GINKGOITES PATAGONICA (BERRY) COMB. NOV. FROM THE EOCENE OF PATAGONIA, LAST GINKGOALEAN RECORD IN SOUTH AMERICA

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Premise of research. The ginkgophytes are an ancient group of gymnosperms with a long history starting during the late Paleozoic and reaching the present with the unique species *Ginkgo biloba* L. In order to better characterize the early and middle Eocene (ca. 52.2 and 47.7 Ma) leaf species *Ginkgo patagonica* Berry from northwest Patagonia, Argentina, new specimens were studied, focusing on their morphological and anatomical characters.

Methodology. The specimens were studied with LM, epifluorescence, SEM, and TEM.

Pivotal results. The diagnosis of the species *Ginkgoites patagonica* comb. nov. is enlarged to include anatomical and ultrastructural epidermal characters. Herein, the species *Ginkgo patagonica* is shown to have characteristics that clearly separate it from the genus *Ginkgo* L., and it is therefore recombined to the genus *Ginkgoites* Seward.

Conclusions. Eocene *Ginkgoites patagonica* was present in plant communities, and it is the last representative of a still poorly understood southern ginkgophyte lineage that was distinct from the ancestors of *G. biloba* of the Northern Hemisphere.

Keywords: Ginkgoales, cuticles, early-middle Eocene, Patagonia, Argentina.

Introduction

The ginkgophytes are an ancient group of gymnosperms with a long history starting during the late Paleozoic and reaching the present with the unique species *Ginkgo biloba* L. (Taylor et al. 2009). Their origin has been associated with Permian families such as the Trichopytiaceae and the Dicranophyllaceae, from which true ginkgoaleans are thought to have evolved during the Mesozoic (Archangelsky and Cúneo 1990; Stewart and Rothwell 1993; Villar de Seoane 1997; Del Fueyo and Archangelsky 2001; Crane 2013; Del Fueyo et al. 2013).

Based on the limited record of reproductive organs, the genus *Ginkgo* L. can be traced back into the Middle Jurassic (Zhou and Zhengh 2003). However, an earlier origin is hypothetically possible when considering the high abundance of isolated *Ginkgo*-like leaves found in several Permian formations of Argentina (Feruglio 1933, 1942; Cúneo 1987). Unfortunately, there are no methods for attributing isolated *Ginkgo*-like leaves to the living genus *Ginkgo* with confidence based only on foliar characters. Discussions on this matter date to the late nineteenth century (see Watson et al. 1999, among others), and as a result, in order to deal with the prolific record of *Ginkgo*-like leaves, Seward (1919) erected the genus *Ginkgoites* to differentiate many fossil leaves from the modern species *Ginkgo biloba*. Nevertheless, the morphological boundaries of Seward's concept were not very precise. Debate continued on this matter of whether to use other generic fossil names or the genus *Ginkgo* for isolated fossil leaves (see, e.g., Harris and Middleton 1974). Some of these disagreements were settled when *Ginkgo*-like leaves, including *Ginkgoites*, were found associated with reproductive structures very different from those of *G. biloba*, for example, in *Yimaia*, *Karkenia*, and even *Ginkgo*, demonstrating a larger past generic diversity (see Del Fueyo and Archangelsky 2001; Zhou et al. 2002, 2012; Zhou and Zheng 2003; see below for additional discussion).

Herein, a complete morphological, anatomical, and ultrastructural cuticle study from new and historic specimens of *Ginkgo patagonica* Berry (1935, 1938) from the Eocene of Patagonia is presented. Based on these remains, the species is more properly recombined to the extinct genus *Ginkgoites*, and its diagnosis is expanded by adding new epidermal characters. Additionally, hypotheses regarding possible causes for the disappearance of the ginkgophyte clade from the Southern Hemisphere are suggested.

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The Ginkgophyte Fossil Record from Southern South America

In Argentina, the ginkgophytes, represented by vegetative and reproductive structures, show a continuous record since Carboniferous times. Interestingly, they were never the dominant component in any plant community (Del Fueyo et al. 2013).

The leaf genera *Ginkgoites* Seward and *Ginkgophyllum* (Saporta) Neuburg occur in Carboniferous and Permian strata from Patagonia (Feruglio 1933, 1942; Cúneo 1987; Escapa and Cúneo 2003) and northwest of Argentina (Archangelsky and Arrondo 1974; Archangelsky and Leguizamón 1980). The three Patagonian Permian species, *Ginkgoites eximia* (Feruglio) Cúneo, *Ginkgoites crassipes* (Feistmantel) Feruglio, and *Ginkgoites feruglioi* (Feruglio) Cúneo, look almost identical to modern *Ginkgo* leaves (Feruglio 1933; Cúneo 1987; Rothwell and Holt 1997).

During the Triassic, *Ginkgoites* became more diverse with several taxa inhabiting Patagonia, such as *Ginkgoites dutoitii* Anderson et Anderson, *Ginkgoites palmate* (Ratte) Gnaedinger et Herbst, and *Ginkgoites waldeckensis* (Anderson et Anderson) Gnaedinger et Herbst, all representing leaf impressions from the El Tranquilo Group, Santa Cruz Province (Azcuy and Baldoni 1990; Gnaedinger and Herbst 1999). Records from other areas of Argentina include *Ginkgoites truncata* Frenguelli (1946) from the Potrerillos Formation, Mendoza Province.

The oldest Argentinean record of *Ginkgo*-like cutinized leaves is the species *Ginkgo taeniata* Geinitz from the Lower Jurassic Paso Flores Formation, Neuquén Province, and it was described as having amphistomatic leaves that are divided into four to eight lobes (Frenguelli 1937). In lower Cretaceous strata, ginkgophyte remains are relatively more common and diverse in Patagonia. In the Aptian sediments of the Anfiteatro de Ticó Formation (Baqueró Group, Santa Cruz Province), multilobed leaves described as *Ginkgoites ticoensis* Archangelsky and *Ginkgoites tigrensis* Archangelsky were exhumed from two localities (Archangelsky 1965). The latter species occurs intimately associated with the multiovulate reproductive organ *Karkenia incurva* Archangelsky (Archangelsky 1965; Del Fueyo and Archangelsky 2001) that has proven to represent a separate lineage (Karkeniaceae) of the ginkgophyte clade (Crane 2013).

From the slightly younger Albian Kachaike Formation (Santa Cruz Province), Lundblad (1971), Del Fueyo et al. (2006, 2013), and Passalia (2007) described *Ginkgoites skottsbergii* Lundblad, a leaf taxon with 8–12 lobes and preserved epidermis that was ultrastructurally described by Del Fueyo et al. (2006, 2013). Finally, recent findings in the latest Cretaceous portion of the Lefipán Formation (Chubut Province) also include ginkgophyte leaves and pollen, including specimens with preserved cuticles (Cúneo et al. 2007; Barreda et al. 2012).

In Patagonia and almost the entire Southern Hemisphere, the last record of ginkgoalean leaves is the focus of this contribution. *Ginkgo patagonica* Berry (1935, 1938) was first described from the middle Eocene Río Pichileufú locality, La Huitrera Formation, Río Negro Province. Later, Traverso (1964) incorporated into the same species additional remains collected by Frenguelli in 1939–1940 from the early Eocene Tufolitas Laguna del Hunco (Chubut Province) by describing the epidermis of several leaves of *Ginkgo patagonica* using LM.

Material and Methods

Material

Specimens were collected from two different localities (fig. 1). Geographic and stratigraphic data have been previously given by Wilf et al. (2003, 2005). Specimens from the Laguna del Hunco locality in northwestern Chubut Province were collected from lacustrine caldera sediments belonging to the Tufolitas Laguna del Hunco (Aragón and Mazzoni 1997). Based on the ^{40}Ar-^{39}Ar ages of three intercalated ash layers aligned with two paleomagnetic reversals, this unit is currently assigned to the early Eocene. The most reliable datum is a ^{40}Ar-^{39}Ar age on sanidine from a tuff yielding a recently recalibrated age of 52.2 ± 0.22 Ma (Wilf et al. 2003, 2005; Wilf 2012). The Laguna del Hunco ginkgophyte leaves are exquisitely preserved and occur in low percentages in a megaflora dominated by dicot leaves and secondarily by conifers (Wilf et al. 2005). Additional specimens were recently exhumed at the Río Pichileufú locality in lacustrine deposits of the La Huitrera Formation that crops out in southwestern Río Negro Province. Volcanic tuffs immediately above the plant fossils yielded a high-precision ^{40}Ar-^{39}Ar age that was recently recalibrated to 47.5 ± 0.05 Ma, approximately 4.5 Myr younger than the fossil lake beds of the Tufolitas Laguna del Hunco (Wilf et al. 2005; Wilf 2012). The ginkgophyte leaves at Río Pichileufú also occur as a minor component of a highly diversified dicot-dominated taphoflora (Berry 1938; Wilf et al. 2005).

In this article, several specimens of *Ginkgo patagonica* were analyzed: (1) the original specimens from Río Pichileufú described by Berry (1935, 1938) that are housed at the Smithsonian Institution (USNM), including both the figured material housed in the Paleobotany Type Collection and previously unreported cohort material that was found in the Paleobotany Stratigraphic Collection; (2) recently collected macrofossils deposited at the Palaeobotanical Collection of the Paleontological Museum "Egidio Feruglio" (MPEF-Pb, for Laguna del Hunco, sites LH6–22) and the Paleontological Museum of Bariloche (BAR, for Río Pichileufú, sites RP1–3); and (3) the additional Laguna del Hunco specimens of Frenguelli's from the Paleobotanical Collection of the La Plata Natural Sciences Museum (LPPb), originally described by Traverso (1964). Slides for LM, SEM, and TEM specimens are deposited at the Paleobotanical Collection of the Argentine Museum of Natural Sciences "Bernardino Rivadavia" with the acronyms BA Pb. The precise locality data for the historic material studied by Berry and Traverso are not available.

