FOSSIL GINKGOALES FROM THE TICÓ FLORA, SANTA CRUZ PROVINCE, ARGENTINA

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By SERGIO ARCHANGELSKY

SYNOPSIS

The present paper deals with Lower Cretaceous Ginkgoales and associated seeds found in the Ticó Flora, Santa Cruz Province, Argentina. The plants were collected from two different localities, Ticó Amphitheatre and Bajo Tigre Estancia. Two new species of leaves are referred to the genus *Ginkgoites* (*G. tigrensis* and *G. ticoensis*). A female structure found in close association with *G. tigrensis* is referred to a new genus, *Karkenia*. Fragments of short shoots probably belonging to the same plant and roots found in the same bed are described. A new seed, associated with *G. ticoensis*, is described as *Allicospermum patagonicum* sp. n.

INTRODUCTION

THE material described in the present paper was collected by the writer during the years 1958–59 (Ticó) and 1962–63 (Bajo Tigre). The first two excursions covered only the Ticó Amphitheatre and included only a short visit to a new exposure with similar sediments bearing mummified plants in the Estancia Bajo Tigre. A longer excursion to this new locality was undertaken in 1962 when it became evident that the same formation known from Punta del Barco and the Ticó Amphitheatre extended N. and E. to cover a large area. In the Bajo Tigre the fossil plants are preserved in the same way as in Ticó and occur in similar lenticular beds of brownish colour which makes them easy to distinguish in the field from the typical, mostly sterile, white tuffs. Several plant beds were discovered, the three main ones containing (1) *Ginkgoites* and other remains described here, (2) *Ptilophyllum* and associated conifers of *Brachyphyllum* type, and (3) one long-leaved conifer with male and female cones in organic connexion, together with abundant freshwater mollusca.

In 1963, further collecting in the same locality was undertaken, and several short excursions made to new areas which confirmed the extension of the same formation more than 100 km. northwards. Among the new localities discovered, one yielding excellent plant mummifications is known as Bajo Grande situated a few kilometres SW of the Petrified Forest of Santa Cruz (containing the petrified female cones of *Araucaria mirabilis* Speggazini). In Bajo Grande a rich plant association was found composed of many conifers (some with cones), Bennettitales and cutinized fern-like fronds, but no Ginkgoales.

As a result of these excursions, a large amount of material has been collected, the description of which will take some years of future work. The age of the plant bearing beds (and the whole formation) has previously been considered as Upper Jurassic or Lower Cretaceous. However, the pollen content of the strata seems to confirm a Lower Cretaceous age, possibly Barremian to Hauterivian and the flora may well be the last plant association before the advent of the Angiosperms ; it may mark the uppermost limit of survival of some important fossil taxa.

Little is known about Upper Mesozoic Ginkgoales in Argentina. The most comprehensive papers deal mainly with the abundant Triassic impressions. There are no records of *Ginkgoites* in the Lower and Middle Jurassic strata, but they are

present in Upper Jurassic and Lower Cretaceous formations from Lago San Martin, Santa Cruz Province and from Graham Land, Antarctica (Halle 1913). Other records are from Tertiary strata in Chubut Province, Patagonia. The present material fills a gap in the knowledge of the cuticle of *Ginkgoites* leaves in Argentina and throws further light on the development of the female structures in this group.

SYSTEMATIC DESCRIPTIONS

GINKGOALES

Genus ***GINKGOITES*** Seward 1919

Ginkgoites ticoensis sp. n.

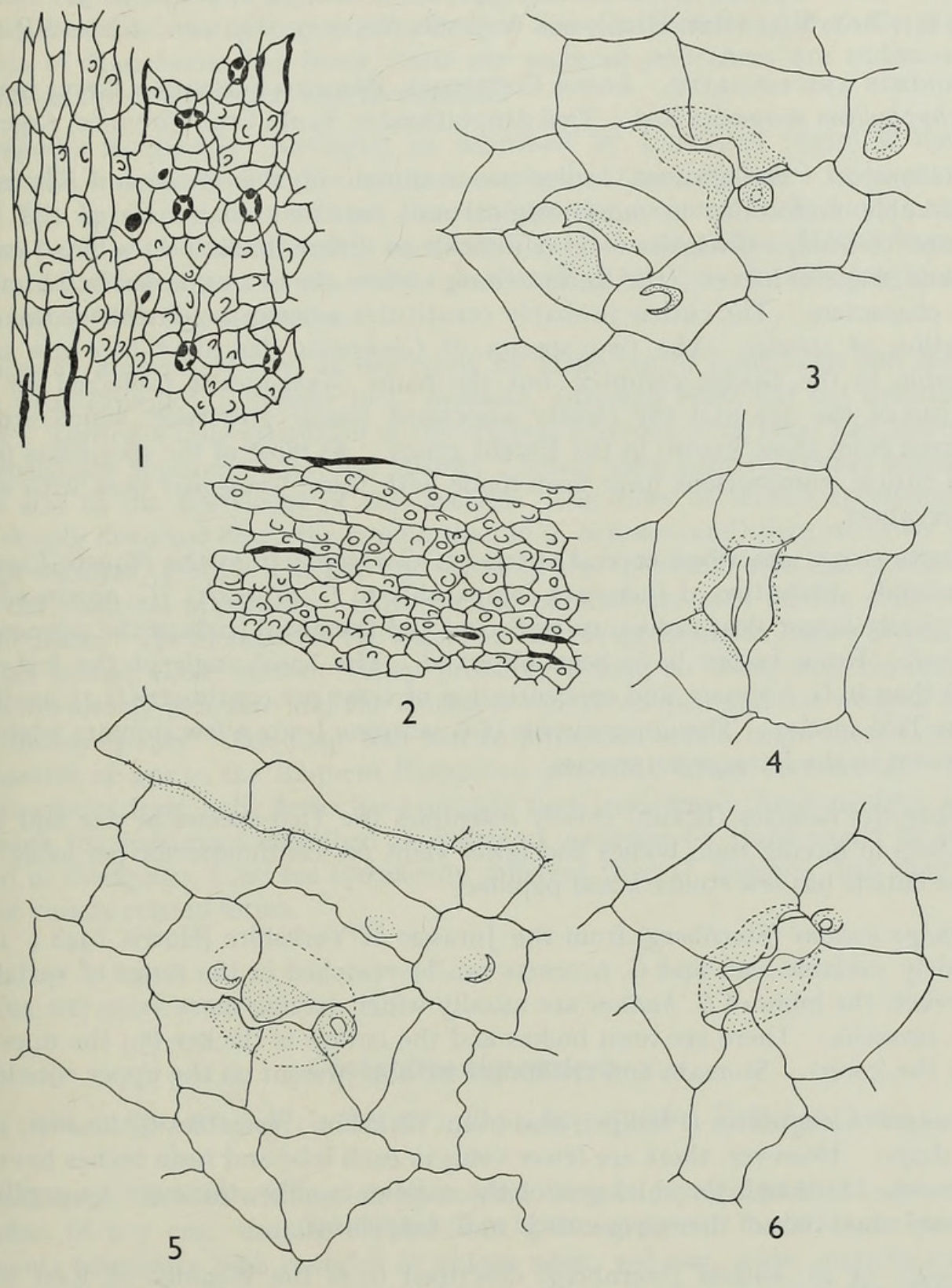
(Pl. 1, figs. 5, 6 ; Pl. 3, figs. 19–21 ; Pl. 4, fig. 27 ; Text-figs. 1–6)

