Comparative study between *Ginkgoites tigrensis* Archangelsky and *Ginkgo biloba* Linn. leaves

Liliana Villar de Seoane

Liliana Villar de Seoane 1997. Comparative study between *Ginkgoites tigrensis* Archangelsky and *Ginkgo biloba* Linn. leaves. *Palaeobotanist* 46(3) : 1-12.

A comparative study between leaves of *Ginkgoites tigrensis* Archangelsky 1965, which belong to the family Karkeniaceae and those of *Ginkgo biloba* L. included within the family Ginkgoaceae is realized, using light microscopy (LM) and scanning and transmission electron microscopy (SEM and TEM). The fossil cuticles occur in the sediments located in Baqueró Formation (Lower Cretaceous), Santa Cruz Province, Argentina. The morphological, anatomical and ultrastructural analyses indicate great similarities between fossil and extant leaves.

Key-words—Ginkgoalean leaves, Baqueró Formation, Lower Cretaceous, Santa Cruz Province, Argentina.

Liliana Villar de Seoane, CONICET, División Paleobotánica, Museo Argentino de Ciencias Naturales "B. Rivadavia". Av. A. Gallardo 470, (1405) Buenos Aires, Argentina.

RESUMEN

En el presente trabajo se realiza el estudio comparado entre hojas de la especie fósil *Ginkgoites tigrensis* Archangelsky 1965, perteneciente a la familia Karkeniaceae, y de la especie actual *Ginkgo biloba* L. perteneciente a la familia Ginkgoaceae, ambas familias incluidas dentro del orden Ginkgoales. Para efectuar el análisis cuticular se utilizó microscopía óptica (MO) y microscopía electrónica de barrido y transmisión (MEB y MET). Los restos fósiles analizados fueron extraídos de sedimentitas organógenas halladas en la Formación Baqueró de la Provincia de Santa Cruz (Cretácico Inferior). Los resultados obtenidos con los análisis realizados, han demostrado la existencia de grandes semejanzas morfológicas, anatómicas y ultraestructurales entre las hojas de las especies *Ginkgoites tigrensis* y *Ginkgo biloba*.

सारांश

***गिन्क्गोइटिस टाइग्रेन्सिस* आर्केन्जेल्सकी एवं *गिन्क्गो बाइलोबा* लिन्नॅयस की पत्तियों का तुलनात्मक अध्ययन**

लिलिआना विलर दॅ सिओने

प्रकाश सूक्ष्मदर्शी, क्रमवीक्षण एवं पारगमन इलेक्ट्रान सूक्ष्मदर्शी के अध्ययन के आधार पर *गिन्क्गोइटिस टाइग्रेन्सिस* आर्केन्जेल्सकी 1965 (कार्केनिएसी कुल) एवं *गिन्क्गो बाइलोबा* लिन्नॅयस (गिन्क्गोएसी कुल) की पत्तियों का तुलनात्मक अध्ययन किया गया है। ये अश्मित उपचर्म अर्जेन्टीना में सान्ता क्रुज़ प्रदेश की बाकेरो शैल-समूह के अवसादों से प्राप्त हुई थीं। आकारिकीय, शारीरीय एवं परासंरचनात्मक विश्लेषण से अश्मित एवं वर्तमान दोनों ही प्रकार की पत्तियों में काफी समानता देखने को मिली है।

THE generic concept of *Ginkgo* (Lower Jurassic to modern times) and *Ginkgoites* (Upper Triassic to Lower Cretaceous) in the sense of Harris (1935) includes recent and fossil specimens of congeneric state in the genus *Ginkgo* L.

Seward (1919) founded the genus *Ginkgoites* for fossil leaves belonging to vegetative remains generically identical with the modern genus *Ginkgo* or closely related to it. A change of concept has been undertaken by Florin (1936) who stressing the importance of anatomical structures of the epidermis, did not consider to apply the name of *Ginkgoites* as Seward did, merely because the plant was fossil. According to Florin, the generic name of *Ginkgoites* is used when the remains differ considerably from modern *Ginkgo*.

The purpose of this paper is to describe the morphology, anatomy and ultrastructure of the leaves of the fossil species *Ginkgoites tigrensis* Archangelsky 1965 (Karkeniaceae) and to compare them with those of the extant species *Ginkgo biloba* L. (Ginkgoaceae), using light microscopy (LM) and scanning and transmission electron microscopy (SEM and TEM). Both families belong to the order Ginkgoales. The species *Ginkgoites tigrensis* was

described by Archangelsky (1965) with light microscopy (LM).

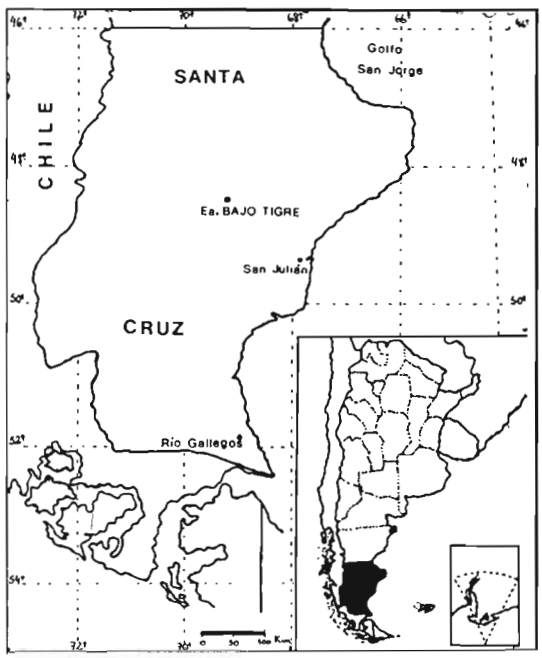
In Argentina, ginkgophyte leaves have been recorded from the Lower Permian of Chubut Province (Cúneo, 1987). The genus *Ginkgoites* occurs in the Triassic of Neuquén and Mendoza Province (Frenguelli, 1946), the Lower Jurassic of Chubut Province (Feruglio, 1933), the Upper Jurassic and Lower Cretaceous of the Lago San Martín, Santa Cruz Province and Graham Land, Antarctica (Halle, 1913), and in the Tertiary strata of Chubut Province (Archangelsky, 1965) and Río Negro Province (Berry, 1938). The studied cuticles were found in the Baqueró Formation, Santa Cruz Province, associated with seed-bearing structures belonging to the species *Karkenia incurva* Archangelsky 1965.

Among living plants there is no more striking example of a species which recalls the past than *Ginkgo biloba* that occurs naturally in Chekiang Province, China; only known in cultivation in Japan, Korea and Manchuria where it is used principally around temples. Used as a street tree in Japan and introduced into Europe from Japan in 1727 (Gifford & Foster, 1989).

