseudoctenis* and *Taeniopteris*), while others have longer time ranges that reach the Jurassic. This is the case for the species of *Anomozamites* and *Ctenis* and for some

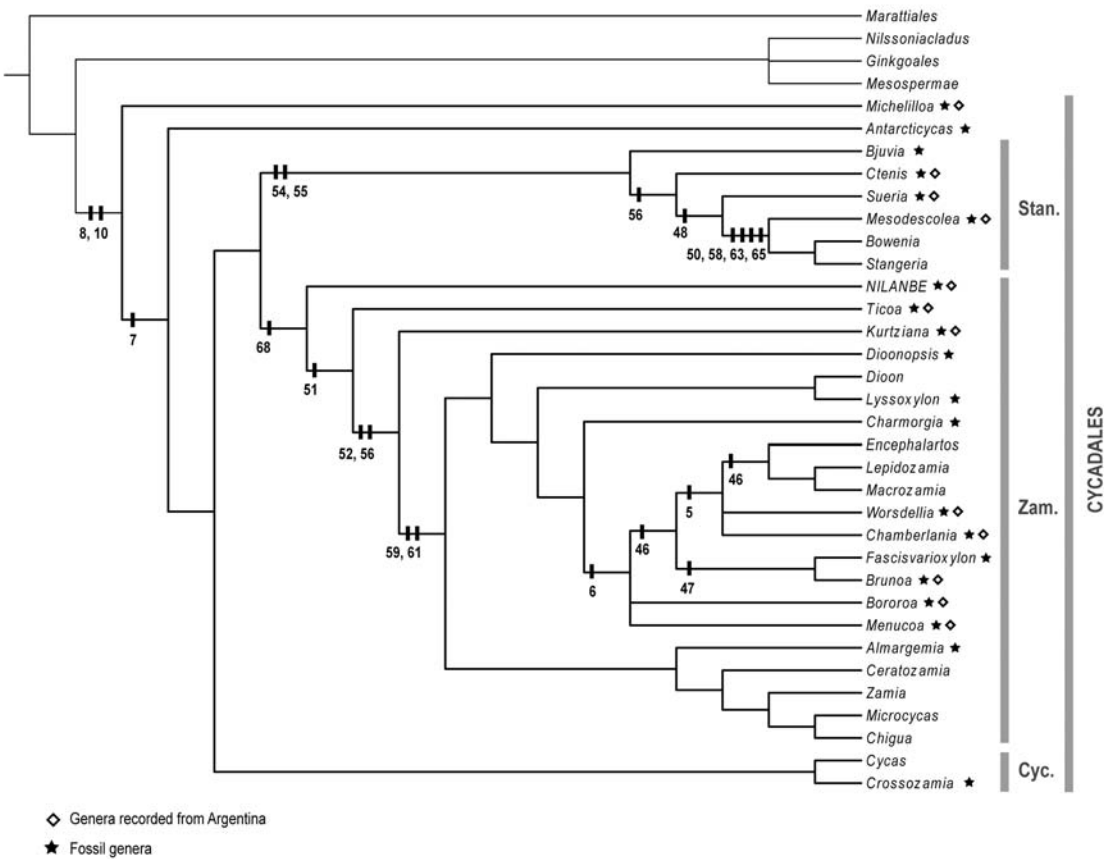


Fig. 9.8. Most parsimonious tree obtained in the cladistic analysis by TNT, based on the morphological matrix of Brenner et al. (2003) and Hermsen et al. (2006). *Brunoa, Worsdellia,* and *Chamberlainia* are included for the first time. Cyc = Cycadaceae; Zam = Zamiaceae; Stan = Stangeriaceae.

species of *Pseudoctenis*, *Nilssonia*, and *Taeniopteris*. In their bio- and chronostratigraphic characterization of the Argentinian Triassic, Spalletti et al. (1999) do not consider cycadophytes as time markers, with the exception of a few species of the possible cycadophyte genera *Yabeiella* and *Kurtziana*.

During the Jurassic, several species of the bennettitalean genus *Otozamites* are typical of the Early Jurassic plant assemblages from a biochronostratigraphic perspective ("the *Otozamites* flora"), but not much can be said for the Middle–Late Jurassic.