DIAGNOSIS. Leaves with petiole 1 cm. long × 1 mm. wide ; lamina with radius of 2–3 cm., divided into 4 segments ; basal angle about 90°. Segments linear to oblong, 4–6 mm. wide, apices blunt, rounded, sometimes slightly lobed. Veins conspicuous, dichotomously forked, up to 12 per lobe at a concentration of 2 per mm. ; margins entire, substance dense, mesophyll thick, transversely cracked. Resin bodies absent.

Both cuticles of same thickness (1–2μ, measured in folds). Upper cuticle having no stomata ; cells polygonal, not forming rows or bands, each cell bearing a strong hollow papilla ; cells between veins 25–35μ in diameter, on veins somewhat rectangular or elongated, also bearing papillae. Anticlinal walls straight, delicate, closely pitted. On veins, lateral anticlinal walls sometimes strongly thickened. Periclinal walls finely granular ; granules also present on papillae.

Lower cuticle showing bands of rectangular cells along veins and margins, alternating with bands of polygonal cells between veins. Vein bands 6–10 cells wide, marginal bands more than 10 cells wide. Cells along veins 15–20μ wide ; lateral anticlinal walls may be strongly cutinized. Cells between veins polygonal, isodiametric, about 20μ ; anticlinal walls straight or slightly sinuous, closely pitted ; periclinal walls finely granular, but not as densely as on upper cuticle. A strong hollow papilla usually present on each cell, but sometimes absent.

Stomata not placed in files, well spaced, variably orientated, rarely sharing subsidiary cells. Stomatal apparatus round, more often oval. Subsidiary cell group round or oval, composed of 5, sometimes 6 similar cells. Encircling cells usually present but not forming a complete ring, not differentiated from neighbouring epidermal cells. Subsidiary cells sometimes differentiated into polar and lateral, usually thickened on the edge of the pit, almost closing the pit and forming a cutinized ring ; occasionally (especially on polar subsidiary cells) there is a strong hollow papilla. Rarely there is no thickening on subsidiary cells. Guard cells feebly cutinized or not cutinized, slightly sunken in an oval pit. Mouth of pit 20–25μ long. Trichomes absent.



FIGS. 1–6. *Ginkgoites ticoensis* sp. n. Fig. 1. Lower cuticle showing stomatiferous area. Slide LP 24, ×100. Fig. 2. Upper cuticle. Slide LP 24, ×100. Fig. 3. Two stomata with subsidiary cells in contact. Slide LP 24, ×500. Figs. 4–6. Stomata. Slide LP 24, ×500.

HOLOTYPE. LP 5800*a*.

MATERIAL. In addition to the holotype, LP 5801*a*, 5802, 5803*a*-5805*a* ; LIL PB 2559 (4); Brit. Mus. (Nat. Hist.), nos. V.51566, V.51579, V.51926. Slides LP 21–25.

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, *Brachyphyllum mirandai* Bed ; Ticó Amphitheatre, Santa Cruz Province, Argentina.

DISCUSSION. Ginkgoalean leaves are common in the Mesozoic. There is a remarkable uniformity in morphological and cuticular characters of the leaves referred to *Ginkgo–Ginkgoites*. It is difficult to differentiate species based only on size and shape of leaves ; the Recent *Ginkgo biloba* shows a remarkable variation of such characters. The cuticle probably constitutes a better argument for the differentiation of species. The two species of *Ginkgoites* described here are clearly referable to the *Ginkgo* complex, but the name *Ginkgoites* is preferred for them because of the age and the closely associated female structures which are very different from those known in the Recent genus. As most of the specimens possess good cuticle, comparisons have been made with those *Ginkgoites* taxa with similar preservation.