Methods

The specimens are compressions and have excellently preserved cuticle fragments that are frequently nearly complete leaf surfaces. To prevent immediate loss of cuticle to the wind on discovery, specimens were quickly plastic-wrapped in the field. Fossil cuticle was prepared for both LM and electron microscopy. The cuticle was easily separated from the matrix

Fig. 1   Location of the early Eocene Laguna del Hunco (Chubut Province) and the middle Eocene Río Pichileufú (Río Negro Province) localities, northwest Patagonia, Argentina.

and cleaned with dilute sodium hypochlorite (5%). The preparations were mounted in glycerine jelly for observation with LM or directly on circular stubs and coated with gold palladium for SEM. Observations were performed with a Philips XL30 TMP at the Electron Microscopy Service of the Argen-

tine Museum of Natural Sciences "Bernardino Rivadavia." For TEM studies, some cuticle fragments were treated with OsO_4 and embedded in Spurr low-viscosity resin (Spurr 1969). Transverse sections (TS) of the cuticles were done with a diamond knife on a SORVAL manual ultramicrotome and mounted

in single-hole grids coated with Formvar and stained with KMnO$_4$ (5–10 min) and uranyl acetate (30 s). Observations were made with a Zeiss EM 109 microscope at the Electron Microscopy Service of the Cellular Biology Department, Faculty of Medicine, Buenos Aires University, Argentina. The below-designated lectotype specimen, a cuticle preparation mounted in glass by Berry, was studied nondestructively under epifluorescence at the Penn State Paleobotany Laboratory using the techniques described in Wilf (2012). The terminology of Metcalfe and Chalk (1979) was used for stomata classification; Holloway (1982) and Lyshede (1978, 1982) were used for ultrastructural descriptions.

Results

Genus—Ginkgoites *Seward 1919*

Type Species—Ginkgoites sibirica *(Heer) Seward 1919*

Ginkgoites patagonica *(Berry) comb. nov. (Figs. 2–5)*

1935. Ginkgo patagonica Berry, Torreya 35, p. 11, figured p. 12.
1938. Ginkgo patagonica Berry, Geol Soc Am Spec Pap 12, p. 58, pl. 10.
1964. Ginkgo patagonica Berry, Traverso, Ameghiniana 3, p. 165, pls. 1, 2.

Emended species diagnosis. Leaves simple, multilobed, hypostomatic, and petiolate. Leaf flabelliform, deeply incised, usually lobed, with two major lobes and with two to eight symmetrical or asymmetrical, secondary, and sometimes tertiary minor lobes with rounded apices. Veins in a pair entering from the petiole and immediately dichotomizing up to five times, converging in the apex of each lobe. Adaxial and abaxial epidermises with striate and rectangular to isodiametric cells irregularly arranged. Tetracytic-actinocytic stomatal apparatuses with four to seven papillate subsidiary cells, randomly arranged on the abaxial epidermis. External wall of the epidermis formed by a cuticle proper, a cuticular membrane, and remnants of the cell wall. Cuticle proper thin and granular. Cuticular membrane formed by two thick and reticulate layers.

Lectotype. USNM 40386c (fig. 3; Berry 1938, pl. 10, fig. 1), Smithsonian Institution Paleobotanical Collection, National Museum of Natural History, Washington, DC.

Syntypes. USNM 40386a (Berry 1938, pl. 10, fig. 4), USNM 40386b (Berry 1935, p. 12, left; Berry 1938, pl. 10, fig. 3), USNM 40386d (Berry 1935, p. 12, middle; Berry 1938, pl. 10, fig. 2), USNM 40386e-l and 545232 (previously unfigured).

Additional material studied. MPEF-Pb 1610A, MPEF-Pb 5656–5666; BAR 4360 B; LPPb 10394, LPPb 10395, LPPb 20441; BA Pb Pm. 514–519; LP Pm. 146; BA Pb MEB 257–259; BA Pb MET 218–220.

All materials housed at the paleobotanical collections of the Smithsonian Institution (USNM) and the Paleontological Museum of Bariloche (BAR) were collected from the Río Pichileufú locality, La Huitrera Formation, Río Negro Province; while those stored at the La Plata Natural Sciences Museum (LPPb), Argentine Museum of Natural Sciences "Bernardino

Rivadavia" (BAPb), and Paleontological Museum "Egidio Feruglio" (MPEF-Pb) were collected at the Laguna del Hunco locality, Tufolitas Laguna del Hunco, Chubut Province.

Type locality and stratigraphic horizon. Rio Pichileufú, Río Negro Province, La Huitrera Formation, middle Eocene.

Age. Middle Eocene (47.7 ± 0.05 Ma).

Type Specimen Remarks

At an unknown time but not long before 1935 (see Berry 1934), E. W. Berry received a single shipment of fossils from the Río Pichileufú locality, then thought to be Miocene in age, from mining geologist J. R. Guiñazú. These were housed and studied at Johns Hopkins University and later transferred to the Smithsonian Institution Paleobotanical Collection. When Berry (1935, p. 11; 1938, p. 58) originally described *Ginkgo patagonica* from Río Pichileufú, he made cuticle preparations and gave a comprehensive description. He illustrated three specimens only as sketches and discussed but did not illustrate cuticle. We were able to correlate two of the three sketches (Berry 1935, p. 12, left and middle) to surviving specimens, whereas the third sketch (Berry 1935, p. 12, right) does not resemble any surviving material from the original collection. In the 1938 article, Berry photographically figured four specimens that all survive, including the two aforementioned from the 1935 article, plus the here-designated lectotype and a fourth specimen (USNM 40386a) that were both not previously illustrated.

It is quite clear from Berry's (1935) writings, which included discussion of cuticle preparation as well as his hand-labeled identifications on all the USNM material, and from the fact that he received only one shipment of material from Río Pichileufú, that USNM 40386c is part of the original gathering (sensu ICBN) of material on which he based the species and is therefore qualified to serve as the lectotype. By the same logic, all the other historic USNM specimens of *Ginkgo patagonica* mentioned above, whether figured in the 1930s or not, are reasonably considered as part of the same original gathering and are here considered syntypes.

Traverso (1964, p. 165) added some epidermal characters using LM to the original morphological descriptions of Berry and included a repository (La Plata Natural Sciences Museum Paleobotanical Collection) for the materials collected by Frenguelli in 1939–1940 from Laguna del Hunco but did not emend the original diagnosis. In this article, Berry's diagnosis was emended with the addition of new cuticular and ultrastructural characters obtained through SEM and TEM observations.

Leaf Morphology

The leaves are simple, multilobed, hypostomatic, and petiolate (fig. 3). The laminae are flabelliform and highly variable in size, reaching up to 8 cm long and 11.5 cm wide in the most deeply incised leaves. They are divided into two to eight symmetrical or asymmetrical lobes. Each lamina shows a deep incision that forms two lobes of the first order that progressively show to second- and third-order lobing with increased incision of the leaf apex (fig. 3). First- to third-order lobes are all lanceolate with rounded apices and have entire margins,

Fig. 2 *Ginkgoites patagonica* (Berry) comb. nov. Petiolate lobed leaf with preserved cuticle, USNM 40386c, lectotype. *A,* General view; scale bars = 1 cm. *B,* Close-up of the lamina cuticle; scale bar = 1 cm. *C,* Details of the cuticle showing two veins and the stomata disposition between them; scale bar = 500 μm.

and they can be up to 2.7 cm long and 0.4–0.5 cm wide (fig. 3*A*, 3*B*, 3*F*). The deep central incision goes to 95% of the leaf length (fig. 3*A*–3*C*, 3*F*). Each lamina has a slender petiole up to 6.5 cm long and 0.3 cm wide (fig. 3*A*–3*C*, 3*F*), with two vascular strands entering the lamina and immedi-
ately dichotomizing up to five times (fig. 3*E*, 3*F*). The veins have radially disposed from the base and are partially convergent at the distal margin of each lobe. Depending on the number of incisions, they have a variable concentration (6–14 veins/cm) in the ultimate lobes (fig. 3*C*–3*F*).

Fig. 3 *Ginkgoites patagonica* (Berry) nov. comb. Morphological variations of different petiolate leaves showing their symmetry, lobing, and incision characters. MPEF-Pb 1610A, MPEF-Pb 5656–5666, BAR 4360 B specimens. Scale bars = 1 cm.

Cuticular Structure and Ultrastructure

Adaxial and abaxial epidermises of the lobes are formed by rectangular (up to 137.7 μm long and 17.9 μm wide) to isodiametric (up to 31.1–42.7 μm wide) cells. All the cells are irregularly disposed among the veins, and their walls are slightly thickened, sinuous, and strongly pitted (fig. 4A). The epidermal cells that cover the veins are formed by five to six rows of rectangular cells (up to 78.2–151.2 μm long and 12.7–29.8 μm wide), with anticlinal sinuous and strongly pitted walls similar to the other epidermal cells (fig. 4B, 4D). The external surfaces of both epidermises are striated (fig. 4F).

Stomata are present only on the abaxial epidermis, irregularly arranged between the veins (fig. 4C). The stomatal density is 20–25/mm^2 (fig. 4C). They show a tetracytic-actinocytic stomatal apparatus that is roughly circular and up to 85.9 μm in diameter, with four to seven subsidiary cells (fig. 4D, 4E). Each subsidiary cell forms a subcircular to elongated papilla of 7.3–9.1 μm in height and 7.6–11.9 μm in width, oriented toward the pit and overarching the suprastomatal aperture (fig. 4F). Guard cells are sunken and reniform (14.8–31.7 μm long and 4.9–8.4 μm wide), with a cuticular ridge surrounding the pit (fig. 4E, 4F).