For the first time, Kaempfer (1712) described this tree and gave the generic name *Ginkgo*. In 1690, he travelled to Orient, where he saw "an uncommon tree in Europe, with adiantiform leaves". In 1771, Linnaeus adopted the genus given by Kaempfer and established the species *G. biloba*. In 1900, Seward and Gowan realized a complete description of the "Maidenhair tree". More recently, the species *Ginkgo biloba* was studied by Chamberlain (1935), Sporne (1965), Napp-Zinn (1966), Gifford and Foster (1989) and Page (1990) with general descriptions. Krüssmann (1985) analyzed its anatomy in relation with the environment.

MATERIAL AND METHODS

The fossil materials occur in the Baqueró Formation, Estancia Bajo Tigre. This Formation is located to the south of the Deseado River, between the parallels 47°-49° and the meridians 68°-69° 30', Santa Cruz Province, Argentina (Text-figure 1). In the Estancia Bajo Tigre the fossil plants occur in lenticular beds of brownish colour. Paleobotanical and palynological studies (Archangelsky & Gamerro, 1966a, 1966b) for the Baqueró Formation suggested a Lower Cretaceous age, 120 million years (Archangelsky, 1967). Fossils are mainly represented by well preserved leaves. Cuticles were prepared for both light and electron microscopy. The material was easily separated from the matrix and cleaned with dilute sodium hypochlorite.



Text-figure 1—Map showing the location of the Estanicia Bajo Tigre (Baqueró Formation).

PLATE 1

1-6. *Ginkgoites tigrensis* Archangelsky

1. General view of the leaves. BA Pb 11557. Scale bar = 1 cm.
2. Internal abaxial epidermis. BA Pb MEB 50. Scale bar = 100 µm.
3. Stomata (arrows) on the external abaxial epidermis. BA Pb MEB 50. Scale bar = 50 µm.
4. Details of cells in the internal adaxial epidermis. BA Pb MEB 50. Scale bar = 50 µm.
5. Details of a stoma. BA Pb MEB 50. Scale bar = 10 µm.
6. Details of guard cells. BA Pb MEB 50. Scale bar = 10 µm

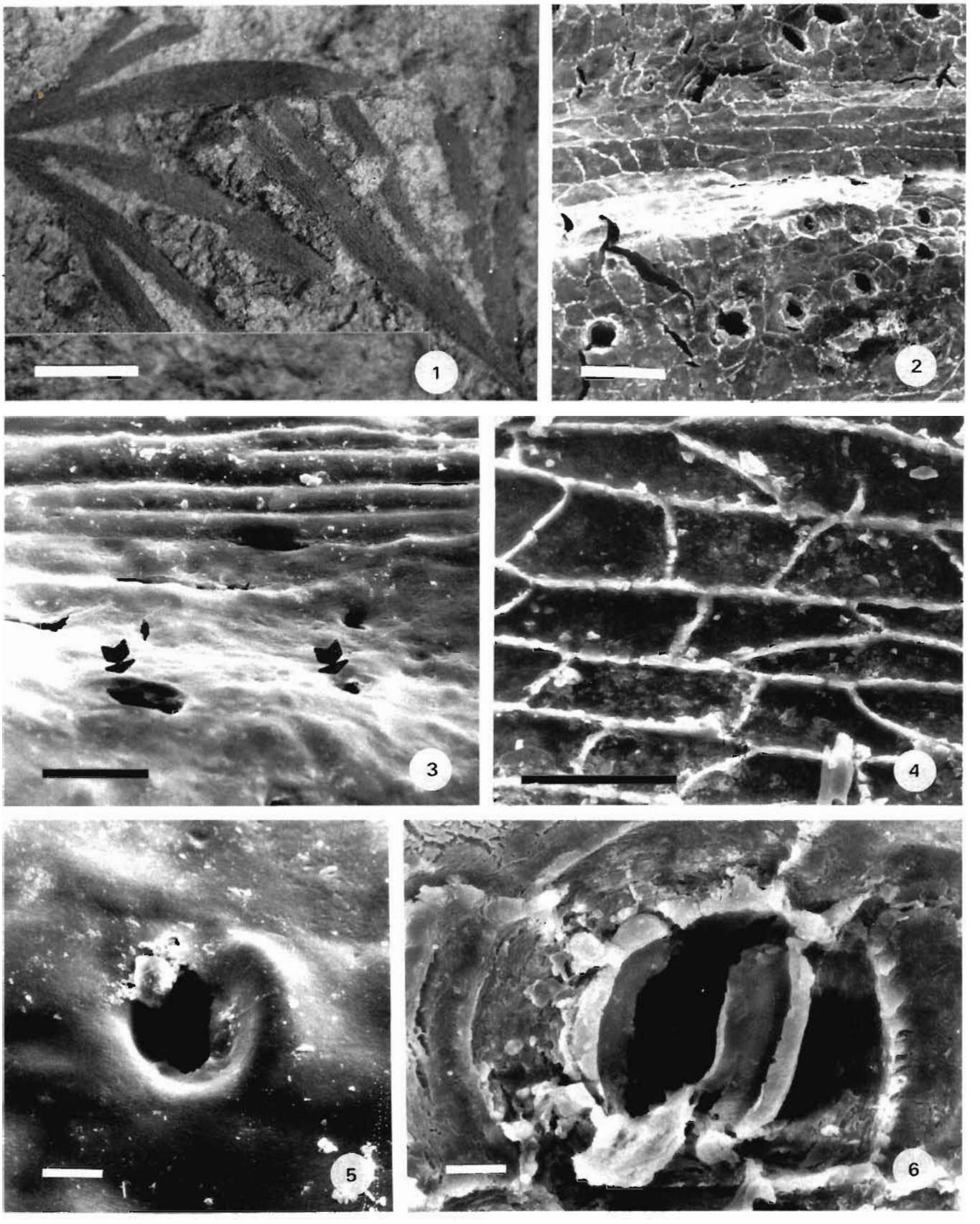


PLATE 1

The recent material was collected at the Buenos Aires Botanical Garden. Fossil and extant leaves were mounted in glycerine-jelly for observation with light microscopy, or directly on cylindrical stubs and coated with gold-palladium for scanning electron microscopy (SEM). Observations were made with a JEOL T-100 SEM at the La Plata Natural History Museum.

For transmission electron microscopy (TEM) cuticle fragments were embedded in Spurr low viscosity resin (Spurr, 1969). Sections were cut with a diamond knife and mounted in single hole grids coated with Formvar. Observations were made on a Zeiss EM 109 of the Electronic Microscopy Service at the Cellular Biology Department, Medicine Faculty, Buenos Aires University.

The fossil type specimens are deposited at the Paleobotanical Collection of the Buenos Aires Natural History Museum (BA Pb) and the recent specimens at the Plant Biology Department, Natural Sciences Faculty, Buenos Aires University. Hickey's classification (1974) was used for the morphological descriptions, whilst terminology of Holloway (1982a, 1982b) and Lyshede (1978, 1982) was used for the ultrastructural analysis.