Harris (1935) described several species of *Ginkgoites* from the Rhaeto-Liassic of Greenland. Only two of them are comparable to *G. ticoensis*. *G. acosima* Harris is typically larger (leaf-radius up to 8 cm.) and the distal parts of the segments are notched. Resin bodies have been observed. The basal angle of the leaf varies more than in *G. ticoensis*, and concentration of veins per centimetre is 15 against 20 in the Ticó species. The upper cuticle of *G. acosima* bears a few stomata while none is present in the Patagonian species.

Ginkgoites taeniata (Braun) closely resembles the Ticó species in size and shape. It differs in having resin bodies and fewer veins per centimetre (or per lobe). The upper cuticle has few stomata and papillae.

Ginkgo huttoni (Sternberg) from the Jurassic of Yorkshire (Harris 1948 : 192) is a widely variable leaf, and *G. ticoensis* can be matched in the range of variability. However, the lobes of *G. huttoni* are usually wider, having more veins (20–40) than in *G. ticoensis*. There are resin bodies and the cuticle is thicker (5μ the upper and 2–3μ the lower). Stomata and trichomes are also present on the upper cuticle.

Ginkgoites longifolius (Phillips), also from Yorkshire, resembles *G. ticoensis* in size and shape. However, there are fewer veins in each lobe and resin bodies have been observed. Although the thickness of the cuticles is alike, there are no papillae on the epidermal cells of the upper cuticle in *G. longifolius*.

Ginkgo ex gr. *huttoni* (Sternberg) described from the Wealden of East Siberia (Vachrameev & Doludenko 1961) approaches the Ticó species in having no resin bodies or stomata on its upper cuticle. But the epidermal cells are larger and trichomes have been observed on the lower cuticle. Also there are more veins per lobe (14–18).

Ginkgoites obrutschewi Seward (1911), from the Jurassic of Chinese Dzungaria, has larger lobes and fewer veins per centimetre. Abundant resin bodies have been observed and there are no papillae on the epidermal cells of the upper cuticle.

Ginkgoites cf. *sibirica* (Heer) as described by Yabe & Oishi (1933) from the Middle Jurassic of Manchuria, has fewer veins per segment and there are rudimentary stomata on the upper cuticle and no papillae.

Ginkgoites marginatus (Nathorst) as described by Lundblad (1959) is usually smaller and has no resin bodies in the mesophyll ; there are more veins per lobe (12). The upper cuticle is without stomata and the epidermal cells have a strong median papilla. Lundblad (1959) considers *Ginkgoites hermelini* (Hartz) from the Liassic of Greenland and *G.* cf. *sibirica* as described by Yabe & Oishi (1933), to be synonymous with *G. marginatus*.

Baiera cf. *australis* M'Coy, as described by Halle (1913) from Lago San Martin, Santa Cruz Province, is similar to *G. ticoensis*, although Halle did not describe its cuticle. During a reinvestigation of the original material from Lago San Martin in the Stockholm Museum of Natural History I found some poor epidermal fragments which add to the knowledge of this species. The lobes of Halle's specimens are more deeply dissected down the lamina than in *G. ticoensis* and there are fewer veins in each segment (5–10). The size and shape of the epidermal cells are similar, and so is the stomatal apparatus. However, no papillae are seen on the cells of the upper cuticle. The inclusion of the Lago San Martin specimens in *Baiera* is questionable (as indeed Halle states). They probably belong to *Ginkgoites*, because the leaves are clearly petiolate and the lamina is well developed and not wedged as are most *Baiera* species. The Lago San Martin formation which bears these fossils, is comparable in age to the Baqueró Formation (probably Lower Cretaceous). Some similar species from both floras have already been mentioned (Archangelsky 1963). Although the specimens described as *Baiera* cf. *australis* by Halle would be better placed in *Ginkgoites*, they are specifically different from *G. ticoensis*, but they may well be closely related forms.

Ginkgoites tigrensis sp. n.

(Pl. 1, figs. 1–4 ; Pl. 3, fig. 22 ; Pl. 4, figs. 23–26 ; Text-figs. 7–11)

Diagnosis. Leaves with petiole up to 5 cm. long × 2·5 mm. wide. Lamina with a radius of 1–5 cm., usually divided into 4–8 segments ; basal angle 90–180°. Segments lanceolate with rounded or obtuse apex, 3–8 mm. wide, margins entire ; veins conspicuous, dichotomously forked, crossing the lamina at a concentration of about 18–24 per centimetre, up to 15 present in a full sized lobe ; two veins seem to be present in the petioles. Oval, round or fusiform bodies between veins are rather few and scattered.

Upper cuticle up to 3–4μ thick (measured in folds). Epidermal cells rectangular on base of lamina and on veins of lobes, 20–25μ wide ; between veins becoming more isodiametric, about 20–25μ in diameter. Anticlinal walls straight, thick, up to 5μ, pitted ; periclinal walls with strong ridges, sometimes forming parallel striae, markedly granular ; papillae occasionally observed. Stomata absent on the petiole and base of lamina, but present on lobes between veins, not forming rows, variably orientated, scattered, sometimes sharing subsidiary cells.