Ultrastructurally, the external wall of the epidermis is formed by a cuticle proper and a cuticular membrane divided into upper and lower layers (Lyshede 1982; fig. 5A, 5C). Epicuticular waxes cover the entire surface and are irregularly disposed. They have a granular structure and a relatively low electron density. In some areas, waxes reach 0.5 μm thickness (fig. 5A, 5E).
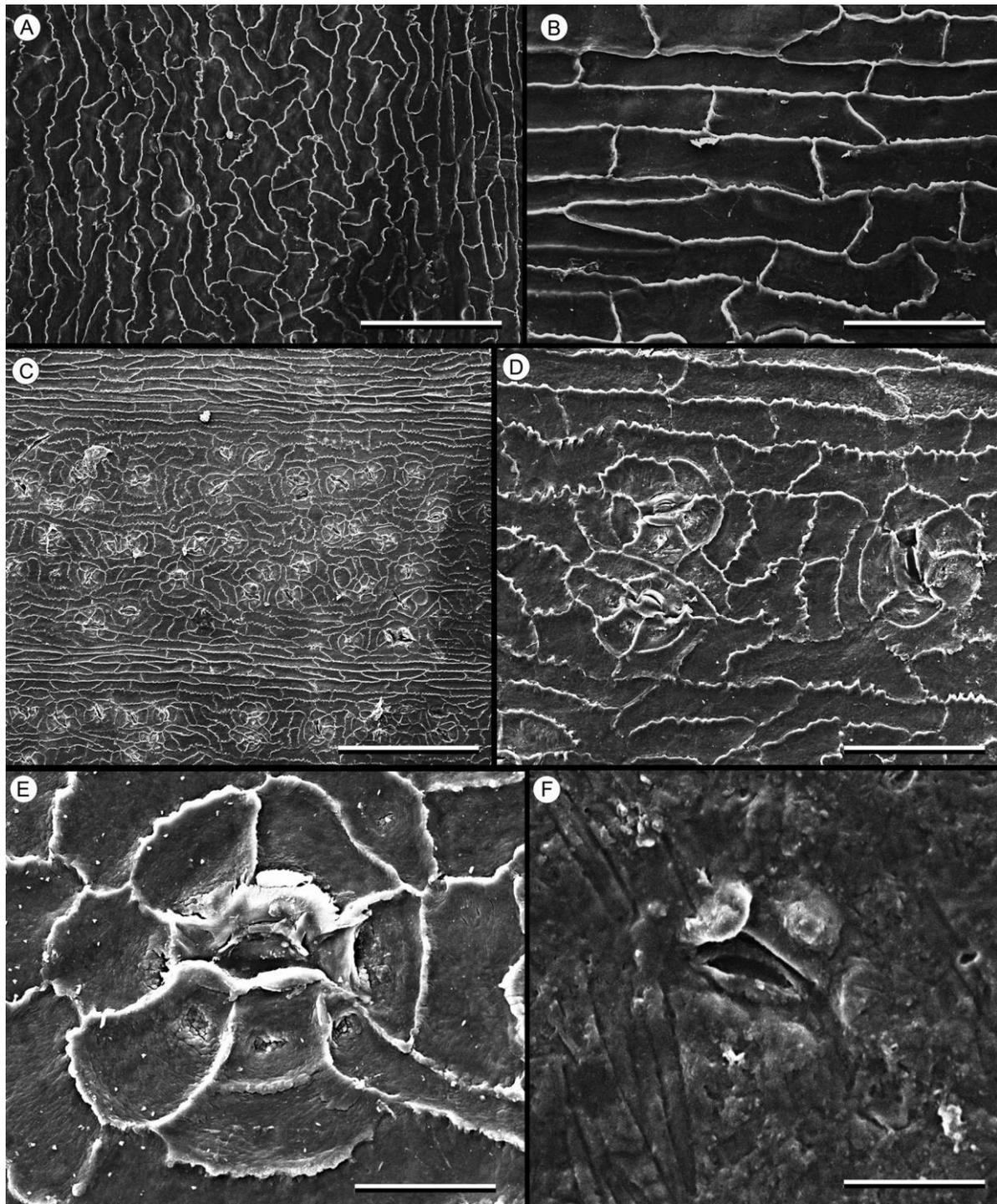
Fig. 4 *Ginkgoites patagonica* (Berry) comb. nov. SEM cuticular anatomy. *A*, Internal view of the adaxial epidermis; BA Pb MEB 257; scale bar = 200 μm. *B*, Detail of the epidermal cells disposition on the veins in the adaxial epidermis; BA Pb MEB 257; scale bar = 50 μm. *C*, Internal view of the abaxial epidermis showing the stomata disposition between two veins; BA Pb MEB 259; scale bar = 200 μm. *D*, Detail of the three stomata in internal view; BA Pb MEB 259; scale bar = 20 μm. *E*, Details of the internal view of a stomatal apparatus; BA Pb MEB 259; scale bar = 10 μm. *F*, Details of the external view of the papillate subsidiary cells and sunken guard cells in a stoma; BA Pb MEB 259; scale bar = 10 μm.
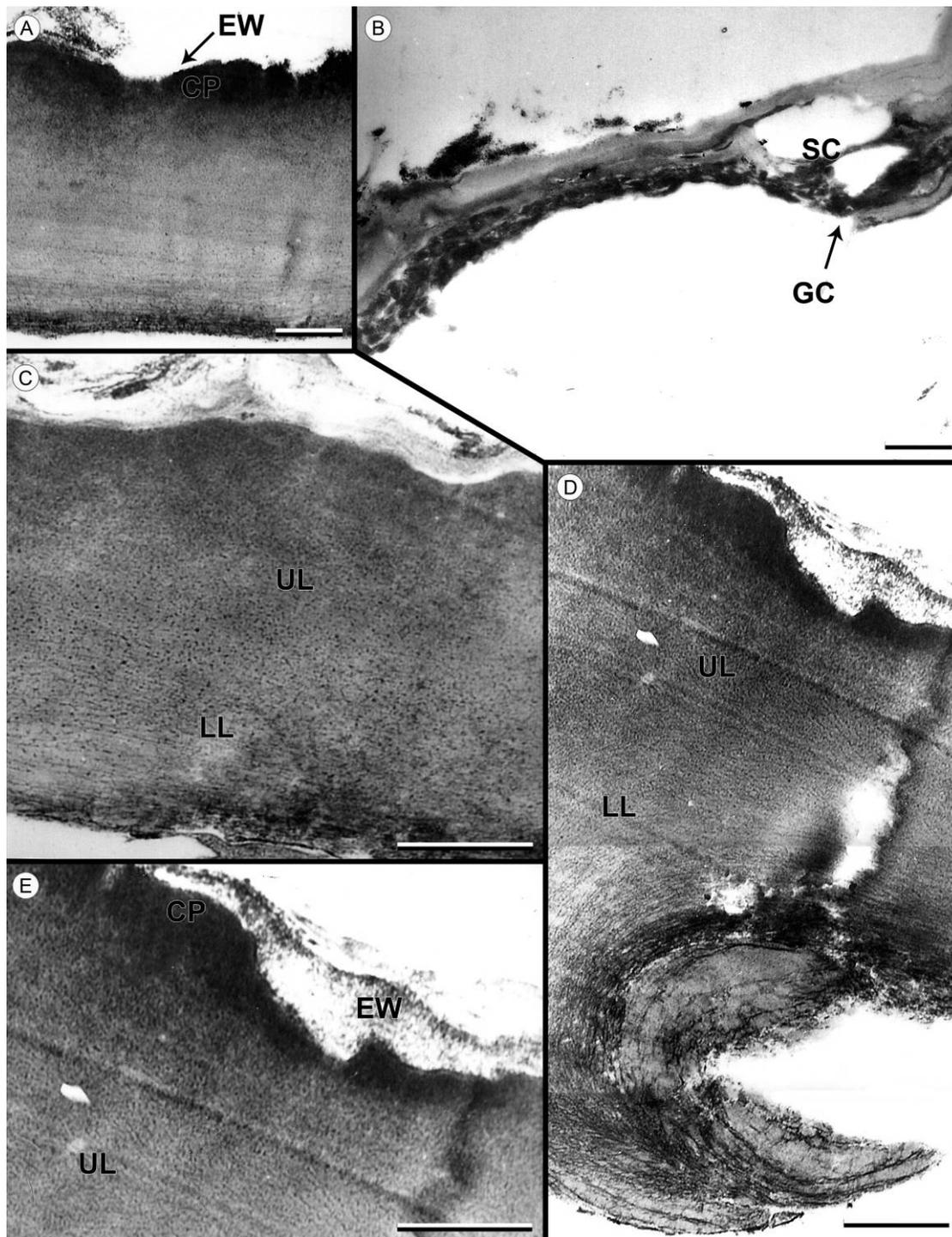
Fig. 5 *Ginkgoites patagonica* (Berry) comb. nov. TEM cuticular ultrastructure. *A*, Transverse sections (TS) of the external wall of the epidermis with epicuticular waxes on the surface (arrow) and details of the cuticle proper; BA Pb MET 219; scale bar = 1 μm. *B*, TS of a stomatal apparatus showing its subsidiary cells and remains of guard cells (arrow); BA Pb MET 219; scale bar = 10 μm. *C*, Detail of the epicuticular waxes and the upper and lower layers; BA Pb MET 220; scale bar = 1 μm. *D*, Detail of the upper and lower layers in a TS of an anticlinal wall; BA Pb MET 220; scale bar = 1 μm. *E*, Detail of the epicuticular waxes, cuticle proper, and upper layer; BA Pb MET 220; scale bar = 1 μm. EW = epicuticular waxes; CP = cuticle proper; UL = upper layer; LL = lower layer; SC = subsidiary cells; GC = guard cells.

The cuticle proper is 0.25–0.5 μm thick and has a granular aspect (fig. 5A, 5E). The cuticular membrane is 3.6 μm thick and formed by upper and lower layers (fig. 5C, 5D). The upper layer is 2.1 μm thick and has a higher electron density (fig. 5E). It is reticulated and forms a strong irregularly distributed net. This net is very dense in the upper zone while it is lax in the middle zone, finishing parallel to the lower layer (fig. 5C, 5D). The lower layer is 1.3 μm thick and has a reticulate structure disposed parallel to the surface (fig. 5C, 5D). The remnants of the cell wall are irregular and have a lower electron density, with a thickness of 0.5 μm (fig. 5C). The anticlinal walls have a major development of the lower layer where the pectinaceous microchannels are anastomosed and parallel to the surface (fig. 5D). The TS of a stoma shows the subsidiary cells and remnants of the guard cells with cutinized walls (fig. 5B).

Discussion

Generic Taxonomy

The use of different names for *Ginkgo*-like leaves has persisted since the nineteenth century (Heer 1881; Seward 1919; Florin 1936; Harris and Millington 1974; Watson et al. 1999, among others). This situation resulted from many attempts to attribute generic significance to observations of morphological and anatomical cuticle variations.

The importance of incorporating reproductive characters in order to be able to identify ginkgoalean fossil taxa was recently agreed upon (Crane 2013). This consensus resulted from analyzing reproductive structures that are extremely rare in the fossil record. In their pioneering article, Zhou and Zhang (1989) proposed to restrict the use of the generic name *Ginkgo* to only fossil species that are essentially similar to modern *Ginkgo biloba*, not only in leaf morphology but also in reproductive organs. The finding of similar fossil leaves in organic attachment to different ginkgoalean reproductive structures confirms the homoplasic nature of the typical ginkgoalean leaf. In this regard, Zhou (1997), in his attempt to perform a cladistic analysis on ginkgoalean taxa, was able to include only very few vegetative characters in his matrix. He also noted that reproductive organs provided most of the characters that could be reliable for phylogenetic interpretations. More recently, Yang et al. (2008) pointed out very clearly that it is uncertain how many isolated fossil leaves assigned to *Ginkgo* really do belong to it since the most informative characters for generic delimitation are features of the ovule-bearing organs. Therefore, the use of the whole-plant concept for ginkgoaleans (Rothwell and Holt 1997; Kvaček et al. 2005) has become essential for understanding natural taxa, including those with modern representatives. Thus, the fossil representation of the living genus *Ginkgo*, with more than 100 records, can be confirmed only by a few examples in which both vegetative and reproductive organs occur attached or at least intimately and repeatedly associated (i.e., taphonomically justified; Yang et al. 2008; Zhou et al. 2012).