SYSTEMATIC DESCRIPTION

Family—Karkeniaceae

Genus—*Ginkgoites* Seward 1919

Type species—*Ginkgoites obovata* (Nathorst) Seward 1919

Ginkgoites tigrensis Archangelsky 1965

Pl. 1, figs 1-6; Pl. 2, figs 1-4

Ginkgoites tigrensis Archangelsky, *Bull. Brit. Mus. (Nat. Hist.) Geol.*, 10 (5), pp. 125-128, pl. 3, fig. 22 and pl. 4, figs 23-26 (1965).

Specimens studied—BA Pb 11556, 11557, 11558, 11559, 11560, 11561, 11581, 11582, 11583, 11584, 11585, 11586, 11587 and 11588; BA Pb Pm 237, 238, 239, 240 and 253; BA Pb MEB 50; BA Pb MET 153.

Locality—Meseta Baqueró, Estancia Bajo Tigre.

Stratigraphic horizon—Baqueró Formation, Lower Cretaceous.

Emended diagnosis—Ultrastructurally, the external wall of the epidermis is composed by a cuticular membrane and a cellular wall. A thin cuticle proper, a compact upper layer and a reticulate lower layer formed the cuticular membrane. Cellular wall with a lower electronic density.

Description—The leaves are simple and small to medium. They are flabelliform, up to 4.5 cm long and 5 cm wide. The laminae are divided in three to six segments. The segments are loriform, up to 4 cm long and 0.7 cm wide, united by only one decurrent base. They have rounded apex and straight margins (Pl. 1, fig. 1). The petioles are slender, up to 3 cm long and 0.1 cm wide. The veins radiate from the base, dichotomously forked, with a concentration of about 18-20 veins per centimetre, up to 14 present in each segment. Two veins seem to be present in the petioles.

The leaf surfaces are covered with epicuticular waxes. Adaxial epidermis has rectangular to isodiametric cells, 31-70 µm long and 18-26 µm wide. They often occur in rows, have microgranular surface, their walls are thickened and have irregular margins with sinuosities up to 2.5 µm wide (Pl. 1, fig. 4). Stomata absent on the petiole and the base of the lamina, but present on segments between veins. They are irregularly disposed.

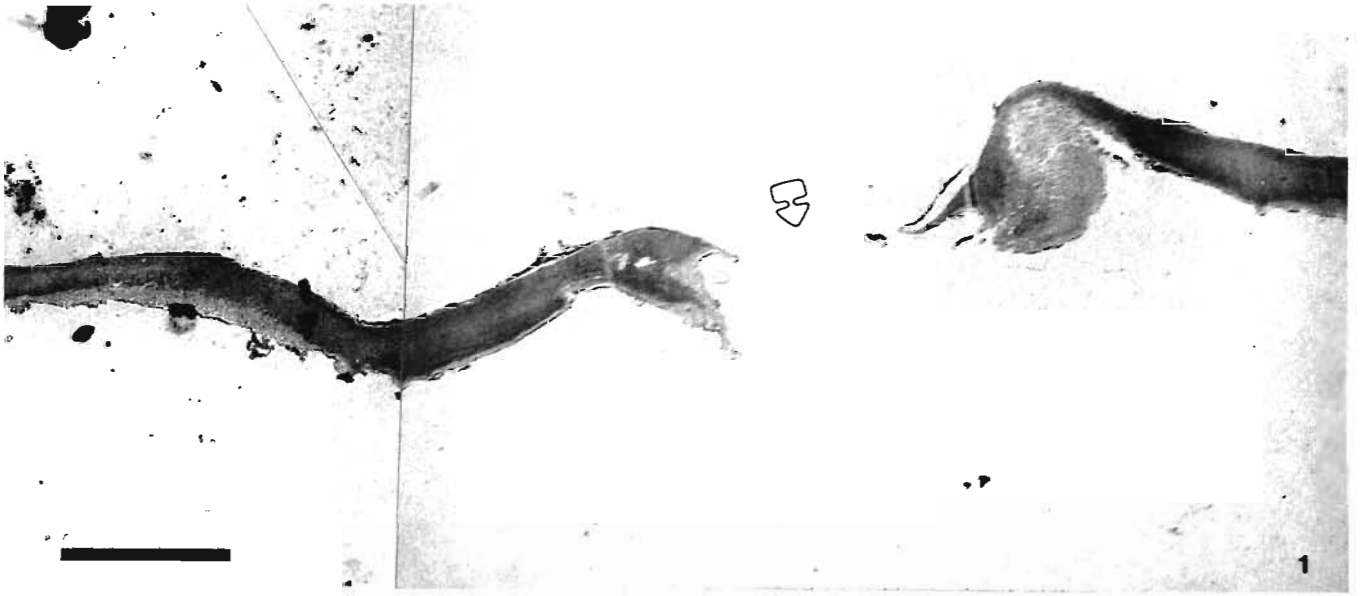
Abaxial epidermis has rectangular to isodiametric cells, 39-78 µm long and 18-34 µm wide. The cells have the same characters and dispósition in the