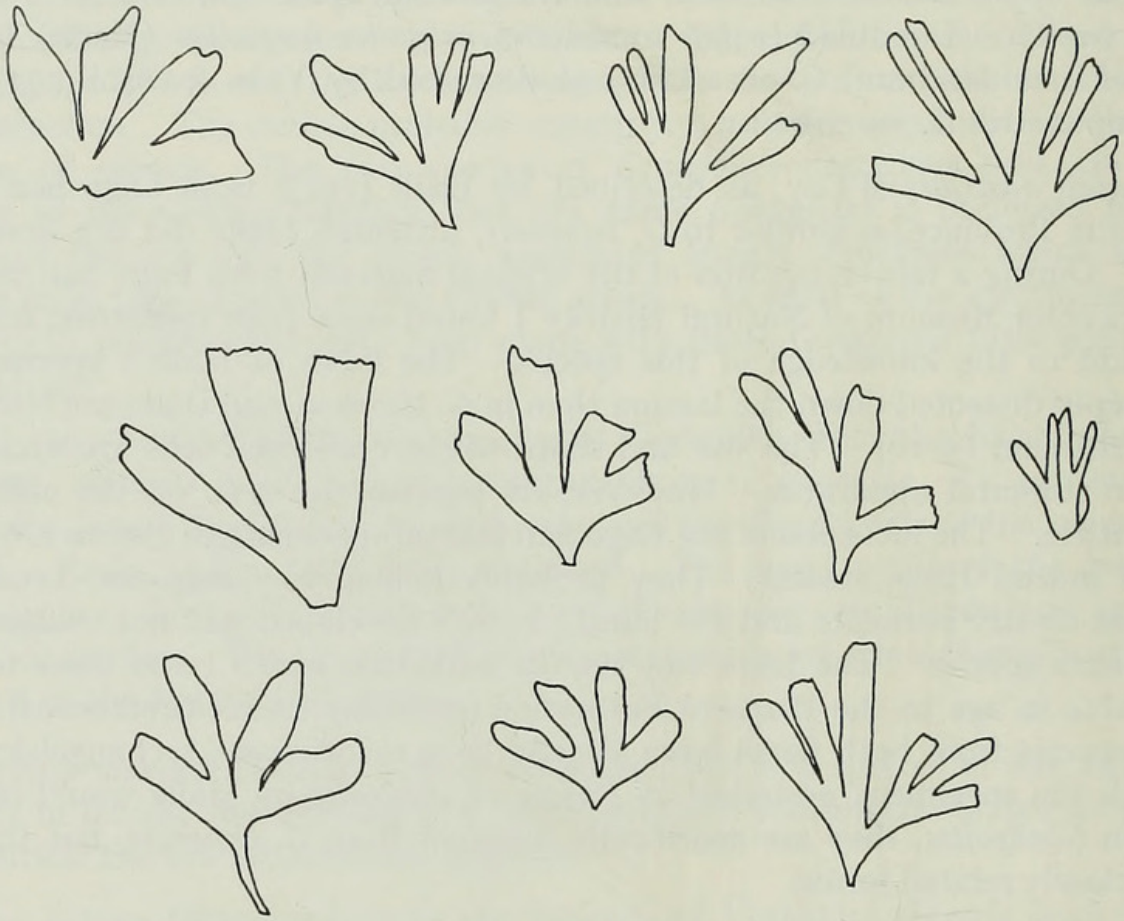


FIG. 7. *Ginkgoites tigrensis* sp. n. Outlines of different leaves to show variation in shape and size. All × 1.

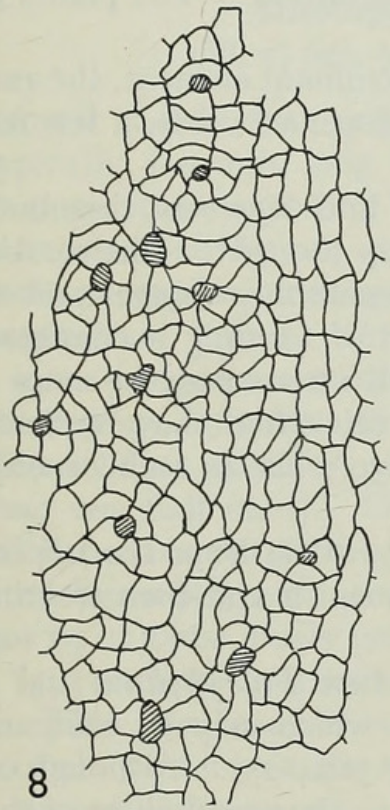
Lower cuticle very thin ; shape and sculpturing on epidermal cells as for upper cuticle. Anticlinal cell walls thin (1–2μ), pitted. Stomata present.

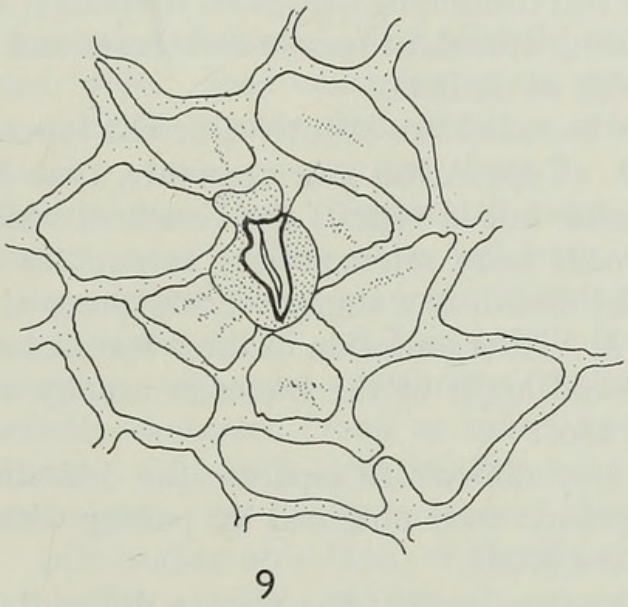
Stomatal apparatus on both cuticles circular or oval, with 4–7 similar haplocheilic subsidiary cells (usually 5–6). Encircling cells sometimes present (apparatus imperfectly dicyclic). Sculpturing on subsidiary cells as for common epidermal cells, except for marked thickening (which occasionally is a papilla) on edge of pit ; thickenings sometimes fused to form a continuous rim of cutin. Guard cells feebly cutinized, slightly sunken. Mouth of pit 25–40μ long.