A different situation occurs in the Early Cretaceous, a time when both cycads and bennettitaleans become major components of the vegetation in Patagonia, reversing the strangely absent role that they played during most of the Jurassic. Archangelsky (2003), for example, was able to define a *Ptilophyllum* biozone on the basis of the presence of highly diversified bennettitaleans and cycads in the Deseado Massif of southern Patagonia. Interestingly, bennettitaleans disappear in the younger *Gleichenites* biozone and only the cycads remain. Thus, the Bennettitales become completely extinct by the beginning of the Late Cretaceous, while cycads, although diminished, remain until the early Paleogene, after which they finally disappear from the Patagonian region. Nevertheless, it is quite possible that the cycads in particular could have persisted

in the northern part of the Argentinian territory until later in the Paleogene or early Neogene, at which point they definitely abandoned their midlatitudinal distribution in this part of South America.

Paleoecological and Paleoclimatic Implications

Middle–Late Triassic plant communities in Argentina have been extensively analyzed by Artabe et al. (2001), who showed that cycadophytes were likely minor components. In these floras, cycadophytes are interpreted as shrubby plants that, along with the peltasperms, were part of the understory vegetation in various forest types (evergreen, deciduous, or sclerophyllous) dominated by corystosperms, or occupied open areas as shrubs. These types of vegetation grew on the alluvial plains with lakes and rivers under subtropical, but seasonal, climatic conditions that were apparently more humid during the Middle and early Late Triassic than in the latest Triassic.

By the Jurassic, plant communities in this region were represented by extensive conifer forests mainly dominated by the Araucariaceae and Cupressaceae (Archangelsky and Del Fueyo 2010), which occupied terrestrial or littoral settings with constant volcanic activity. There, the bennettitaleans and the ferns seem to have represented the understory vegetation, particularly during the Early Jurassic, when they were probably favored by warm and humid climatic conditions. During the Middle–Late Jurassic, the role of the cycadophytes in the local plant communities became restricted, apparently as a result of some kind of paleoclimatic control (displacement of arid belts, for instance; Rees et al. 2000). This sort of gap in southern South America is in stark contrast to coeval floras in the rest of the world, which show a climax in the role of cycadophytes in terrestrial plant communities.

Later, during the Early Cretaceous, cycads and bennettitaleans began to recover their former prominence in plant communities in Patagonia. This situation has been analyzed extensively in the Baqueró Group, where the two groups occur in great abundance. Interestingly, both cycads and bennettitaleans show marked adaptations to dry conditions—for example, reduced leaves, sculptured surfaces with strongly ornamented epidermis (trichomes, papillae, and hairs), sunken and protected stomata, and thick cuticles. Apparently, these autoecological features were a response to the warm and strongly seasonally dry climates constantly influenced by volcanic activity, which especially increased during sedimentation of the upper Baqueró Group (Archangelsky et al. 1995; Archangelsky 2003).

Cycadophytes probably occupied various niches in different plant communities (Cúneo 2003). During the sedimentation of the lower Baqueró Group, bennettitaleans and cycads were major components of the local vegetation, which, along with the pteridosperms and ferns, formed a low stratum of a relatively closed community dominated by

conifers (podocarps, araucarians, and cheirolepidiaceans). This scenario changes toward the upper part of the Baqueró Group, when the bennettitaleans disappear and cycads (*Pseudoctenis*, *Nilssonia*, and *Mesosingeria*) remain present as midsized plants associated with gleicheniaceous/dipteridaceous ferns and araucarian conifers in a more open community structure (Cladera and Cúneo 2002).

Late Cretaceous and early Paleogene plant communities show an increased role on the part of the dicots, although conifers, ferns, and cycads still occur in differing amounts in the flora. Cycads in particular have been intensively recorded in northern Patagonia, which documents their northward retreat away from their more southern distribution in the Early Cretaceous. On the basis of the paleoecological and sedimentological settings in which they have been found, cycads could have been part of low, open communities in coastal areas, where they normally occurred alongside palms (Petriella 1972). Paleoclimatic analyses of latest Cretaceous–Paleocene floras suggest warm and humid conditions (Petriella and Archangelsky 1975; Iglesias et al. 2007; Cúneo et al. 2007) favorable for plant communities with thermophilic plants such as cycads. In this regard, the dominance of the Encephalartineae cycads, with xeric traits like mucilage channels and persistent leaf bases, also supports seasonal dry conditions.