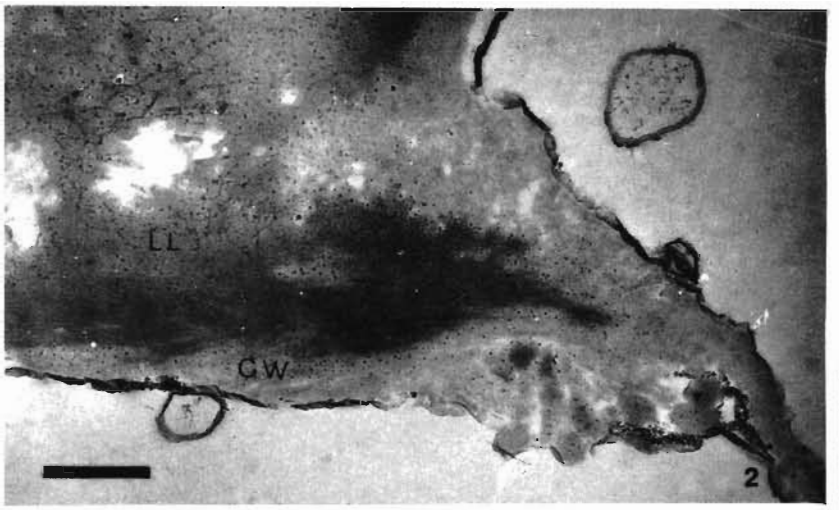
PLATE 2 →

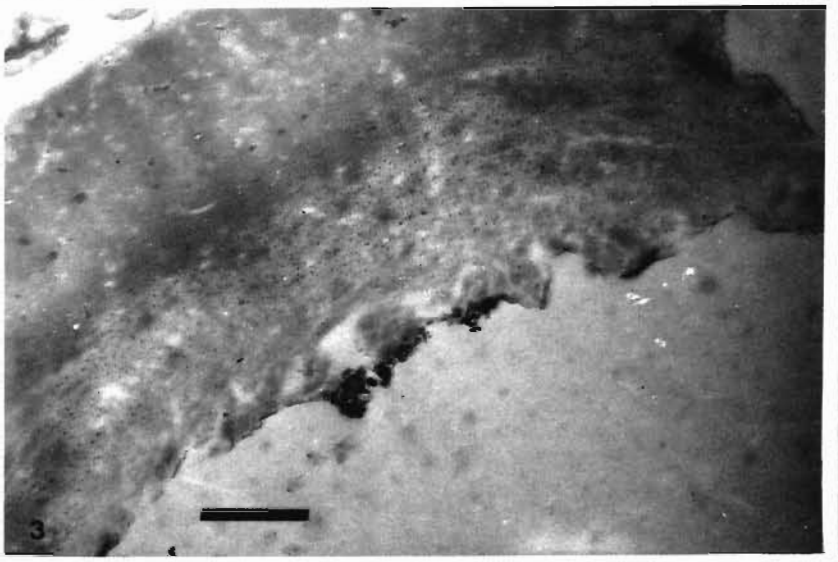
C = cuticle proper; UL = upper layer; LL = lower layer; CW = cellular wall.

1-4. *Ginkgoites tigrensis* Archangelsky

1. TS section of the external wall of the epidermis with stoma (arrow). BA Pb MET 153. Scale bar = 10 µm.
2. TS section of a stoma. BA Pb MET 153. Scale bar = 1 µm.
3. TS section of a periclinal wall. BA Pb MET 153. Scale bar = 1 µm.
4. TS section of the external wall of the epidermis. Detail. BA Pb MET 153. Scale bar = 1 µm.







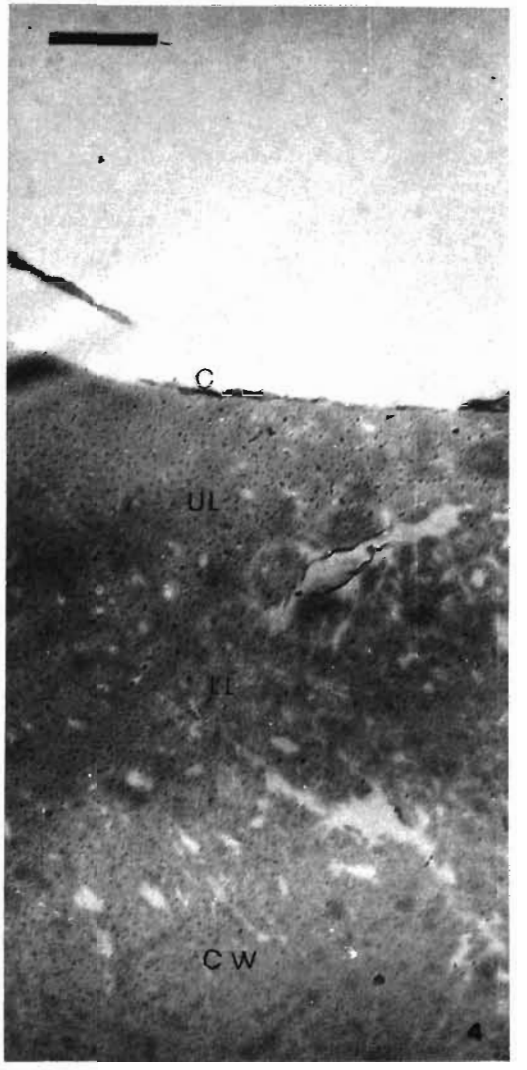


PLATE 2

adaxial epidermis, but the walls are more thin (Pl. 1, fig. 2).

Stomata are irregularly disposed (Pl. 1, fig. 3). Stomatal apparatus up to 62 µm in diameter and are circular or oval on both cuticles. They are actinocytic or tetracytic with 6 or 4 subsidiary cells, respectively. The subsidiary cells have striate walls that form a ring of 2-3 µm high surrounding the guard cells (Pl. 1, fig. 5). Guard cells slightly sunken in a pit and cutinized (Pl. 1, fig. 6).

Ultrastructurally, the external wall of the epidermis is composed by a cuticular membrane and a cellular wall (Pl. 2, fig. 1). The cuticle proper is 0.25 µm thick (Pl. 2, fig. 4), the upper layer is 1.0 µm thick, compact and homogeneous and the lower layer is 1.5 µm thick, slightly reticulate with thin channels irregularly distributed (Pl. 2, figs 2-4). The channels are anastomosed. Near the cellular wall they are parallel to the surface, but near the upper layer they may arch up to 90^0 and are perpendicular to the surface. Both layers have small and irregular holes (Pl. 2, figs 3, 4). The rest of the cellular wall is 1.5 µm thick and has a lower electronic density (Pl. 2, fig. 4). The anticlinal walls have an important development of the upper layer. The periclinal walls of the stomata have the lower layer very developed.

Comparisons—*Ginkgoites ticoensis* Archangelsky 1965, the other species described in the Baqueró Formation, differs from *Ginkgoites tigrensis* in shape, size and anatomical structures. *Ginkgoites ticoensis* has smaller leaves divided in 4 segments, smaller segments with 12 veins per centimetre, polygonal epidermal cells with a strong hollow papilla that not form rows and smaller stomata only present in the abaxial cuticle. Ultrastructurally, Taylor, W. *et al.* (1989) studied cuticle fragments of *Ginkgoites tigrensis* finding "approaching the outer cuticle surface, a well developed poly-lamellate region of 25-44 nm in overall extent". That poly-lamellate region has not been found in the cuticles described in the present paper.

Ginkgoites digitata (Brgn.) from the Lower Jurassic of Chubut Province, differs in having entire leaves, bilobed or divided in several segments (Feruglio, 1933); *Ginkgoites patagonica* Berry 1938 from the Lower Tertiary of Neuquén Province, has leaves deeply divided in several segments; *Ginkgoites crassipes* Feistmantel from the Lower Permian of Chubut Province, differs in having entire leaves; *Ginkgoites eximia* Feruglio 1942 from Piedra Shotel, Chubut Province (Lower Jurassic), has entire and bilobed leaves with long petioles; *Ginkgoites taeniata* (Geinitz) Frenguelli 1946 from the Triassic of Neuquen Province, has small leaves divided in few segments, small stomata only present in the abaxial cuticle and few stomata and papillae in the adaxial cuticle; and *Ginkgoites truncata* Frenguelli 1946 from Potrerillos Basin, Mendoza Province (Upper Triassic), differs in having entire and triangular leaves with truncate apex.