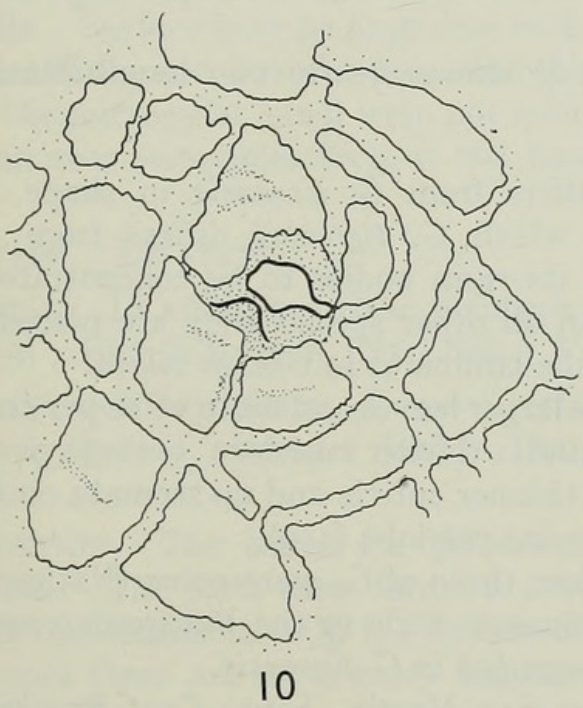
Trichomes absent.

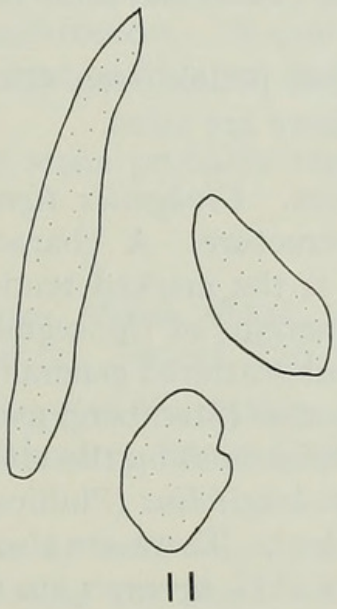
HOLOTYPE. LP 5806. Counterpart, B.M. (N.H.) no. V.51571.

MATERIAL. In addition to the holotype, LP 5541–54, 5557–71, 5573–74, 5593*a*, 5594*a*, 5631–33*b*, 5636–39, 5643*a*, 5644*a*, 5647–49*b*, 5650, 5672, 5807–14, 5824–25; British Museum (Nat. Hist.) Nos. V.51490–V.51501, V.51572–78, V.51924-25. Slides LP 30–40, 145.









FIGS. 8–11. *Ginkgoites tigrensis* sp. n. Fig. 8. Upper cuticle showing distribution of stomata. Slide LP 30, ×100. Figs. 9, 10. Stomata. Slide LP 30, ×500. Fig. 11. Resin bodies. Slide LP 32, ×40.

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member; Bajo Tigre, Santa Cruz Province, Argentina.

DESCRIPTION. This species occurs in the Estancia Bajo Tigre, about 10 miles E. of Ticó. Several fossiliferous beds have been discovered in sediments of similar colour and texture to those found in the Ticó Amphitheatre. The plants are also mummified in the same way.

In the bed containing *Ginkgoites tigrensis* it is the dominant element, the associated plants being abundant female structures and their dispersed seeds, a few ferns and some twigs of conifers.

I have included two slightly different types of leaf in *G. tigrensis*, they both occur together. Type A has four segments, type B has up to eight. Their cuticles are very similar but in type B the anticlinal walls are sometimes thinner and the subsidiary cells more often project as papillae instead of forming a continuous rim round the mouth of a stoma. Sculpturing of the cell surface may be more marked in type A. Intergradation in these features of the cuticle does, however, occur.

The basal angle of the leaves is usually about 130°, but in small specimens it is up to 180°.

It is very difficult to separate the delicate lower cuticle from the upper, but a few fragments were obtained by pulling with nail varnish and then treating them with dilute KOH.

In the same locality but from a different bed (where *Ptilophyllum* and *Brachyphyllum* are abundant) I collected two small leaves which may be compared with the small specimens found in the *G. tigrensis* Bed (LP 5824–25). Although cuticular fragments are small and show no important characters, the morphology of the leaves coincides.

The largest petiole seen (Pl. 1, fig. 4) shows clearly two longitudinal furrows which I believe are veins.

DISCUSSION. *Ginkgoites tigrensis* differs from *G. ticoensis* in shape, size and cuticular structure. A character in which *G. tigrensis* differs from all other *Ginkgoites*, is the marked tendency of its resin bodies to be concentrated mainly along the margins of the segments. In all other species they are placed between the veins but scattered generally over the lamina as in *Ginkgo biloba*.

Ginkgo huttoni (Sternberg) usually has larger leaves and more veins per centimetre; it also has trichomes on the epidermis and a thicker cuticle.

Ginkgoites longifolius (Phillips) has a thinner cuticle and no stomata on the upper side of the leaf. There are also fewer veins per lobe (4–9).

The lobes of *G. tigrensis* are wider than those of *G. marginatus* (Nathorst). The concentration of veins is 4–18 per centimetre while in the Patagonian species it is 18–24 ; also there are more veins per segment in *G. tigrensis*.