Acknowledgments

We extend our highest respect and friendship to our good friend Ted Delevoryas for an entire life dedicated to paleobotany. We congratulate Carole Gee on this volume and thank her for the kind invitation to participate in Ted's Festschrift. The TNT program is freely available thanks to a subsidy from the Willi Hennig Society.

References Cited

Anderson, J. M., and H. M. Anderson. 1989. *Paleoflora of Southern Africa, Molteno Formation (Triassic)*, vol. 2, *Gymnosperms (Excluding* Dicroidium*)*. *National Botanic Institute* 2: 1–167. Rotterdam: Balkema.

Archangelsky, A. 1997. *Pseudoctenis giganteus*, nueva cycadal de la Formación Baqueró, Cretácico inferior de Argentina. *Ameghiniana* 34: 387–391.

Archangelsky, A., R. R. Andreis, S. Archangelsky, and A. E. Artabe. 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. 1963a. A new Mesozoic flora from Ticó, Santa Cruz Province, Argentina. *Bulletin of the British Museum (Natural History), Geology* 8: 45–92.

———. 1963b. Notas sobre la flora fósil de la zona de Ticó, Provincia de Santa Cruz. 2. Tres nuevas especies de *Mesosingeria*. *Ameghiniana* 3: 113–122.

———. 1966. New gymnosperms from the Ticó flora, Santa Cruz Province, Argentina. *Bulletin of the British Museum (Natural History), Geology* 13: 261–295.

———. 1976. Vegetales fósiles de la Formación Springhill, Cretácico, en el subsuelo de la Cuenca Magallánica, Chile. *Ameghiniana* 13: 141–158.

———, ed. 2003. La flora cretácica del Grupo Baqueró, Santa Cruz, Argentina. *Monografias Museo Argentino Ciencias Naturales* 4 (CD-ROM). Buenos Aires.
Archangelsky, S., and A. Baldoni. 1972. Notas sobre la flora fósil de la Zona de Ticó, Santa Cruz. X. Dos nuevas especies de *Pseudoctenis* (Cycadales). *Ameghiniana* 9: 241–257.
Archangelsky, S., and D. Brett. 1963. Studies on Triassic fossil plants from Argentina. II. *Michelilloa waltonii* nov. gen. et sp. from the Ischigualasto Formation. *Annals of Botany* 27: 147–154.
Archangelsky, S., and G. M. Del Fueyo. 2010. Endemism of Early Cretaceous conifers in Western Gondwana. In C. T. Gee (ed.), *Plants in Mesozoic Time: Morphological Innovations, Phylogeny, Ecosystems*, pp. 247–268 Bloomington: Indiana University Press.
Archangelsky, S., and B. Petriella. 1971. Notas sobre la flora fósil de la zona de Ticó, Santa Curz. IX. Nuevos datos acerca de la morfología foliar de *Mesodescolea plicata* Arch. (Cycadales, Stangeriaceae). *Boletin Sociedad Argentina Botanica* 14: 88–94.
Archangelsky, S., and L. Villar de Seoane. 2004. Cycadean diversity in the Cretaceous of Patagonia, Argentina. Three new *Androstrobus* species from the Baqueró Group. *Review of Palaeobotany and Palynology* 131: 1–28.
Arrondo, O. G., and B. Petriella 1980. Alicurá, nueva localidad plantífera liásica de la provincia de Neuquén, Argentina. *Ameghiniana* 17: 121–133.
Artabe, A. 1994. Estudio al microscopio electronico de barrido (MEB) de dos cycadópsidas fósiles de Argentina. *Pseudoctenis dentata* Archangelsky Baldoni 1972 y *Sueria rectinervis* Menendez 1965. *Ameghiniana* 31: 115–124.
Artabe, A., and S. Archangelsky. 1992. Estudio al microscopio electronico de barrido y transmisión de una Stangeriaceae (Cycadales) *Mesodescolea plicata* Archangelsky emend. Archangelsky et Petriella 1971. *Ameghiniana* 28 (1–2): 202.
Artabe, A., and D. W. Stevenson. 1999. Fossil Cycadales of Argentina. *Botanical Review* 65: 219–238.
Artabe, A., A. Zamuner, and S. Archangelsky. 1991. Estudios cuticulares en Cycadopsida fósiles. El género *Kurtziana* Frenguelli. *Ameghiniana* 28: 365–374.
Artabe, A., E. M. Morel, and L. A. Saplletti. 2001. Paleoecología de las Floras triásicas argentines. In A. E. Artabe, E. M., Morel, and A. B. Zamuner (eds.), *El Sistema Triásico en la Argentina*, pp. 199–225. La Plata, Argentina: Fundación Museo La Plata.
———. 2003. Caracterización de las provincias fitogeográficas triásicas del Gondwana. *Ameghiniana* 40: 387–405.
Artabe, A., A. B. Zamuner, and D. W. Stevenson. 2004. Two new petrified cycad stems *Brunoa* gen. nov. and *Worsdellia* gen. nov., from the Cretaceous of Patagonia (Bajo de Santa Rosa, Río Negro province), Argentina. *Botanical Review* 70: 121–133.
———. 2005. Fossil cycad stems (Zamiaceae–Encephalartoideae) from the Late Cretaceous of Argentina, with reappraisal of the known forms. *Alcheringa* 29: 87–100.
Artabe, A., E. M. Morel, and D. G. Ganuza. 2007. Las floras triásicas de la Argentina. *Ameghiniana 50° Aniversario, Publicación Especial* 11: 75–86.
Baldoni, A. 1974. Revisión de las Bennettitales de la Formación Baqueró (Cretácico Inferior) Provincia de Santa Cruz. II. Brácteas. *Ameghiniana* 11: 328–356.
———. 1977. *Ptilophyllum ghiense* n. sp., una nueva Bennettital de Paso Roballos, Provincia de Santa Cruz. *Ameghiniana* 14: 53–58.