Family—Ginkgoaceae

Genus—*Ginkgo* Linnaeus 1771

Type species—*Ginkgo biloba* Linnaeus 1771

Ginkgo biloba Linn.

Pl. 3, figs 1-6; Pl. 4, figs 1-4

Description—The leaves are simple and small to medium. Laminae flabelliform, up to 8 cm wide, entire, but more frequently bilobed, or subdivided into several wedge-shaped lobes. Leaves with rounded apex slightly serrate, straight margins and decurrent base (Pl. 3, fig. 1). The petioles are slender, up to 3 cm long and 0.1 cm wide. The veins are radially disposed from the base. They are subparallel, dichotomously forked, with a concentration of about 18-20 veins per centimetre. Two veins are present in the petioles. The foliage leaves occur on long shoots or crowded at the apex of short shoots.

PLATE 3 →

1-6. *Ginkgo biloba* L.

1. Leaf. BA 74784. Scale bar = 0.5 cm.
2. Details of adaxial epidermal cells. BA Pb MEB 51. Scale bar = 50 µm.
3. Stomata (arrows) on the abaxial epidermis. BA Pb MEB 51. Scale bar = 100 µm.
4. Details of the stomata (arrows). BA Pb MEB 51. Scale bar = 50 µm.
5. Details of the guard cells. BA Pb MEB 51. Scale bar = 10 µm.
6. Details of the subsidiary cells. BA Pb MEB 51. Scale bar = 10 µm.

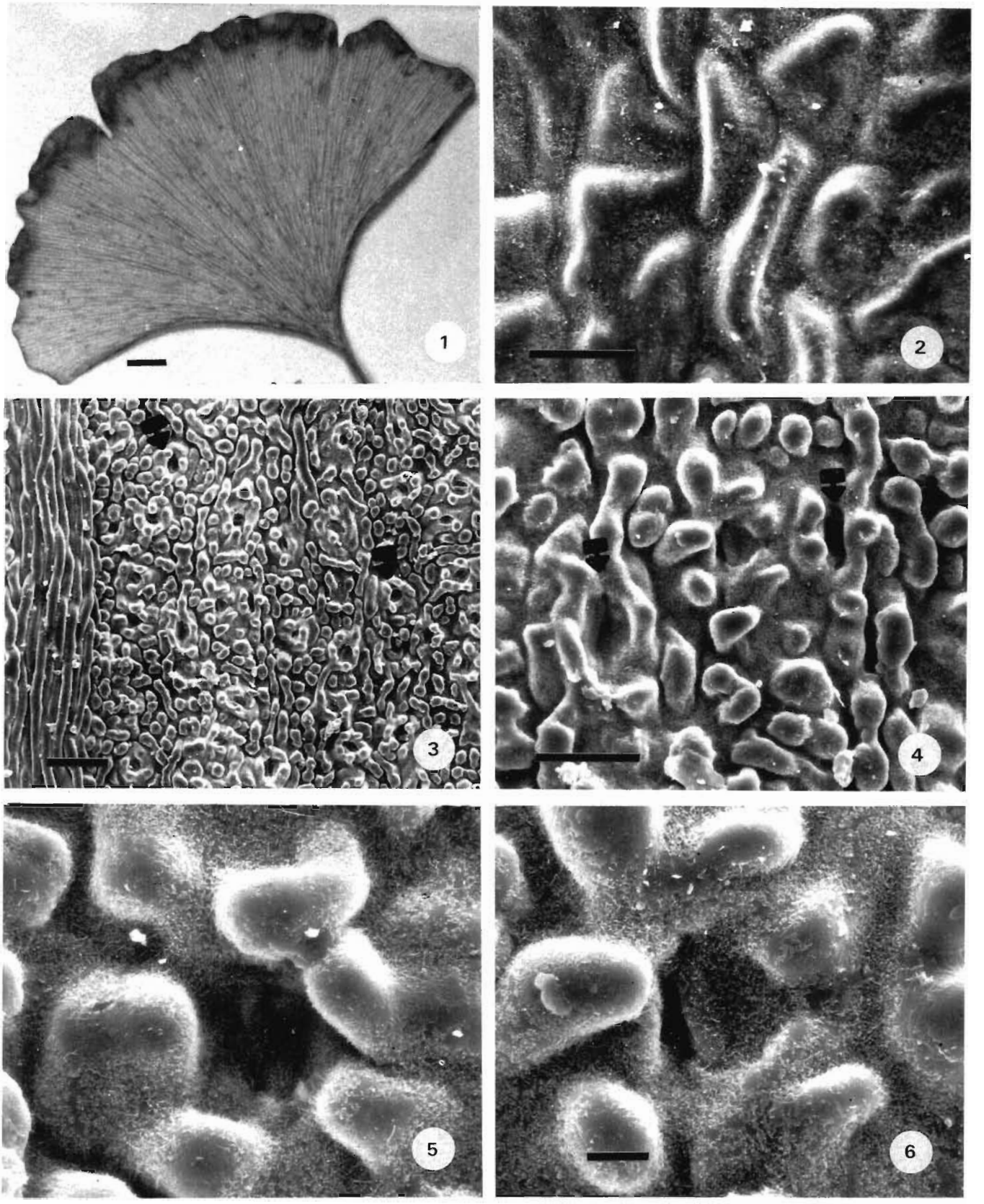


PLATE 3

Surface covered with abundant epicuticular waxes of thin and short fibrous aspect (Pl. 3, figs 5, 6). Adaxial and abaxial epidermis are formed by rectangular to polygonal cells irregularly disposed (Pl. 3, figs 2, 3). Their walls are slightly thickened and sinuous. Each abaxial epidermal cell forms one or two papillae of 17 µm in diameter and 15-28 µm height (Pl. 3, fig. 4).

Stomata on the abaxial epidermis, irregularly disposed between veins. Actinocytic stomatal apparatus, up to 90 µm in diameter, with 6 to 7 subsidiary cells (Pl. 3, figs 5, 6). Each subsidiary cell forms a papilla oriented to the pit. Guard cells sunken, with cuticular ridge surrounding the mouth (Pl. 3, figs 5, 6).

Ultrastructurally, the external wall of the epidermis is formed by a cuticular membrane and a cellular wall. A thin cuticle proper, a compact upper layer and a reticulate lower layer formed the cuticular membrane (Pl. 4, figs 1, 2). The cuticle proper is 0.25 µm thick; the upper layer, up to 0.75 µm thick, is compact and homogeneous (Pl. 4, fig. 4). The lower layer, up to 1.0 µm thick, is reticulate, with pectinaceous microchannels that are perpendicular to the surface. The cellular wall is lamellate, up to 2.0 µm thick, with superposed lamellae separated by translucent channels that anastomose, and are parallel to the surface (Pl. 4, fig. 4). The anticlinal walls have an important development of the upper layer (Pl. 4, fig. 3). The subsidiary and guard cells have a thick cuticle and their cellular wall is very lignified, especially the external periclinal wall.