Baiera cf. *australis* M'Coy from Lago San Martin, Santa Cruz Province (Halle 1913) is smaller and the lobes are deeply dissected.

Ginkgo biloba is clearly different in shape and size. The distribution of the resin bodies is also different as well as the stomatal apparatus.

SEEDS AND FEMALE STRUCTURES CLOSELY ASSOCIATED WITH *GINKGOITES* LEAVES

ALLICOSPERMUM Harris 1935

Allicospermum patagonicum sp. n.

(Pl. 1, figs. 7–9 ; Pl. 5, fig. 28 ; Text-fig. 12)

DIAGNOSIS. Seeds oval, originally somewhat flattened, with slightly acuminate apex, typically 4–5 mm. long by 3 mm. wide. Seed consisting of an outer flesh and an inner stone enclosing various cuticles. Outer flesh about 1 mm. thick (usually represented by an empty space) ; stone 3·0–3·5 mm. long by 2·5 mm. wide, with micropilar prolongation 0·5–1·0 mm. long. Surface of stone marked with longitudinal bulges. On maceration, seed yielding the following cuticles. (1) The inner (megaspore membrane), densely and finely granular, showing no cell walls, thick (2–3μ in folds) and resistant to maceration. (2) Thin cuticle (1–1·5μ in folds) described as nucellus, partly covering megaspore membrane (probably not more than one half of it). Cells markedly elongated (120μ or more) and 8–10μ wide. Cell surface flat, not ornamentated. Cell walls straight, becoming thicker and pitted towards apex ; end walls straight. (3) Poorly preserved thin cuticle (less than 1μ in folds), finely granular ; cells isodiametric (15μ) or slightly elongated (24μ × 15μ) with straight walls. Small hollow papillae, one per cell, are sometimes present. This membrane is regarded as the inner lining of the integument. (4) Thick cuticle (outer cuticle of integument) enclosing stone and flesh. Cuticle faintly marked with somewhat isodiametric cells, 10–15μ in diameter, with straight thick walls. Surface may be granulose with many adherences. Stomata absent.

The apex of the nucellus where a pollen chamber might be situated, and a cutinized lining of the micropylar canal were not seen.

A round scar sometimes seen at the base of the stone probably represents the hilum.

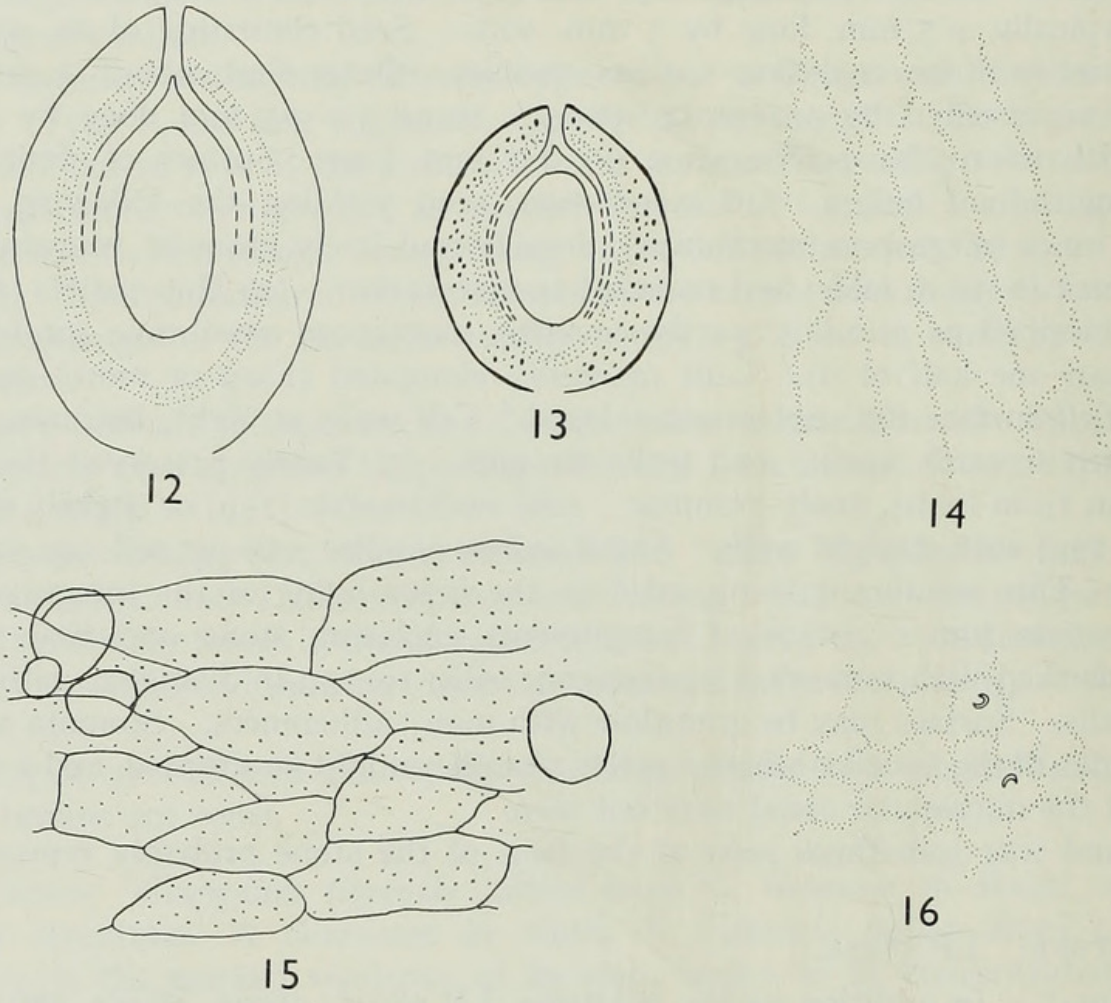
HOLOTYPE. LP 5821*a*.