Even though the whole-plant standard is obviously more realistic, it fails to provide a working approach for the innumerable records of isolated *Ginkgo*-like leaves that occur all over the world from the Permian through the Neogene. These *Ginkgo*-like leaves are often included in a ginkgoalean taxa (see, e.g., Zhou 1997; Naugolnykh 2007) because they might belong to more than one natural biological entity at family or generic level. This is why the name *Ginkgoites*, in spite of some morphological overlap with other similar taxa, for instance, *Baiera* (Watson et al. 1999), is highly useful as one of the generic names when such fossils cannot be attributed to any natural genus with certainty. Therefore, we propose to transfer the species *Ginkgo patagonica* to the genus *Ginkgoites* sensu Watson et al. (1999) based on the preserved morphological, anatomical, and ultrastructural characters of its cuticle.

Comparisons and Species Delimitation

Leaves of *Ginkgoites patagonica* were compared with the majority of known Cenozoic, Mesozoic, and Paleozoic ginkgoalean leaf species and also with leaves of the living *Ginkgo biloba*, which are summarized in tables 1 and 2, bringing out their morphologic, anatomic, and ultrastructural epidermal characters. In the following paragraphs, only *Ginkgo* and *Ginkgoites* species that have anatomical and ultrastructural cuticular descriptions are compared with *Ginkgoites patagonica*.

Ginkgo biloba L. has simple and small flabelliform leaves divided into two lobes. The veins are dichotomously forked, and there is a concentration of 18–20 veins/cm. Adaxial and abaxial epidermises have rectangular to polygonal cells. The abaxial epidermal cells are papillate. Stomatal apparatuses are actinocytic, with six to seven papillate subsidiary cells, and are present only on the abaxial surface. The external wall of the epidermis shows a cuticular membrane formed by a compact upper layer and a reticulate lower layer (Villar de Seoane 1997).

Ginkgo cranei Zhou, Quan et Liu 2012 from the late Paleocene Sentinel Butte Formation of the Fort Union Group, North Dakota, and *Ginkgo jiayinensis* Quan, Sun et Zhou 2010 from the Wuyun Formation (early Paleocene) of northeastern China differ in having semicircular leaves with smooth adaxial epidermis and slightly papillate abaxial epidermis. Stomata are on lower surfaces, are irregularly distributed, and have four to eight papillate subsidiary cells (Quan et al. 2010; Zhou et al. 2012).

Sun et al. (2008) described *Ginkgo longifolius* (Phillips) Harris and *Ginkgo shiguaiensis* Sun et al. from the Middle Jurassic of inner Mongolia, China, which differ in having amphistomatic four-lobed leaves. In addition, adaxial and abaxial epidermal cells are smooth, and stomatal apparatuses have four to six papillate subsidiary cells.

Ginkgo taeniata Geinitz has small and flabelliform leaves, six to eight lobed. The veins are dichotomous, with a concentration of 30–40 veins/cm. These impressions were found near Paso Flores, Lower Jurassic of Neuquén Province (Frenguelli 1937).

Ginkgoites patagonica has a similar morphology to *Ginkgo coriacea* (Sun 1993) except for the anatomy of the epidermal cells that are papillate in the Chinese species. Its ultrastructure was not studied.

Table 1

Morphological and Anatomical Features of *Ginkgo* Extant and Fossil Species

Species	Period	Origin	Morphology					Anatomical characters				Ultrastructure		
			Laminae	Size (width × length; cm)	Lobes	Veins/cm	Petiole width (cm)	Adaxial cells	Abaxial cells	Stomata	Subsidiary cells	Cuticle proper (μm)	Upper layer (μm)	Lower layer (μm)
Ginkgo biloba L. 1771 Villar de Seoane 1997	Recent	China	Lobed hypostomatic	8 (width)	2	18–20	.1	Smooth	Papillate	Actinocytic	6–7 papillate	.25, lamellate	.75, granular	1, reticulate
Ginkgo australis (Mc Coy) Drinnan et Chambers 1986	Paleogene	Tasmania	Lobed	5.0 × 8.0	6	...	...	...	...	...	...	...	...	...
Ginkgo cranei Zhou et al. 2012	Paleocene	United States	Entire hypostomatic	3.2–11.3 × 2.8–8.3	...	11–14	...	Smooth	Papillate	Incomplete bicyclic	4–8 papillate	...	...	...
Ginkgo coriacea Florin 1936, Sun 1993	Lower Cretaceous	China	Lobed hypostomatic	3.8–8.0 × 2.0–4.3	4	15–20	.1–.2	Papillate	Papillate	Actinocytic monocyclic	5–6 papillate	...	...	...
Ginkgo apodes Zheng et Zhou 2004	Lower Cretaceous	China	Lobed	1.5–3.0 × 1.4–2.3	5–8	8–15	.2	...	...	...	...	...	...	...
Ginkgo polaris Nathorst 1900, Florin 1936	Lower Cretaceous	North Pole	Lobed hypostomatic	2.5 × 3.5	4–8	25–35	...	Papillate	Papillate	Actinocytic	Papillate	...	...	...
Ginkgo longifolius Harris 1974, Sun et al. 2008	Middle Jurassic	China	Lobed amphistomatic	12 × 6–7	4	14–20	.1–.2	Smooth	Smooth	Actinocytic	4–6 papillate	...	...	...
Ginkgo shiguaiensis Sun et al. 2008	Middle Jurassic	China	Lobed amphistomatic	6–7 × 3–4	4	20–24	.1–.2	Smooth	Smooth	Actinocytic	4–6 papillate	...	...	...
Ginkgo yimaensis Zhou et Zhang 1989	Lower Jurassic	China	Lobed hypostomatic	4–13 × 3.3–8.0	4–8	7–18	.1–.3	Smooth	Smooth	Anomocytic	6–8 papillate	Polylamellate	Granular	Fibrillar
Ginkgo taeniata Geinitz (Frenguelli, 1937)	Lower Jurassic	Argentina/ Greenland	Lobed amphistomatic	2.2 × 2.7	4–8	30–40	...	Papillate	Smooth	Actinocytic	5 papillate	...	...	...

Table 2

Morphological and Anatomical Features of *Ginkgoites* Species, Including *Ginkgoites patagonica*

Species	Period	Origin	Morphology					Anatomical characters				Ultrastructure		
			Laminae	Size (width × length; cm)	Lobes	Veins/cm	Petiole width (cm)	Adaxial cells	Abaxial cells	Stomata	Subsidiary cells	Cuticle proper (μm)	Upper layer (μm)	Lower layer (μm)
Ginkgoites patagonica (Berry) comb. nov. (this article)	Eocene	Argentina	Lobed hypostomatic	8 × 11.5	4–8	6–14	.3	Striate	Striate	Tetracytic-actinocytic	4–7 papillate	.25–.5, granular	2.1, reticulate	1.3, reticulate
Ginkgoites skottsbergii Lundblad 1971, Del Fueyo et al. 2006	Albian	Argentina	Lobed amphistomatic	4 × 5	8–12	...	...	Smooth	Smooth	Actinocytic	6–8 papillate	.35, granular	.7, reticulate	.5, reticulate
Ginkgoites ticoensis Archang. 1965, Del Fueyo et al. 2013	Aptian	Argentina	Lobed hypostomatic	3 × 4	4	12	.1	Papillate	Papillate	Actinocytic	5–7 papillate	.6–1, granular	.6, reticulate	.13, fibrillar
Ginkgoites tigrensis Archang. 1965, Villar de Seoane 1997	Aptian	Argentina	Lobed amphistomatic	5 × 4.5	3–6	18–20	.1	Smooth	Smooth	Tetracytic-actinocytic	4–6 striated	.25, compact	1.0, compact	1.5, reticulate
Ginkgoites myrioneurus Yang 2004	Barremian	China	Lobed hypostomatic	8 × 3.8	8–18	20–30	.1–.2	Papillate	Papillate	Actinocytic bicyclic	6–8 papillate	...	...	...
Ginkgoites pluripartita Seward 1919, Tralau 1968	Lower Cretaceous	Germany	Lobed hypostomatic	1.5–10 × 2.5	4–10	20–30	.1–.2	Papillate	Papillate	Actinocytic	4–8 papillate	...	...	...
Ginkgoites brauniana Watson et al. 1999	Lower Cretaceous	Germany	Lobed hypostomatic	1.5–10 × 2.5	9–17	18–20	.1–.2	Smooth	Papillate	Actinocytic	5–7 papillate	...	...	...
Ginkgoites multiloba Douglas 1970	Lower Cretaceous	Australia	Lobed hypostomatic	2.5–3.5 (length)	6–8	13–15	.2	Haired	Haired	Actinocytic	5–7 papillate	...	...	...
Ginkgoites obrutschewii Seward 1919	Middle Jurassic	China	Lobed hypostomatic/ amphistomatic	.8–1.8 × 2–5	2–4	9–11	.1–12	Smooth	Smooth	Actinocytic	4–7 papillate	...	...	...
Ginkgoites buttonii Heer 1881, Tralau 1968	Middle Jurassic	England	Lobed amphistomatic	...	2–12	...	...	Smooth	Papillate	Actinocytic	6 papillate	...	...	...
Ginkgoites regnellii Tralau 1968	Middle Jurassic	Sweden	Lobed hypostomatic	.8–6 × 6.7	3–8	10	.1	Smooth	Smooth	Actinocytic monocytic	4–6 papillate	...	...	...
Ginkgoites sibirica Seward 1919, Tralau 1968	Middle Jurassic	Siberia	Lobed hypostomatic	...	8–10	10–14	...	Papillate	Papillate	Actinocytic	Papillate	...	...	...
Ginkgoites truncata Frenguelli 1946	Triassic	Argentina	Entire	.8–2.5 × 2.5–4.6	0	31–32	...	...	...	...	...	...	...	...
Ginkgoites feruglioi Cúneo 1987	Permian	Argentina	Entire	3.3 × 1.6	0	30	.15	...	...	...	...	...	...	...
Ginkgoites eximia Feruglio 1942	Permian	Argentina	Entire or lobed	3.0–5.0 × 1.9–3.0	0–2	32–45	.2	...	...	...	...	...	...	...
Ginkgoites crassipes Feistmantel (Feruglio 1933)	Permian	Argentina	Entire	2.6 × 4	0	...	...	...	...	...	...	...	...	...