DISCUSSION

The order Ginkgoales appears in the Upper Paleozoic. The oldest fossil materials from the Lower Permian were represented by different types of leaves which are referred to three genera: *Trichopitys* Saporta, *Phylladoderma* Zalessky and *Sphenobatera* Florin.

During the Mesozoic, the Ginkgoales have their greatest prominence, especially in the Jurassic and Lower Cretaceous, their polymorphic leaves were grouped in two families, the Ginkgoaceae and the Phoenicopsiaceae. The family Ginkgoaceae was represented by *Ginkgo* L., *Ginkgoidium* Yokoyama, *Ginkgoites* Seward and *Batera* F. Braun; whilst the family Phoenicopsiaceae was represented by *Phoenicopsis* Heer, *Culgoweria* Florin, *Windwardia* Florin, *Eretmophyllum* Thomas, *Stephenophyllum* Florin, *Pseudotorellia* Florin, *Arctobatera* Florin, *Hartzia* Harris, *Czekanowskia* Heer, *Sphenobatera* Florin and *Glossophyllum* Kräusel During the Upper Cretaceous, the order Ginkgoales begins to disappear and in the Lower Cenozoic the group was only represented by the family Torelliaceae with the genera *Torellia* Heer (Tralau, 1968).

The oldest fossils belonging to the genus *Ginkgo* were found in the Lower Jurassic of Fergana in the southern Asiatic part of the Soviet Union, and were described as *G. digitata* (Brik, 1953; Vasiljevskaja, 1956). During the Lower Cretaceous, the polymorphy in foliar remains indicates the rise of new species. At the Middle Tertiary, the genus retained its circumpolar distribution, being known throughout Eurasia and Northern America. At the Upper Miocene, *Ginkgo* becomes to be extinct in North America and during the Pliocene the genus seems to be confined to Eurasia, taking place in China between the Upper Pliocene and the modern times.

At the beginning of the Mesozoic, there exist several lineages of Ginkgoales, characterized by different leaves and seed-bearing structures. Accord-

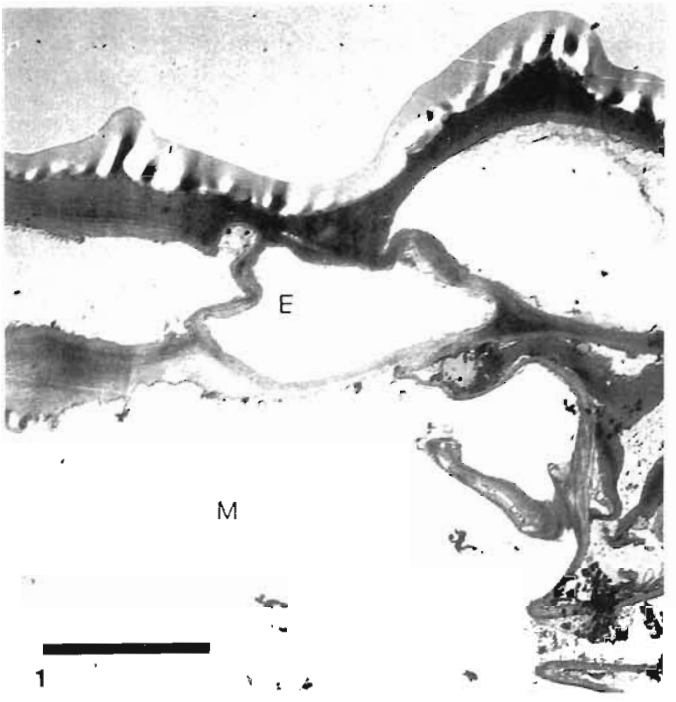
---

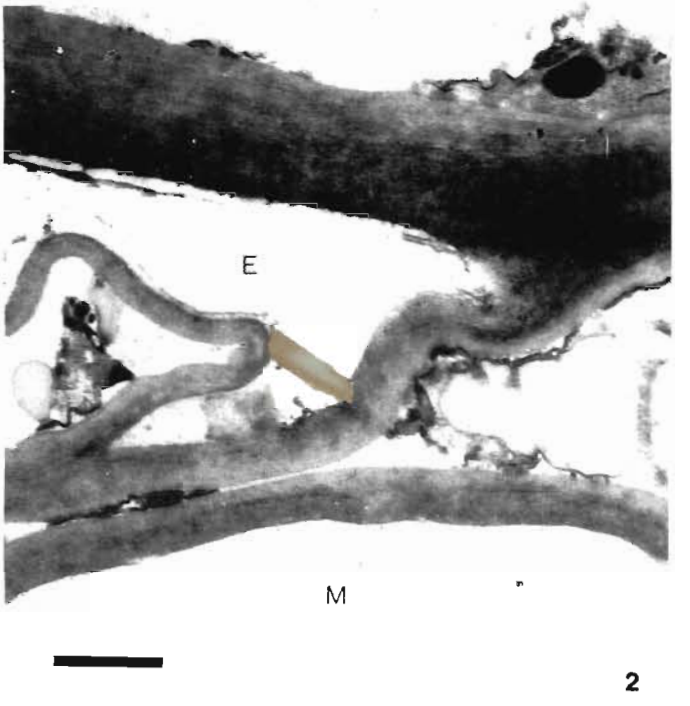
PLATE 4 →

E = epidermis; M = mesophyll; C = cuticle proper; UL = upper layer; LL = lower layer; CW = cellular wall.

1-4. *Ginkgo biloba* L.

1. TS section of the abaxial epidermis. BA Pb MET 161. Scale bar = 10 µm.
2. TS section of the abaxial epidermis. Detail. BA Pb MET 161. Scale bar = 1 µm.
3. TS section of an anticlinal wall (arrows). Detail. BA Pb MET 161. Scale bar = 1 µm.
4. TS section of the external wall of the epidermis. Detail. BA Pb MET 161. Scale bar = 1 µm.