———. 1978. Plantas fósiles jurásicas del subsuelo de Plaza Huincul, provincia de Neuquén. *Boletin Asociación Latinoamericana Paleobotánica y Palinología* 5: 1–12.
———. 1981. Tafofloras Jurásicas y Eocretácicas de América del Sur. In W. Volkheimer and E. Mussachio (eds.), *Cuencas Sedimentarias del Jurásico y Cretácico de América del Sur* 2: 359–391.
Baldoni, A., and T. N. Taylor. 1983. Plant remains from a new Cretaceous site in Santa Cruz, Argentina. *Review of Palaeobotany and Palynology* 39: 301–311.
Bateman, R., J. Hilton, and P. J. Rudall. 2006. Morphological and molecular phylogenetic context of the angiosperms: contrasting the "top-down" and "bottom-up" approaches used to infer the likely characteristics of the first flowers. *Journal of Experimental Botany* 57: 3471–3503.
Berry, E. W. 1924. Mesozoic plants from Patagonia. *American Journal of Science*, ser. 5, 7: 473–482.
Bonetti, M. 1964. Flórula mesojurásica de la zona de Taquetrén (Cañadón del Zaino), Chubut. *Revista del Museo Argentino Ciencias Naturales* 1: 1–43.
———. 1968. Las especies del género *Pseudoctenis* en la flora triásica de Barreal (San Juan). *Ameghiniana* 5: 433–446.
———. 1972. Las Bennettitales de la flora triásica de Barreal (Prov. de San Juan). *Revista Museo Argentino de Ciencias Naturales "B. Rivadavia"* 1: 307–322.
———. 1974. Flórula jurásica del Lago Argentino (Santa Cruz). *I Congreso Argentino Paleontología y Bioestratigrafía, Resúmenes*, Tucumán, p. 9.
Brenner, E. D., D. Stevenson, and R. W. Twigg. 2003. Cycads: evolutionary innovations and the role of plant-derived neurotoxins. *Trends in Plant Science* 8: 446–452.
Chaw, S. M., A. Zharkikh, H. M. Sung, T. K. Lau, and W. H. Li. 1997. Molecular phylogeny of extant gymnosperms and seed plant evolution, analyses of 18S rRNA sequences. *Molecular Biology and Evolution* 14: 56–68.
Chaw, S. M., C. Parkinson, Y. Cheng, T. M. Vincent, and J. D. Palmer. 2000. Seed plant phylogeny inferred from all three plant genomes: monophyly of gymnosperms and sistehood of Gnetales and Pinaceae. *Proceedings of the National Academy of Sciences U.S.A.* 97: 4086–4091.
Chaw, S. M., T. W. Walter, C. C. Chang, S. H. Hu, and S. Chen. 2005. A phylogeny of cycads (Cycadales) inferred from chloroplast *matK* gene, *trnK* intron, and nuclear rDNA ITS region. *Molecular Phylogenetics and Evolution* 37: 214–234.
Cladera, G., and R. Cúneo. 2002. Fossil plants buried by volcanic ash in the Lower Cretaceous of Patagonia. In M. De Renzi, M. V. Pardo Alonso, M. Belinchón E. Peñalver, P. Montoya, and A. Márquez-Aliaga (eds.), *Current Topics on Taphonomy and Fossilization, Third Encounter Taphos 2002*, pp. 399–403. Valencia: Ayuntamiento de Valencia.
Crane, P. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. *Annals of the Missouri Botanical Garden* 72: 716–793.
———. 1988. Major clades and relationships in "higher" gymnosperms. In C. B. Beck (ed.), *Origin and Evolution of Gymnosperms*, pp. 218–272. New York: Columbia University Press.
Crepet, W. L., and D. W. Stevenson. 2010. The Bennettitales (Cycadeoidales): a preliminary perspective on this arguably enigmatic group. In C. T. Gee (ed.), *Plants in Mesozoic Time: Morphological Innovations, Phylogeny, Ecosystems*, pp. 215–244. Bloomington: Indiana University Press.
Cúneo, N. R. 2003. Early Cretaceous terrestrial ecosystems from Patagonia: the Baquero Group, a case study. Terrestrial paleobiology of South America, Cretaceous through Neogene (Paleont. Soc.). *Geological Society of America Annual Meeting-Exposition, Seattle* 35 (6): 58.