Ginkgoites skottsbergii Lundblad (1971) from the Kachaike Formation, Albian of Santa Cruz Province, has flabelliform and amphistomatic leaves divided into 8–12 lobes with veins dichotomously forked. Adaxial and abaxial epidermises have isodiametric to polygonal cells and actinocytic stomatal apparatuses with six to eight papillate subsidiary cells. The epidermis wall has a granular external layer and reticulate middle and internal layers (Del Fueyo et al. 2006, 2013).

In the Anfiteatro de Ticó Formation, Aptian of Santa Cruz Province, two ginkgoalean species were found. *Ginkgoites tigrensis* Archangelsky has simple and small flabelliform leaves with three to six segments. The veins dichotomously forked, and there is a concentration of 18–20 veins/cm. Adaxial and abaxial epidermises have rectangular to isodiametric cells and actinocytic stomatal apparatuses with four to six striated subsidiary cells. The external wall of the epidermis shows a cuticular membrane formed by a compact upper layer and a reticulate lower layer (Villar de Seoane 1997). *Ginkgoites ticoensis* Archangelsky shows flabelliform leaves divided into four lobes with veins dichotomously forked. Adaxial and abaxial epidermises show papillate cells. Stomata are present in the abaxial surface and have five to seven papillate subsidiary cells. The external wall of the epidermis has a granular external layer, a reticulate middle layer, and a fibrillose internal layer (Del Fueyo et al. 2006, 2013).

Ginkgoites truncata Frenguelli (1946) from the Cacheuta Series, Triassic of Mendoza Province, presents entire and flabelliform leaves of different sizes (24.5–46 mm long and 8–25 mm wide).

In the valley of Río Genoa (Permian of Chubut Province), the impressions of three species were described: *Ginkgoites crassipes* Feistmantel shows an entire and flabelliform leaf with a long petiole (Feruglio 1933); *Ginkgoites eximia* Feruglio (1942) shows entire or bilobed leaves with thin petioles (the veins are radially disposed from the base, with a concentration of 32–45 veins/cm); and *Ginkgoites feruglioi* Cúneo (1987) has flabelliform and entire leaves with long petioles and veins dichotomously forked, with a concentration of 30 veins/cm in the upper margin.

Hill and Carpenter (1999) compared *Ginkgoites patagonica* with new specimens of *Ginkgo australis* (Mc Coy) Drinnan and Chambers 1986 from the Paleogene (probably Eocene) of Tasmania. Since the Australian materials are only impressions, they were able to compare only the leaf morphology. Thus, these authors indicated that the species from Argentina was more deeply lobed and perhaps slightly asymmetrical. However, these are highly variable traits, suggesting that *G. australis* and *Ginkgoites patagonica* might be more closely related than previously thought. This idea is consistent with the large and expanding list of plant taxa that have been found from Paleogene sediments of both southern Australia and Patagonia, indicating large trans-Antarctic paleodistributions (e.g., Wilf et al. 2013).

Evolution of Ginkgophytes in Argentina

The Ginkgoales were an important component of the plant communities of Patagonia from Permian to middle Eocene, with a climax during the early Cretaceous. The comparison of the foliar morphology and diversification among Paleozoic, Mesozoic, and Tertiary ginkgoalean species with *Ginkgo bi-*

loba showed a multilobed fossil leaf in opposition to a bilobed living leaf (fig. 6). Permian species (*Ginkgoites crassipes*, *Ginkgoites eximia*, and *Ginkgoites feruglioi*) are characterized by impressions of entire to bilobed flabelliform leaves from the valley of Río Genoa (Chubut Province).

Ginkgoites truncata, another entire flabelliform leaf, is the only species that was found outside of Patagonia, in the Triassic strata of Cacheuta, Mendoza Province. During the Lower Jurassic, the ginkgoalean species were represented by multilobed leaves of *Ginkgo taeniata* from Paso Flores, Neuquén Province. At the beginning of Cretaceous, the Ginkgoaceae increased in amount and diversity. In the Aptian sediments of the Anfiteatro de Ticó Formation (Baqueró Group), a larger number of multilobed leaves were found, such as *Ginkgoites ticoensis* and *Ginkgoites tigrensis*. Some specimens of the latter species appeared in organic connection with the female reproductive organ *Karkenia incurva* Archangelsky 1965, being the first member (at present day, the unique species) belonging to the Karkeniaceae found in the Southern Hemisphere. In the Albian of Kachaike Formation, *Ginkgoites skottsbergii* was found, a leaf with 8–12 lobes.

Finally, in the early/middle Eocene of Chubut Province, tetralobed leaves of *Ginkgoites patagonica* were found. After this time, no ginkgoalean leaf remains appeared in the Cenozoic strata of Argentina.

Morphologically, the flabelliform leaves of the Argentinean species show a varied type of laminae though the geological time. They are entire or bilobed in the Permian and Triassic, multilobed in Jurassic and Cretaceous, and tetralobed in Eocene. This variance in the lamina is similar to the variability in the lamina of the Northern Hemisphere species (Tralau 1968), except in the Cenozoic specimens where *Ginkgo adiantoides* (Unger) Heer shows flabelliform to reniform leaves with entire to bilobed lamina (Shaparenko 1935).

Ginkgo adiantoides, whose leaves show the modern biloba type, appeared in the early Cretaceous of Siberia and was very abundant during the late Cretaceous and Paleogene of the Northern Hemisphere (Tralau 1968). It had a large distribution in the Cretaceous of Greenland and in the early Cretaceous of Montana, Wyoming, and South Dakota (Shaparenko 1935).

Zhou (1991) made a cladistic analysis of Mesozoic ginkgos, including in the order Ginkgoales (Gorozhankin 1904) the female reproductive organs and leaves of the following taxa: *Trichopitys* (Saporta) Florin, *Karkenia* Archangelsky, *Toretzia* Stanislavsky, *Umaltolepis* Krassilov, *Yimaia* Zhou and Zhang, *Ginkgo yimaensis* Zhou and Zhang, and *Ginkgo* L. In this analysis, Zhou observed that *Ginkgo* leaves have had a general tendency toward transformation from deeply divided to less divided lamina through geological time, and he indicated that leaves and bracts of Ginkgoales tend to be laminated and petiolate due to planation, webbing, and fusion of telomes and mesomes. In other words, the Argentinean species began with entire or bilobed laminae during Permian and Triassic times, then showed multilobed leaves in Jurassic and Cretaceous strata, and finished with tetralobed laminae in the Eocene.

Disappearance of the Ginkgophytes from the Southern Hemisphere

In the Southern Hemisphere, *Ginkgoites* is found only in Argentina and apparently Australia, where in each case no fos-

sils thus far can be confidently assigned to the genus *Ginkgo*. In Argentina, *Ginkgoites* (*Ginkgoites crassipes*, *Ginkgoites eximia*, and *Ginkgoites feruglioi*) first appears in sediments of Permian age (Feruglio 1933, 1942; Cúneo 1987), and its last appearance is recorded during the middle Eocene (Berry 1935, 1938; this article). In Australia, a probable *Ginkgoites* (*G. australis*) is recorded only for the early Cretaceous and Paleogene (Douglas 1970). In contrast, both *Ginkgo* and *Ginkgoites* are known from the Northern Hemisphere. *Ginkgoites* is recorded from the middle Jurassic to the Barremian, while the oldest record for *Ginkgo* was registered in the early Jurassic of China (where it still grows naturally; Zhou and Zhang 1989), reaching its maximum diversity globally during the Cretaceous (see tables 1, 2).

Possible causes for the disappearance of the clade in the Southern Hemisphere and for its extreme decline in the Northern Hemisphere have been traditionally linked to major climatic, biological, or ecological shifts that probably started during the middle Cretaceous (Seward 1900; Florin 1949; Tralau 1968; Tiffney 1984; Rothwell and Holt 1997; Royer et al. 2003; Crane 2013). However, as in many other extinction events, a combination of causes is probably the most plausible explanation.

The principal cause for the disappearance of the ginkgoalean clade may be associated with climatic changes. Cooling conditions have been suggested in both hemispheres approximately during the Paleogene-Neogene transition as well as a major shift to lower moisture levels at middle latitudes worldwide. In this regard, Uemura (1997) suggested lower moisture levels as a possibility for explaining the decrease of the ginkgophytes after the Paleogene. During the Neogene, the climatic conditions of most of Asia and North America changed, but less so in southeastern Asia (including southern China), where warmer and wetter conditions were maintained and therefore helped to protect *Ginkgo* during the Quaternary (Shaparenko 1935; Tralau 1968).

Southern-latitude floras suffered the loss of many taxa during and at the end of the Eocene, but the majority of losses occurred through the Oligocene and Miocene (Askin and Spicer 1995). The climatic deterioration by the late Eocene–early Oligocene was a result of different factors, especially the dramatic decrease in the ability of the ocean to transport heat into the Southern Hemisphere and especially in Patagonia, where the deepwater opening of the Drake Passage and Tasman Gateway with the rapidly expanding Antarctic ice sheets (Zachos et al. 2001, 2008; Huber and Nof 2006). During the Oligocene, Patagonia had a drastic decrease in plant diversity due to major tectonic and climatic changes. Surface temperatures became colder, and the floras suffered the loss of many mesothermal taxa and communities. A similar decrease in diversity is observed at northern high latitudes (Askin and Spicer 1995).

Ginkgoites patagonica occurred as a minor component in both the Laguna del Hunco (early Eocene) and Río Pichileufú (middle Eocene) floras, which were mostly dominated by dicot taxa with a strong secondary representation of conifers. Remarkably, the mean annual temperature (MAT) and precipitation have been estimated for the Laguna del Hunco flora as 16.6° ± 2.0°C and 1.1 m/yr, respectively, while for Río Pichileufú, a higher though preliminary MAT of 19.2° ± 2.4°C was estimated (Wilf et al. 2003, 2005). Modern *Ginkgo*

grows naturally in mixed mesophytic forest communities of the Yangtze River Valley in China (Wang 1961; Zheng 1992; Ke et al. 1994; Tang et al. 2012). The paleoclimate parameters would indicate a similar climate present at the time of fossil deposition. Both Patagonian floras were part of a subtropical–tropical-like, possibly montane rainforest biome (Wilf et al. 2009) bounded by cooler winters to the south and arid conditions to the north (Wilf et al. 2005).