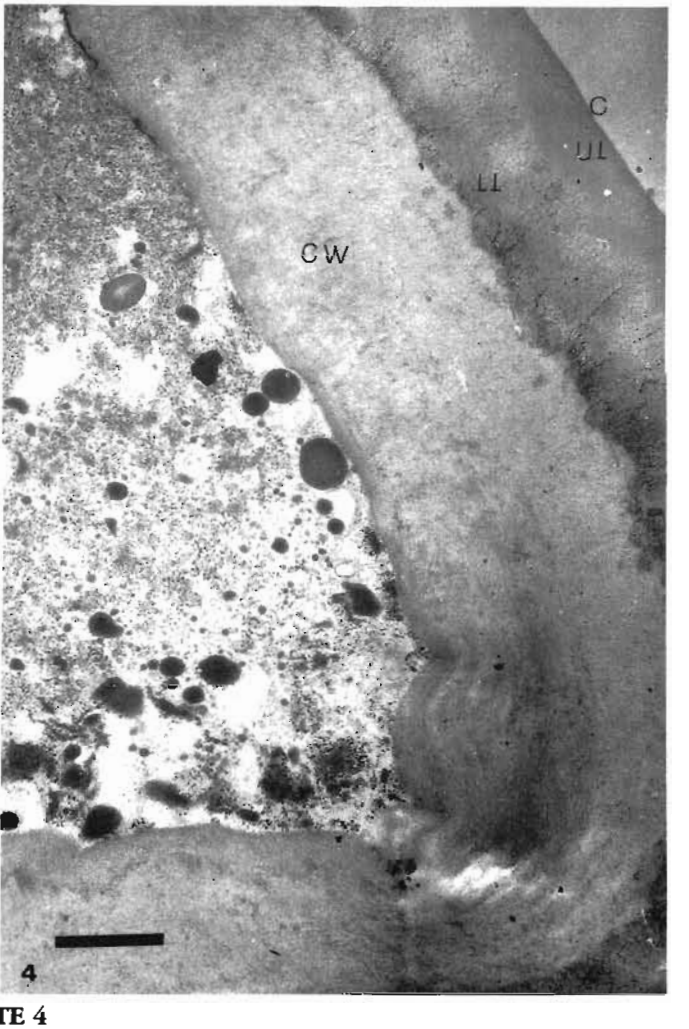


PLATE 4

ing to the inflorescence associated, the leaves were re-grouped in four different families, such as Trichopityaceae, Umaltolepidaceae, Karkeniaceae and Ginkgoaceae (Zhou Zhiyan,1991).

The Trichopityaceae was the oldest family and disappeared at the end of the Paleozoic; the Umaltolepidaceae and Karkeniaceae were Mesozoic families that disappeared in the Upper Cretaceous; and the Ginkgoaceae is the modern family with the only one living species *Ginkgo biloba.*

The family Trichopityaceae was represented by *Trichopitys heteromorpha* Saporta 1875 and Florin (1949) described the species *T. heteromorpha* from the Lower Permian of Lodéve (France), as vegetative shoots with leaves spirally arranged and divided in 4 to 8 segments. In their middle region the long shoots carry furcated ovulate shoots with 3 to 20 terminal, inverted and orthotropous ovules.

Krassilov (1970, 1972) studied the tafoflora from the Bureja River Basin of Siberia (Upper Jurassic-Lower Cretaceous). Within the order Ginkgoales, he described two different types of female inflorescences (*Karkenia* and *Umaltolepis*) and several types of leaves. *Umaltolepis vachrameevii* from the Talunjan Formation of this area (Upper Jurassic) was described as the Type species, but there is another species of *Umaltolepis, U. rarinervis* from the Ulgar Formation of the same area (Lower Cretaceous). This type of female reproductive organ consists of a stalk and a terminal bract. This bract is elongated, entire or divided into two lobes that abaxially had a single seed. These structures were associated to leaves of the *Pseudotorellia*-type, with laminae undivided, roundish apex and stomata on abaxial epidermis only. The other species *Karkenia asiatica* is composed of a central axis with erect or incurved ovules, densely packed and associated to leaves of *Eretmophyllum* Thomas and *Sphenobatera*-type. *Eretmophyllum* has undivided leaves with roundish apex, stomata on abaxial epidermis only and rounded papillae whilst, *Sphenobatera* has small leaves deeply lobed.

Stanislavsky (1971, 1973) described *Toretzia angustifolia* from the Upper Triassic of Novoraick Formation (Ukraine). The vegetative shoots bear buds covered with scales spirally arranged. 2 to 3 ovule-bearing organs are given off from the axils of bracts on the short shoots. The ovules are inverted. The genera *Umaltolepis* and *Toretzia* belong to the family Umaltolepidaceae and *Karkenia* to the family Karkeniaceae.

Zhou and Zhang (1988) described *Yimaia recurva* from the Middle Jurassic Yima Formation, Henan, Central China. The fertile shoots were composed of a peduncle and up to 9 terminal ovules which were large, sessile, contiguous, orthotropous but mostly recurved. *Yimaia* was associated to primary short shoots with *Batera*-type leaves. These leaves were deeply divided into numerous narrow lobes, forming as a whole one third to one fourth of a circle.

Also, Zhou and Zhang (1988, 1989) described the species *Ginkgo yimaensis* from the Middle Jurassic Yima Formation of Henan, Central China. It differs from *G. biloba* L., in having more deeply divided laminae and normally more (2-4) seeds which were attached terminally to pedicels rather than directly to the peduncle as in the case of the extant species. The extant species has female flowers long stalked, solitary, axillary, with 2 opposing ovules at the end of the thickened stalk apex. The genera *Yimaia* and *Ginkgo* belong to the family Ginkgoaceae.

GENERAL CONCLUSIONS

The family Karkeniaceae was proposed by Krassilov 1970 and includes a single genus with two species from the Upper Jurassic and Lower Cretaceous strata of Siberia and Argentina. *Karkenia incurva* Archangelsky 1965 is the only ginkgoalean fossil known outside Laurasia. *Karkenia* was associated with sessile leaves during the Upper Jurassic and petiolate leaves during the Lower Cretaceous.

In the Baqueró Formation, the family Karkeniaceae is represented by the leaves of *Ginkgottes tigrensis* and the associated ovule-bear-

ing organ *Karkenia incurva*. This structure is composed of a central axis and up to 100 small, incurved and orthotropous ovules, densely packed. On the basis of the close relationship between the Karkeniaceae and Ginkgoaceae, the genus *Ginkgoites* was compared with the extant genus *Ginkgo*.

Morphologically, the leaves of fossil and extant genera are different. The fossil leaves are smaller and divided in several segments whilst, the extant leaves are longer and entire, but more frequently bilobed or subdivided into several wedge-shaped lobes.

The anatomical analysis between *Ginkgoites* and *Ginkgo* has indicated several affinities. The two genera have fan-shaped leaves with veins radially disposed from the base, epicuticular waxes and rectangular to polygonal epidermal cells with sinuous and thick walls. The fossil genus has a smooth epidermal surface and actinocytic or tetracytic stomatal apparatus with a ring surrounding the guard cells whilst, the extant genus has a papillose epidermal surface and actinocytic stomatal apparatus with papillae oriented to the pit.

Ultrastructurally, the comparison of the external wall of the epidermis between *Ginkgoites* and *Ginkgo* has demonstrated that both the genera have a thin cuticle proper, a compact and homogeneous upper layer and a reticulate lower layer. However, *Ginkgoites* has thicker upper and lower layers than *Ginkgo*. The existence of morphological, anatomical and ultrastructural similarities in both of the fossil and living genera corroborates a close relationship between the Karkeniaceae and Ginkgoaceae leaves.