MATERIAL. In addition to the holotype, LP 5804*b*, 5822*a*, 5823*a*, 5863*c* ; LIL PB 2559(3) ; British Museum (Nat. Hist.), V.51580–81(2). Slides LP 49–53, 125–129.

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, *Brachyphyllum mirandai* Bed ; Ticó Amphitheatre, Santa Cruz Province, Argentina.

DESCRIPTION. The seeds are preserved in one of two ways. A. Without compression. The seed then forms a cavity enclosing the stone which is itself filled with fine sediment. On the surface of this stone (or possibly the internal cast of the stone) there are some coaly fragments which yield a few membranes when macerated. These membranes are situated on the outer surface of the coal. Two cuticles are usually present. The outer and thicker is similar to cuticle 4 of the diagnosis, while the inner, poorly preserved, corresponds to cuticle 3 (inner lining of the integument). Cuticles 2 and 1 are sometimes also present, adhering to the inner

surface of the coaly fragments. The gap seen outside the coal may be due to the shrinkage of the stone. B. With compression, but no infilling with sediment. The seed then forms a disc and it is possible to prepare its cuticles. The flesh forms a compressed border round the thicker substance of the stone. In such specimens the megaspore membrane and the nucellus are usually better preserved. Clearly, the nucellus cuticle is single and was not seen fused to the inner lining of the integument as in the seed described by Harris (1944 : 427, text-fig. 3D).



FIGS. 12–16. *Allicospermum patagonicum* sp. n. and *Karkenia incurva* gen. et sp. n.

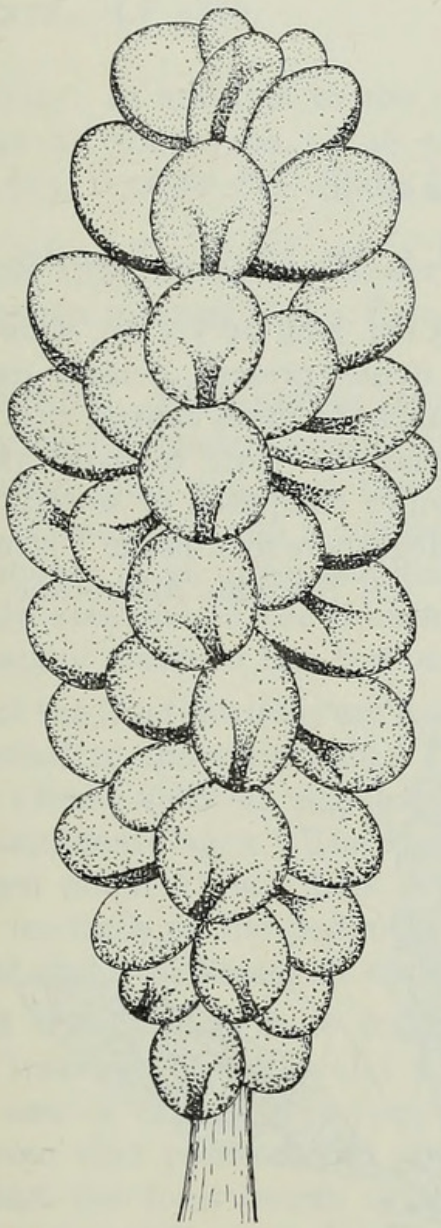
Fig. 12. *Allicospermum patagonicum* sp. n. Diagrammatic section of seed to show the probable extent and position of the different membranes (the stone is dotted). ×10.

Figs. 13–16. *Karkenia incurva* gen. et sp. n. Fig. 13. Diagrammatic section of seed to show the probable extent and position of the different membranes (small dots represent the stone ; thick dots are resin cavities). ×10. Fig. 14. Cells of nucellus. Slide LP 42, ×425. Fig. 15. Outermost layer of cells (outer integument) with a few resin cavities. Slide LP 44, ×500. Fig. 16. Cells of the inner integument, faintly marked. Slide LP 42, ×425.

DISCUSSION. *Allicospermum retimirum* Harris from the Jurassic of Yorkshire is similar in size and shape, though slightly wider. Fine differences are : *A. patagonicum* has a granulose outer cuticle instead of a smooth one, and the stone, on macera-

tion, yields no reticulum as does *A. retimirum*. The Yorkshire species has not been identified with any leaf. Seeds looking rather like *A. patagonicum* are associated with *Ginkgoites* leaves in various floras and have sometimes been more or less definitely linked with them. There is, for example, *A. xistum* with *Ginkgoites taeniata* Harris from Scoresby Sound, Greenland, the cuticles of that seed being known.

A. patagonicum is associated with *Ginkgoites ticoensis* in the *Brachyphyllum mirandai* Bed. Neither of these taxa has been found in other horizons or localities so far studied.