Another possible cause for ginkgophyte decline may be related to their reproductive biology. For instance, Florin (1949) suggested that because ginkgophytes were not able to develop seed cones, as in conifers or cycads, their success in reproduction and further distribution was limited. Associated with this, a low seed production has also been suggested as a restriction for dispersal. Regarding this, Tiffney (1984) and Rothwell and Holt (1997) have suggested that the post-Cretaceous ginkgophyte decline was related to the extinction of the dinosaurs, since these were probably the main dispersers of their seeds; however, there is no evidence that supports this claim (Hori et al. 1997). Other agents of dispersions could have been the early mammals of the extinct family Multituberculata (Del Tredici 1989); these animals, often known as the rodent of the Mesozoic, were found in the temperate parts of the Northern Hemisphere from the late Jurassic through the Oligocene. Rothwell and Holt (1997 and citations therein) indicated that there is evidence that modern *Ginkgo* seeds are consumed and dispersed by small mammals such as the red-bellied squirrel (*Callosciurus flavimanus* var. *ningpoens*, which lives in the natural *Ginkgo* populations in China), the eastern grey squirrel (*Sciurus carolinens*, found in planted *Ginkgo* populations in Canada), and the masked palm civet (*Paguma larvata*, also from China; Del Tredici et al. 1992).

Finally, paleoenvironmental changes could have also affected the distribution of ginkgophytes; however, Royer et al. (2003) have demonstrated that for the Northern Hemisphere there were no major changes from the Cretaceous through the Eocene in the paleoenvironments occupied by the fossilized ginkgophytes, which mostly grew in riparian zones and up the slopes of adjacent levees. In the Patagonian region, known plant communities including ginkgophytes grew in riparian zones on extensive open plains during the early Cretaceous or deltaic environments in the latest Cretaceous, while by the Eocene, *Ginkgoites patagonica* was part of plant communities that mostly grew on the margins of lacustrine settings that probably developed at mid- to high altitudes (Wilf 2012). In all cases, ginkgophyte communities were linked to warm and relatively moist (but most probably seasonal) climatic conditions that definitely changed to cooler and drier ones from the middle-late Eocene in southern South America.

Overall, since ginkgophytes represented a mid- to high-latitude lineage, their growth and development were limited by light and temperature. Therefore, major post-Eocene climatic changes, which first affected high latitudes, promoted the ginkgoalean decline in both hemispheres. As mentioned earlier, at least *Ginkgo* reached its maximum diversity during the Cretaceous at the same time that the angiosperms started to be more prominent within the communities (Wing and Boucher 1998), so it is possible that the angiosperm competition also played a role in the same process that affected all gymnosperms in both hemispheres (Royer et al. 2003;
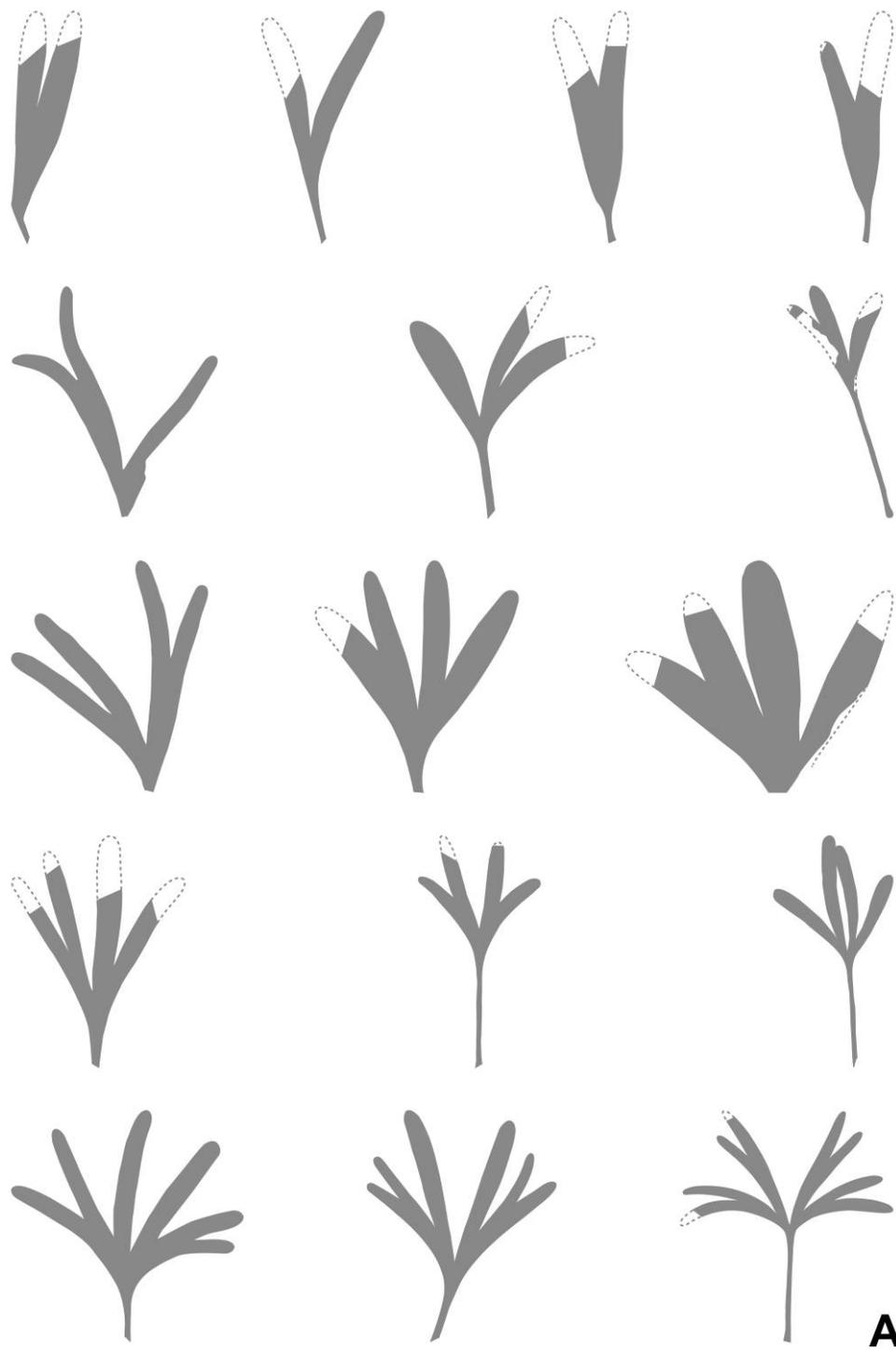
Fig. 6 *A*, *Ginkgoites patagonica* (Berry) comb. nov. Leaf morphology variations. *B*, *Ginkgo biloba* L. leaf morphology variations. Modified from Tralau (1968).
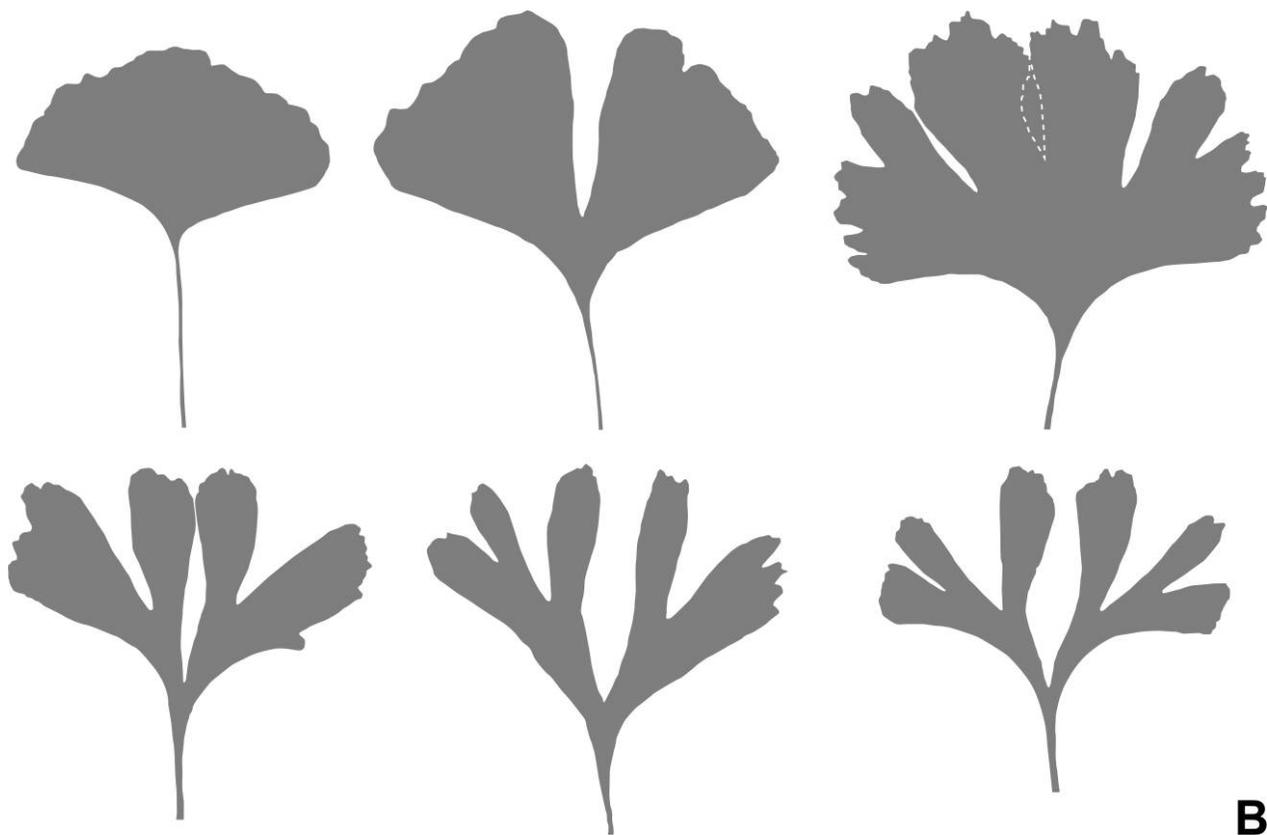
B

Fig. 6   (*Continued*)

Archangelsky et al. 2009), perhaps more accentuated for the ginkgophytes in southernmost regions.