Cúneo, N. R., K. Johnson, P. Wilf, R. Scasso, A. Gandolfo, and A. Iglesias. 2007. A preliminary report on the diversity of latest Cretaceous floras from northern Patagonia, Argentina. *Geological Society of America Annual Meeting, Abstracts with Programs, Denver* 39: 584.

De Laubenfeld, D. J. 1999. The families of the Cycadaceae. *Encephalartos* 59: 7–9.

Delevoryas, T. 1955. The Medullosae—structure and relationships. *Palaeontographica*, Abt. B, 97: 114–167.

Donoghue, M., J. Doyle, J. Gauthier, A. G. Kluge, and T. Rowe. 1989. The importance of fossils in phylogeny reconstructions. *Annual Review of Ecology and Systematics* 20: 431–460.

Doyle, J. 1996. Seed plant phylogeny and the relationships of Gnetales. *International Journal of Plant Sciences* 157: 3–39.

Doyle, J., and M. Donoghue. 1992. Fossils and seed plant phylogeny reanalyzed. *Brittonia* 44: 89–106.

Gee, C. T. 1989. Revision of the Late Jurassic/Early Cretaceous fossil flora from Hope Bay, Antarctica. *Palaeontographica*, Abt. B, 213: 149–214.

Gnaedinger, S. 1999. La flora triásica del Grupo El Tranquilo, Provincia de Santa Cruz (Patagonia). Parte VII. Cycadophyta. In *Ameghiniana*, *Publicación Especial* 6: 27–32.

Gnaedinger, S., and R. Herbst. 1998. La flora triásica del Grupo El Tranquilo, provincia de Santa Cruz (Patagonia). Parte V. Pteridophylla. *Ameghiniana* 35: 53–65.

———. 2004. Pteridophylla del Triásico del Norte Chico de Chile. I. El género *Taeniopteris* Bgt. *Ameghiniana* 41: 91–110.

Goloboff, P., J. S. Farris, and K. Nixon. 2009. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.

Herbst, R. 1965. La flora fósil de la Formación Roca Blanca, provincia de Santa Cruz, Patagonia. Con consideraciones geológicas y estratigráficas. *Opera Lilloana* 12: 7–101.

———. 1966a. Revisión de la flora liásica de Piedra Pintada, provincia de Neuquén, Argentina. *Revista del Museo de la La Plata*, n.s., 5: 27–53.