ACKNOWLEDGEMENTS

Thanks are due to Dr Sergio Archangelsky for useful comments and providing the fossil material; to Dr Elena Ancibor for valuable discussions; to Isabel Farías for technical assistance in the preparation of materials for TEM; La Plata Natural History Museum for the SEM and Cellular Biology Department (Medicine, UBA) for the TEM.

REFERENCES

Archangelsky S 1965. Fossil Ginkgoales from the Ticó flora, Santa Cruz Province, Argentina. *Bull. Brit. Mus. (Nat. Hist.) Geol.* **10**(5): 119-137.

Archangelsky S 1967. Estudio de la Formación Baqueró, Cretácico Inferior de Santa Cruz, Argentina. *Rev. Mus. La Plata (N.S.) Pal.* **5**: 63-171.

Archangelsky S & Gamerro JC 1966a. Estudio palinológico de la Formación Baqueró (Cretácico), provincia de Santa Cruz. II. *Ameghiniana* **4**(6): 201-209.

Archangelsky S & Gamerro JC 1966b. Estudio palinológico de la Formación Baqueró (Cretácico), provincia de Santa Cruz. III. *Ameghiniana* **4**(7): 229-236.

Berry EW 1938. Tertiary flora from the Río Pichileufú, Argentina. *Special Paper Geol. Soc. Americana* **12**: 1-140.

Brik MJ 1953. *The Mesozoic flora of the Vostotjno-Fergana coal basin.*

Cúneo R 1987. Sobre la presencia de probables Ginkgoales en el Pérmico Inferior de Chubut, Argentina. *Actas VII Simposio Argentino Paleobot. Palinol.* : 47-49. Buenos Aires.

Chamberlain J 1935. *Gymnosperms structure and evolution.* The University of Chicago Press, Chicago.

Feruglio E 1933. Fossili Liassici della Valle del Rio Genua (Patagonia). *In: Giorn. di Geologia (Ann. R. Mus. Geol. Bologna)* **9**: 1-64. Imola.

Feruglio E 1942. La Flora Liásica del Valle del Río Genoa. Ginkgoales et Gymnospermae incertae sedis. *Notas del Museo de La Plata. Paleontol.* **7**(40): 93-110.

Florin R 1936. I. Die fossilen Ginkgophyten von Franz-Joseph-Land nebst Erörterungen über vermeintliche Cordaitales mesozoischen Alters, and III. Allgemeiner Teil. *Palaeontographica* **B81-82**.

Florin R 1949. The morphology of *Trichopitys heteromorpha* Saporta, a seed plant of Palaeozoic age, and the evolution of the female flowers in the Ginkgoinae. *Acta Horti Bergiani* **15**(5): 79-109.

Frenguelli J 1946. La Flora del Gondwana Superior en la Argentina. *Notas del Museo de La Plata. Paleontol.* **11**(87): 101-127.

Gifford EM & Foster AS 1989. *Morphology and evolution of vascular plants.* Freeman WH (Editor). New York.

Halle TG 1913. Some Mesozoic plant-bearing deposits in Patagonia and Tierra del Fuego and their floras. *K. svensk. VetenskAkad. Handl.* **51**(3): 1-58.

Harris TM 1935. The fossil flora of Scoresby Sound, East Greenland, 4. Ginkgoales, Coniferales, Lycopodiales and isolated fructifications. *Medd. Grönland* **112**, 1.

Hickey L 1974. Clasificación de la arquitectura de las hojas de Dicotiledóneas. *Bol. de la Soc. Arg. de Bot.* **16**(1-2): 1-150.

Holloway PJ 1982a. Structure and histochemistry of plant cuticular membranes: an overview. *In* : Cutler DF, Alvin KL & Price CE (Editors)—*The plant cuticle* : 1-31. London.

Holloway PJ 1982b. The chemical constitution of plant cutins. *In* : Cutler DF, Alvin KL & Price CE (Editors)—*The plant cuticle*: 45-85. London.

Kaempfer L 1712. *Amaenitates exoticae.*

Krassilov VA 1970. Approach to the classification of Mesozoic "Ginkgoalean" plants from Siberia. *Palaeobotanist* **18**: 12-19.

Krassilov VA 1972. *Mesozoic flora from the Bureja River (Ginkgoales and Czekanowskiales).* Moskow.

Krüssmann G 1985. *Manual of cultivated conifers.* Hans-Dieter Warda (Editor), Oregon.

Linnaeus CA 1771. *Mantissa Plantarum.* Holmiae.

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

Lyshede OB 1982. Structure of the outer epidermal wall in xerophytes. *In* : Cutler DF, Alvin KL & Price CE (Editors)—*The plant cuticle*: 87-97. London.

Napp-Zinn K 1966. Anatomie des Blattes. I. Blattanatomie der Gymnospermen. *Handbuck der Pflanzenanatomie.* 2nd Edn. Berlin.

Page CN 1990. Coniferophytina (Conifers and ginkgoids). In: *The families and genera of vascular plants,* **1**. Kubitzki K (Editor)—Springer-Verlag, Berlin.

Saporta G de 1875. Sur la découverte de deux types nouveaux de Coniferes dans les schistes permiens de Lodéve (Hérault). *C.R. Acad. Sci. Paris* **80**: 1017-1022.

Seward AC 1919. *Fossil plants : A text-book for students of Botany and Geology,* IV. Cambridge.

Seward AC & Gowan J 1900. The Maidenhair Tree (*Ginkgo biloba* L.). *Annals Bot.* **14**(53): 109-154.

Sporne KR 1965. *The morphology of gymnosperms.* The structure and evolution of primitive seed-plants. Hutchinson Univ. Library, London.

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

Stanislavsky FA 1971. *Fossil flora and stratigraphy of Upper Triassic sediments in the Donetz Basin (Rhaetian Flora from Raick).* Naukova Dumka, Kiev.

Stanislavsky FA 1973. The new genus *Toretzia* from the Upper Triassic of the Dontez Basin and its relation to the genera of the order Ginkgoales. *Paleontol. Zh.* **1**: 88-96.

Taylor WA, Taylor TN & Archangelsky S 1989. Comparative ultrastructure of fossil and living gymnosperm cuticles. *Rev. Palaeobot. Palynol.* **59**: 145-151.

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

Vasiljevskaja ND 1956. *New Lower Jurassic plants from eastern Fergana.* T. 15.

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

Zhou Zhiyan & Zhang Bole 1988. Two new ginkgoalean female reproductive organs from the Middle Jurassic of Henan Province. *Kexue Tongbao* (*Sci. Bull.*) **33**(14): 1201-1203.

Zhou Zhiyan & Zhang Bole 1989. A Middle Jurassic *Ginkgo* with ovule-bearing organs from Henan, China. *Palaeontographica* **B211**: 113-133.