From a taxonomical viewpoint, however, it would be of particular interest to elucidate which particular internal ginkgophyte lineage (or clade) disappeared from the Southern Hemisphere record. According to Zhou (1997) and Del Fueyo and Archangelsky (2001), the ginkgophytes were represented by three clades or evolutionary lineages. Based on a whole-plant record, only the Mesozoic family Karkeniaceae has been clearly recorded in the Southern Hemisphere (Archangelsky 1965). This had prompted Krassilov (1970), after discovering similar materials in Asia, to define the family Karkeniaceae, thus taxonomically separating multiovulate organs (Karkeniaceae) from the classical two- to three-ovulate Ginkgoaceae (see also Zhou et al. 2002). However, a major point is how homologous *Karkenia* and *Ginkgo* reproductive structures are. In his recent contribution on *Ginkgo*, Crane (2013, p. 116) explicitly said on *Karkenia*, "I was skeptical whether they had anything to do with living ginkgo," although he accepted ginkgoalean affinity of *Karkenia* after these reproductive structures with clearly *Ginkgo*-like leaves were found in intimate association in different and far-distant regions such as Asia and South America, as recorded by Archangelsky (1965), Krassilov (1970), and Zhou et al. (2002). In any case, as Crane (2013) suggested, *Karkenia*-like plants probably represent an ancient ginkgo lin-

eage that we still do not understand. It is noteworthy that all Cretaceous-Paleogene leaf records belong to the multilobed type, including those of *Ginkgoites patagonica* in the Southern Hemisphere. A similar case seems to be present in Australia, with the species *G. australis* apparently extending its range throughout the Paleogene (Drinnan and Chambers 1986; Douglas 1994; Hill and Carpenter 1999). In this case, as pointed out by Crane (2013), it is quite possible that all of these Southern Hemisphere ginkgoaleans were *Karkenia*-like plants that survived the K-Pg boundary event. On the contrary, the Northern Hemisphere record suggests that a trend from lobed to entire leaves existed from the Jurassic through the Paleogene, culminating with the modern *Ginkgo biloba*. Does this mean that the ginkgoaeceous (true ginkgophyte) lineage or clade (?) was never present in the Southern Hemisphere? It could be the case; however, it can be tested only after reproductive organs associated with late Cretaceous and Paleogene leaves are found.

Conclusions

Based on the evidence herein provided, the new combination *Ginkgoites patagonica* for the Patagonian Eocene fossils previously assigned to *Ginkgo patagonica* is proposed. This new combination and emended diagnosis are supported by morphological, anatomical, and ultrastructural studies and

comparison of the Patagonian materials and other *Ginkgoites* and *Ginkgo*-like leaves from both hemispheres.

The comparison between *Ginkgoites patagonica* and the other *Ginkgoites* Argentinian species showed the following similarities: *Ginkgoites patagonica* and *Ginkgoites ticoensis* have hypostomatic lobed leaves, a granular cuticle proper, and a reticulate upper layer in the cuticular membrane. *Ginkgoites patagonica* and *Ginkgoites tigrensis* have tetracytic-actinocytic stomatal apparatuses with papillate subsidiary cells and a reticulate lower layer in the cuticular membrane. *Ginkgoites patagonica* and *Ginkgoites skottsbergii* have a granular cuticle proper and reticulate upper and lower layers in the cuticular membrane. On the other hand, *Ginkgoites patagonica* differs from *Ginkgo biloba* in having four- to eight-lobed leaves, striate adaxial and abaxial epidermal cells, tetracytic-actinocytic stomatal apparatuses, granular cuticle proper, and reticulate upper layer in the cuticular membrane.

The homoplastic nature of most of the foliar characters identified in fossil and living ginkgophytes does not allow a clear and natural affinity for isolated leaves, although some of these characters can be useful for species delimitation. Temperatures of the southern oceans show a striking change during the Eocene-Oligocene transition. The dramatic climatic deterioration at the beginning of the Oligocene that occurred in the Southern Hemisphere probably influenced the extinction of *Ginkgoites* in Patagonia and the whole Southern Hemi-sphere. At the beginning of the Eocene, *Ginkgoites patagonica* was present in the plant communities and can be considered the last representative of a poorly understood (at the whole-plant level) southern ginkgophyte lineage distinct from the lineage of *Ginkgo biloba* in the Northern Hemisphere.

Literature Cited

Aragón E, MM Mazzoni 1997 Geología y estratigrafía del complejo volcánico piroclástico del Río Chubut medio (Eoceno), Chubut, Argentina. Rev Asoc Geol Argent 52:243–256.

Archangelsky S 1965 Fossil Ginkgoales from the Ticó flora, Santa Cruz Province, Argentina. Bull Br Mus (Nat Hist) Geol 10:119–137.

Archangelsky S, OG Arrondo 1974 Dos especies de *Ginkgophyllum* del Paleozoico Superior de la Provincia de La Rioja. Ameghiniana 11:357–365.

Archangelsky S, V Barreda, M Passalía, MA Gandolfo, M Prámparo, E Romero, NR Cúneo, et al 2009 Early angiosperm diversification: evidence from southern South America. Cretac Res 30:1073–1082.

Archangelsky S, RN Cúneo 1990 *Polyspermophyllum*, a new Permian gymnosperm from Argentina, with considerations about the Dicranophyllales. Rev Palaeobot Palynol 63:117–135.

Archangelsky S, R Leguizamón 1980 El registro de *Ginkgophyllum diazii* en el Carbónico de Sierra de Los Llanos, Provincia de La Rioja. Bol Acad Nac Cienc Cordoba 53:211–219.

Askin R, R Spicer 1995 The late Cretaceous and Cenozoic history of vegetation and climate at northern and southern high latitudes: a comparison. Pages 156–173 *in* Effects of past global change on life: studies in geophysics. Board on Earth Sciences and Resources, Commission on Geosciences, Environment, and Resources, National Research Council, ed. National Academy, Washington, DC.

Azcuy CA, AM Baldoni 1990 La flora triásica del Grupo El Tranquilo, provincia de Santa Cruz (Patagonia). Pt 3. Ginkgoales. 5th Congr Argent Paleontol Bioestratigr (Tucumán, Argentina) Actas 7:109–115.

Barreda VD, NR Cúneo, P Wilf, ED Currano, RA Scasso, H Brinkhuis 2012 Cretaceous/Paleogene floral turnover in Patagonia: drop in diversity, low extinction, and a *Classopollis* spike. PLoS ONE 7: e52455.

Berry EW 1934 Miocene Patagonia. Proc Natl Acad Sci USA 20:280–282.

——— 1935 A tertiary *Ginkgo* from Patagonia. Torreya 35:11–13.

——— 1938 Tertiary flora from the Río Pichileufu, Argentina. Geol Soc Am 12:1–49.

Crane PR 2013 *Ginkgo*. Yale University Press, New Haven, CT.

Cúneo NR 1987 Sobre la presencia de probables Ginkgoales en el Pérmico Inferior de Chubut, Argentina. Pages 47–50 *in* Actas del VII Simposio Argentino de Paleobotánica y Palinología, Buenos Aires.

Cúneo NR, K Johnson, P Wilf, R Scasso, MA Gandolfo, 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, 584.

Del Fueyo GM, S Archangelsky 2001 New studies on *Karkenia incurva* Archang. from the Early Cretaceous of Argentina: evolution of the seed cone in Ginkgoales. Palaeontogr Abt B 256:111–121.

Del Fueyo GM, G Guignard, L Villar de Seoane, S Archangelsky 2013 Leaf cuticle anatomy and the ultrastructure of *Ginkgoites ticoensis* Archang. from the Aptian of Patagonia. Int J Plant Sci 174:406–424.

Del Fueyo GM, L Villar de Seoane, S Archangelsky, G Guignard 2006 Estudios cuticulares de *Ginkgoites* Seward del Cretácico Inferior de Patagonia. Rev Mus Argent Cienc Nat 8:143–149.

Del Tredici P 1989 Ginkgos and multituberculates: evolutionary interactions on the Tertiary. Biosystems 22:327–339.

Del Tredici P, H Ling, G Yang 1992 The Ginkgos of Tian Mu Shan. Conserv Biol 6:202–209.

Douglas JG 1970 *Ginkgoites multiloba*: a new *Ginkgo*-like leaf. Min Geol J 6:28–31.

——— 1994 Cretaceous vegetation: the macrofossil record. Pages 171–188 *in* RS Hill, ed. History of Australian vegetation: Cretaceous to recent. Cambridge University Press, Cambridge.

Drinnan A, TC Chambers 1986 Flora of the Lower Cretaceous Koonwarra fossil bed (Korumburra Group), South Gippsland, Victoria. Mem Assoc Aust Palaeontol 3:1–77.

Escapa I, NR Cuneo 2003 Una nueva especie de *Ginkgophyllum* Saporta *ex* Neuburg en el Pérmico temprano de Chubut, Argentina. Rev Mus Argent Cienc Nat 5:181–184.

Feruglio E 1933 Fossili Liassici della Valle del Rio Genua (Patagonia). Estratto G Geol Ann R. Mus Geol Bologna 9:1–64.

——— 1942 La Flora Liásica del Valle del Río Genoa (Patagonia): Ginkgoales et Gymnospermae incertae sedis. Not Mus La Plata Paleontol 7:93–110.

Florin R 1936 Die fossilen Ginkgophyten von Franz-Joseph-Land nebst Erörterungen uber vermeintliche Cordaitales mesozoischen Alters. I. Spezieller Teil. Palaeontogr Abt B 81:71–173.

——— 1949 The morphology of *Trichopitys heteromorpha* Saporta, a seed-plant of Palaeozoic age, and the evolution of the female flowers in the Ginkgoinae. Acta Hortic Bergiani 15:79–109.

Frenguelli J 1937 La flórula jurásica de Paso Flores en el Neuquén. Con referencias a la de Piedra Pintada y otras floras jurásicas argentinas. Rev Mus La Plata Paleontol 1:67–108.

——— 1946 Contribuciones al conocimiento de la flora del Gondwana Superior en la Argentina XXXIII. Not Mus La Plata Paleontol 11:101–127.