———. 1966b. La flora liásica del Grupo Pampa de Agnia, Chubut, Patagonia. *Ameghiniana* 4: 337–347.

———. 1968. Las floras liásica argentines con consideracioines estratigráficas. *III Jornadas Geológicas Argentinas* 1: 145–162.

———. 1980. Flórula fósil de la Fm. Los Patos (Sinemuriano) del río Los Patos (San Juan), Argentina. *II Congreso Argentino Paleontologia y Bioestratigrafia*, *I Congreso Latinoamericano Paleontología*, *Actas* 1: 175–189.

Herbst, R., and L. Anzotegui. 1968. Nuevas plantas de la flora del Jurásico medio (Matildense) de Taquetrén, provincia de Chubut. *Ameghiniana* 5: 183–190.

Herbst, R., and S. Gnaedinger. 2002. *Kurtziana* Frenguelli (Pteridospermae? incertae sedis) y *Alicurana* nov. gen. (Cycadopsida) del Triásico y Jurásico temprano de Argentina y Chile. *Ameghiniana* 39: 331–341.

Herbst, R., and A. Troncoso. 2000. Las Cycadophyta del Triásico de las Formaciones La Ternera y El Puquén (Chile). *Ameghiniana* 37: 283–292.

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

———. 2007. Cycads from the Triassic of Antarctica: permineralized cycad leaves. *International Journal of Plant Sciences* 168: 1099–1112.

Hunter, M. A. 2005. Mid-Jurassic age for the Botany Bay Group: implications for the Weddell Sea Basin creation and southern hemisphere biostratigraphy. *Journal of the Geological Society* 162: 745–748.

Iglesias, A., P. Wilf, K. Johnson, A. Zamuner, R. Cúneo, S. Matheos, and B. Singer. 2007. A Paleocene lowland macroflora from Patagonia reveals significantly greater richness than North American analogs. *Geology* 35: 947–950.
Jones, D. L. 2002. *Cycads of the World: Ancient Plants in Today's Landscape*, 2nd ed. Washington, D.C.: Smithsonian Institution Press.
Leppe, M., and P. Moisan. 2003. Nuevos registros de Cycadales y Cycadeoidales del Triásico superior del río Biobío, Chile. *Revista Chilena Historia Natural* 76: 475–484.
Loconte, H., and D. Stevenson. 1990. Cladistics of the Spermatophyta. *Brittonia* 42: 197–211.
Longobucco, M. I., C. Azcuy, and B. Aguirre Urreta. 1985. Plantas fósiles de la Formación Kachaike, Cretácico de Santa Cruz. *Ameghiniana* 21: 305–315.
Mamay, S. 1969. Cycads: fossil evidence of Late Paleozoic origin. *Science* 164: 295–296.
Menéndez, C. A. 1965. *Sueria rectinervis* n. gen. et sp. de la flora fósil de Ticó, Provincia de Santa Cruz. *Ameghiniana* 4: 3–11.
———. 1966. Fossil Bennettitales from the Ticó flora, Santa Cruz Province, Argentina. *Bulletin of the British Museum (Natural History)*, *Geology* 12: 1–42.
Passalia, M. 2007. Nuevos registros para la flora cretácica descripta por Halle (1913) en lago San Martín, Sancta Cruz, Argentina. *Ameghiniana* 44: 565–595.
Petriella, B. 1969. *Menucoa cazaui* nov gen. et sp., tronco petrificado de Cycadales, Provincia de Río Negro, Argentina. *Ameghiniana* 6: 291–302.
———. 1972. Estudio de las maderas petrificadas del Terciario inferior del área central de Chubut (Cerro Bororó). *Revista del Museo de La Plata*, n.s., *Paleontología* 6: 159–254.
———. 1978. Nuevos hallazgos de Cycadales fósiles en Patagonia. *Boletin de la Asociación Latinoamericana de Paleobotánica y Palinología* 5: 13–16.
Petriella, B., and S. Archangelsky. 1975. Vegetación y ambiente en el Paleoceno de Chubut. *I Congreso Argentino Paleontologia y Bioestratigrafia*, *Actas*, *Tucumán* 2: 257–270.
Rai, H. S., H. E. O'Brian, P. A. Reeves, R. G. Olmstead, and S. W. Graham. 2003. Inference of higher-order relationships in the cycads from a large chloroplast data set. *Molecular Phylogenetics and Evolution* 29: 350–359.
Rees, P. M., and C. J. Cleal. 2004. Lower Jurassic floras from Hope Bay and Botany Bay, Antarctica. *Special Papers in Palaeontology* 72: 1–90.
Rees, P. M., A. Ziegler, and P. Valdes. 2000. Jurassic phytogeography and climates: new data and model comparisons. In B. T. Huber, K. Macleod, and S. Wing (eds.), *Warm Climates in Earth History*, pp. 297–318. Cambridge: Cambridge University Press.
Rothwell, G., and R. Serbet. 1994. Lignophyte phylogeny and the evolution of the spermatophytes: a numerical cladistic analysis. *Systematic Botany* 19: 443–482.
Rothwell, G. W., and R. A. Stockey. 2010. Independent evolution of seed enclosure in the Bennettitales: evidence from the anatomically preserved cone *Foxeoidea connatum* gen. et sp. nov. In C. T. Gee (ed.), *Plants in Mesozoic Time: Morphological Innovations, Phylogeny, Ecosystems*, pp. 51–64. Bloomington: Indiana University Press.
Spalletti, L., A. Artabe, E. Morel, and M. Brea. 1999. Biozonación paleoflorística y cronoestratigrafía del Triásico argentino. *Ameghiniana* 36: 419–451.
Spalletti, L., E. Morel, J. Franzese, A. Artabe, D. Ganuza, and A. Zuñiga. 2007. Contribución al conocimiento sdimentológico y paleobotánico de la

Formación El Freno (Jurásico temprano) en el valle superior del río Atuel, Mendoza, Argentina. *Ameghiniana* 44: 367–386.
Stevenson, D. W. 1981. Observations on ptyxis, phenology, and trichomes in the Cycadales and their systematic implications. *American Journal of Botany* 68: 1104–1114.
———. 1990. Morphology and systematics of Cycadales. *Memoirs of the New York Botanical Garden* 57: 8–55.
———. 1992. A formal classification of the extant Cycadales. *Brittonia* 44: 220–223.
Stewart, W., and G. Rothwell. 1993. *Paleobotany and the Evolution of Plants*, 2nd ed. Cambridge: Cambridge University Press.
Stipanicic, P. N. 2002. Introducción. In P. N. Stipanicic and C. A. Marsicano (eds.), *Léxico Estratigráfico de la Argentina*, vol. 8, *Triásico. Asociación Geológica Argentina*, Serie "B" 26: 1–24.
Taylor, T. N., E. L. Taylor, and M. Krings. 2009. *Paleobotany: The Biology and Evolution of Fossil Plants*, 2nd ed. San Diego: Academic Press.
Villar de Seoane, L. 1995. Estudio cuticular de nuevas Bennettitales eocretácicas de Santa Cruz, Argentina. *VI Congreso Argentino Paleontología y Bioestratigrafía, Actas*, pp. 247–254.
———. 1997. Estudio cuticular comparado de nuevas Cycadales de la Formación Baqueró (Cretácico Inferior), Santa Cruz, Argentina. *Revista Española de Paleontología* 12: 129–140.
———. 1999. *Otozamites ornatus* sp. nov., a new bennettitalean leaf species from Patagonia, Argentina. *Cretaceous Research* 20: 499–506.
———. 2001. Cuticular study of Bennettitales from the Springhill Formation, Lower Cretaceous of Patagonia, Argentina. *Cretaceous Research* 22: 461–479.
———. 2003. Cuticle ultrastructure of the Bennettitales from the Anfiteatro de Ticó Formation (Early Aptian), Santa Cruz Province, Argentina. *Review of Palaeobotany and Palynology* 127: 59–76.
———. 2005. New cycadalean leaves from the Anfiteatro de Ticó Formation, Early Aptian of Patagonia, Argentina. *Cretaceous Research* 26: 540–550.
Watson, J., and C. A. Sincock. 1992. Bennettitales of the English Wealden. *Monograph of the Palaeontographical Society* 145 (588): 2–228.
Worsdell, W. C. 1906. The structure and origin of the Cycadaceae. *Annals of Botany* 20: 129–155.