Gnaedinger S, R Herbst 1999 La flora triásica del Grupo El Tranquilo, provincia de Santa Cruz, Patagonia. Pt 6. Ginkgoales. Ameghiniana 36:281–296.

Gorozhankin IN 1904 Lekts. Morf Sist Archegon 73.

Harris TM, W Millington 1974 Ginkgoales. Pages 2–78 *in* TM Harris, W Millington, J Miller, eds. The Yorkshire Jurassic flora. Vol 4. Ginkgoales and Czekanowskiales. British Museum (Natural History), London.

Heer O 1881 Zur Geschichte der *Ginkgo*-artigen Bäume. Pages 1–13 *in* HGA Engler, ed. Botanische Jahrbucher für Systematik Pflanzengeschichteund Pflanzengeographie. Engelmann, Leipzig.

Hill RS, RJ Carpenter 1999 *Ginkgo* leaves from Paleogene sediments in Tasmania. Aust J Bot 47:717–724.

Holloway PJ 1982 Structure and histochemistry of plant cuticular membranes: an overview. Pages 1–31 *in* DF Cutler, KL Alvin, CE Price, eds. The plant cuticle. Academic Press, London.

Hori T, RW Ridge, W Tulecke, P Del Tredici, J Trémouillaux-Guiller, H Tobe, eds 1997 *Ginkgo biloba*: a global treasure. Springer, Tokyo.

Huber M, D Nof 2006 The ocean circulation in the southern hemisphere and its climatic impacts in the Eocene. Palaeogeogr Palaeoclimatol Palaeoecol 231:9–28.

Ke YX, F Li-kuo, RR Mill 1994 Ginkgoaceae. Page 453 *in* W Zheng-yi, PH Raven, eds. Flora of China. Vol 4. Cycadaceae through Fagaceae. Science/Missouri Botanical Garden, Beijing/St. Louis.

Krassilov VA 1970 Approach to the classification of Mesozoic ginkgoalean plants from Siberia. Palaeobotanist 18:12–19.

Kvaček J, HJ Falcon-Lang, J Daskova 2005 A new Late Cretaceous ginkgoalean reproductive structure *Nehvizdyella* gen. nov. from the Czech Republic and its whole-plant reconstruction. Am J Bot 92:1958–1969.

Lundblad B 1971 A re-study of the ginkgoalean leaves of the Mesozoic flora of Lago San Martin, Patagonia (*Ginkgoites skottsgergii* n.sp.). J Indian Bot Soc 50:236–241.

Lyshede OB 1978 Studies on outer epidermal cell walls with microchannels in a xerophytic species. New Phytol 80:421–426.

——— 1982 Structure of the outer epidermal wall in xerophytes. Pages 87–97 *in* DF Cutler, KL Alvin, CE Price, eds. The plant cuticle. Academic Press, London.

Metcalfe CR, L Chalk 1979 Anatomy of dicotyledons. Vol 1. Clarendon, Oxford.

Nathorst AG 1900 Fossil plants from Franz Josef Land. Pages 1–26 *in* F Nansen, ed. The Norwegian North Polar expedition 1893–1896. Longmans, Green, London.

Naugolnyk SV 2007 Foliar seed-bearing organs of Paleozoic Ginkgophytes and the early evolution of the Ginkgoales. Paleontol J 41:815–859.

Passalia M 2007 Nuevos registros para la flora Cretácica descripta por Halle (1913) en lago San Martín, Santa Cruz, Argentina. Ameghiniana 44:565–595.

Quan C, G Sun, Z Zhou 2010 A new Tertiary Ginkgo (Ginkgoaceae) from the Wuyun Formation of Jiayin, Heilongjiag, northeastern China and its paleoenvironmental implications. Am J Bot 97:446–457.

Rothwell GW, B Holt 1997 Fossils and phenology in the evolution of *Ginkgo biloba*. Pages 223–230 *in* T Hori, RW Ridge, W Tulecke, P Del Tredici, J Trémouillaux-Guiller, H Tobe, eds. *Ginkgo biloba*, a global treasure: from biology to medicine. Springer, Tokyo.

Royer DL, LJ Hickey, SL Wing 2003 Ecological conservatism in the "living fossil" *Ginkgo*. Paleobiology 29:84–104.

Seward AC 1900 The Jurassic flora. I. The Yorkshire Coast. Vol 3. Catalogue of the Mesozoic Plants in the Department of Geology, British Museum (Natural History), London.

——— 1919 Fossil plants. Vol 4. Ginkgoales, Coniferales, Gnetales. Cambridge University Press, Cambridge.

Shaparenko K 1935 *Ginkgo adiantoides* (Unger) Heer: contemporary and fossil forms. Philipp J Sci 57:1–28.

Spurr AR 1969 A low-viscosity epoxy embedding medium for electron microscopy. J Ultrastruct Res 26:31.

Stewart W, G Rothwell 1993 Paleobotany and the evolution of plants. 2nd ed. Cambridge University Press, Cambridge.

Sun C, DL Dilcher, H Wang, G Sun, Y Ge 2008 A study of *Ginkgo* leaves from the Middle Jurassic of Inner Mongolia, China. Int J Plant Sci 169:1128–1139.

Sun G 1993 Ginkgo Coriacea florin from Lower Cretaceous of Huolinhe, northeastern Nei Monggol, China. Palaeontographica Abt B 230:159–168.

Tang X, Y Wu, TY Belenkaya, Q Huang, L Ray, J Qu, X Lin 2012 Roles of N-glycosylation and lipidation in Wg secretion and signaling. Dev Biol 364:32–41.

Taylor TN, EL Taylor, M Krings 2009 Paleobotany: the biology and evolution of fossil plants. 2nd ed. Elsevier, New York.

Tiffney B 1984 Seed size, dispersal syndromes, and the rise of angiosperms: evidence and hypothesis. Ann Mo Bot Gard 71:551–576.

Tralau H 1968 Evolutionary trends in the genus *Ginkgo*. Lethaia 1:63–101.

Traverso NE 1964 La epidermis de *Ginkgo patagonica* Berry, del Terciario de El Mirador, provincia del Chubut. Ameghiniana 3:163–168.

Uemura K 1997 Cenozoic history of *Ginkgo* in East Asia. Pages 207–221 *in* T Hori, RW Ridge, W Tulecke, P Del Tredici, J Trémouillaux-Guiller, H Tobe, eds. *Ginkgo biloba*, a global treasure: from biology to medicine. Springer, Tokyo.

Villar de Seoane L 1997 Comparative study between *Ginkgoites tigrensis* Archangelsky and *Ginkgo biloba* Linn. Leaves. Palaeobotanist 46:1–12.

Wang CW 1961 The forests of China. Harvard University, Cambridge, MA.

Watson J, SJ Lydon, NA Harrison 1999 Consideration of the genus *Ginkgoites* Seward and a redescription of two species from the Lower Cretaceous of Germany. Cretac Res 20:719–734.

Wilf P 2012 Rainforest conifers of Eocene Patagonia: attached cones and foliage of the extant Southeast Asian and Australasian genus *Dacrycarpus* (Podocarpaceae). Am J Bot 99:562–584.

Wilf P, NR Cúneo, KR Johnson, JF Hicks, SL Wing, JD Obradovich 2003 High plant diversity in Eocene South America: evidence from Patagonia. Science 300:122–125.

Wilf P, NR Cúneo, D Pol, I Escapa, M Woodburne 2013 Splendid and seldom isolated: the paleobiogeography of Patagonia. Annu Rev Earth Planet Sci 41:561–603.

Wilf P, KR Johnson, NR Cúneo, ME Smith, BS Singer, MA Gandolfo 2005 Eocene plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina. Am Nat 165:634–650.

Wilf P, S Little, A Iglesias, M Zamaloa, M Gandolfo, NR Cúneo, K Johnson 2009 *Papuacedrus* (Cupressaceae) in Eocene Patagonia: a new fossil link to Australasian rainforests. Am J Bot 96:2031–2047.

Wing SL, LD Boucher 1998 Ecological aspects of the Cretaceous flowering plant radiation. Annu Rev Earth Planet Sci 26:379–421.

Yang XJ 2004 *Ginkgoites myrioneurus* sp. nov. and associated shootsfrom the Lower Cretaceous of the Jixi Basin, Heilongjiang, China. Cretac Res 25:739–748.

Yang XJ, EM Friis, ZY Zhou 2008 Ovule-bearing organs of *Ginkgo ginkgoidea* (Tralau) comb. nov., and associated leaves from the Middle Jurassic of Scania, South Sweden. Rev Palaeobot Palynol 149:1–17.

Zachos JC, GR Dickens, RE Zeebe 2008 An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature 451:279–283.

Zachos JC, M Pagani, LC Sloan, E Thomas, K Billups 2001 Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–693.

Zheng CZ 1992 Preliminary analysis of flora in Tianmu Mountain Reserve. Page 89 *in* F Yang, ed. Comprehensive investigation report on natural resource of Tianmu Mountain Nature Reserve. Science and Technology, Hangzhou.

Zheng S, Z Zhou 2004 A new Mesozoic *Ginkgo* from western Liaoning, China and its evolutionary significance. Rev Palaeobot Palynol 131:91–103.

Zhou Z 1991 Phylogeny and evolutionary trends of Mesozoic ginkgoaleans—a preliminary assessment. Rev Palaeobot Palynol 68: 203–216.

——— 1997 Mesozoic ginkgoalean megafossils: a systematic review. Pages 183–206 *in* T Hori, RW Ridge, W Tulecke, P Del Tredici, J Trémouillaux-Guiller, H Tobe, eds. *Ginkgo biloba*, a global treasure: from biology to medicine. Springer, Tokyo.

Zhou Z, C Quan, Y Liu 2012 Tertiary *Ginkgo* ovulate organs with associated leaves from North Dakota, U.S.A., and their evolutionary significance. Int J Plant Sci 173:67–80.

Zhou Z, B Zhang 1989 A Middle Jurassic *Ginkgo* with ovule-bearing organs from Henan, China. Palaeontogr Abt B 211:113–133.

Zhou ZY, B Zhang, Y Wang, G Guignard 2002 A new *Karkenia* (Ginkgoales) from the Jurassic Yima formation, Henan, China and its megaspore membrane ultrastructure. Rev Palaeobot Palynol 120: 91–105.

Zhou ZY, SL Zheng 2003 The missing link in *Ginkgo* evolution. Nature 423:821–822.