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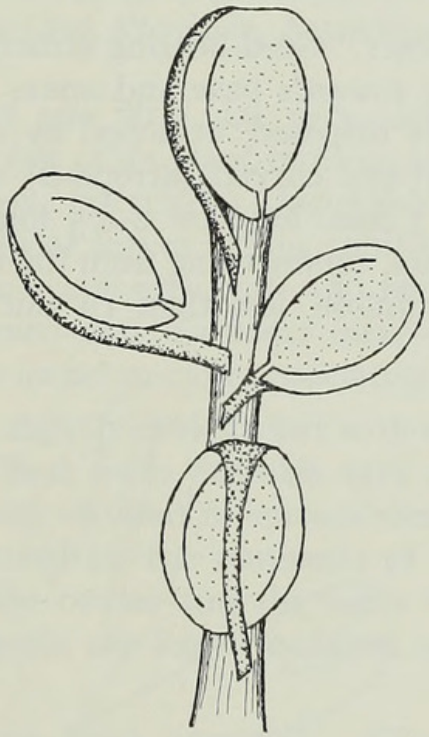

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FIGS. 17–18. *Karkenia incurva* gen. et sp. n. Fig. 17. Reconstruction of the entire female structure (based on LP 5817). ×4·5. Fig. 18. A few inverted ovules inserted on the main axis. ×5. (C. Freile *del.*)

Genus ***KARKENIA*** nov.

The name *Karkenia* is from " karken " which in the language of the Tehuelche Indians (Southern Patagonia) means " female or woman ".

DIAGNOSIS. Oval or elongated seed-bearing structures composed of a central axis with irregularly disposed pedunculate ovules. Ovules round or oval, curved (atropous) facing axis with micropylar end, densely packed, composed of four cutinized membranes belonging to the megaspore, nucellus, inner and outer integuments. Seeds developing a conspicuous stone.

For discussion of genus see below.

TYPE SPECIES. *Karkenia incurva* sp. n.

Karkenia incurva sp. n.

(Pl. 1, fig. 10 ; Pl. 2, figs. 11, 14, 16, 18 ; Pl. 5, figs. 29–32 ; Text-figs. 13–19)

DIAGNOSIS. Seed-bearing structure up to 4·5 cm. long by 1·3 cm. wide, tapering gradually towards base and apex. Up to 100 ovules present, densely packed and irregularly disposed, attached by delicate peduncle to main central axis 1–2 mm. wide. Ovules curved (atropous) with micropylar end close to main axis, round or oval, 3 mm. long by 2–2·5 mm. wide. Ovules composed of several cutinized membranes, commencing from the inside : (1) Megaspore membrane ; structureless, finely granulose, less than 1μ thick (in folds). (2) Nucellus membrane ; usually

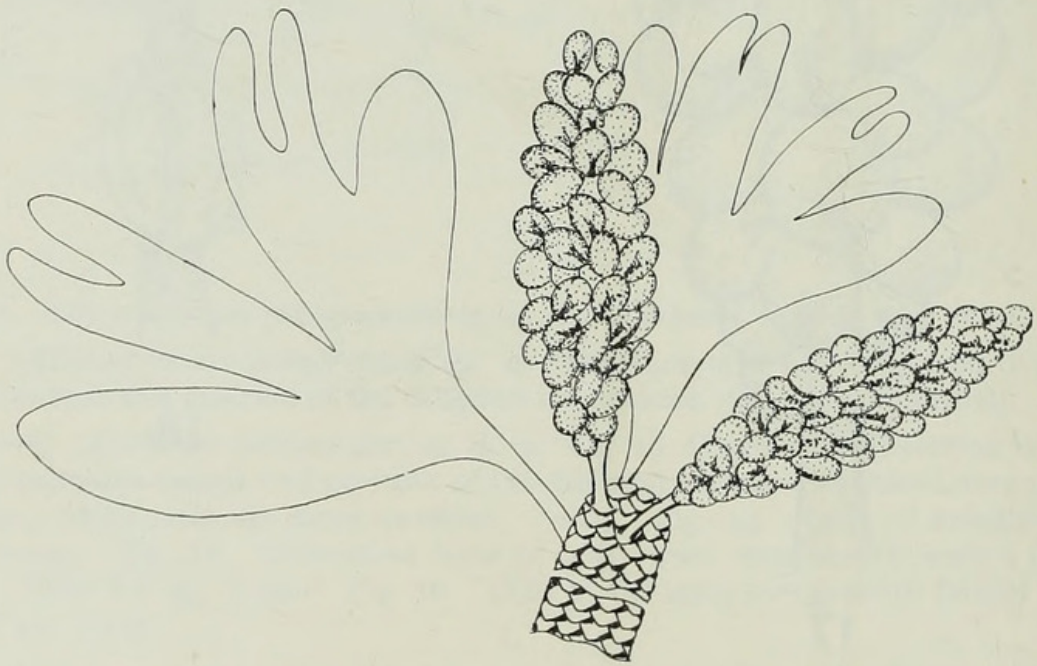

FIG. 19. Tentative reconstruction based on the dwarf-shoots, leaves (*Ginkgoites tigrensis*) and female structures (*Karkenia incurva*). ×2. (C. Freile *del.*)

closely fused to membranes 1 and 3, extending down to near base, 1–1·5μ thick (in folds), showing markedly elongated cells more than 100μ long by 15μ wide, surface flat, not granulose. At the top, nucellus projecting as a short acute micropylar beak. (3) Inner layer of integument, probably extending down to near base of ovule, showing no definite structure but small granules. (4) Outer layer of integument, faintly cutinized membrane, showing cells about 50μ long by 15–25μ wide, finely granulose with occasional small hollow papillae.

Between membranes 3 and 4, small round resin bodies (?) from 2–30μ in diameter occur.

HOLOTYPE. LP 5816.

MATERIAL. In addition to the holotype, LP 5580–84, 5598*a*, 5599, 5631*a*–33*a*, 5635, 5640–41, 5647*a*–49*a*, 5814*b*, 5815*a*, 5817*b*–5819; British Museum (Nat. Hist.), V.51499–503, V.51582–84. Slides LP 41–47, 131–144.

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, *Ginkgoites tigrensis* Bed ; Bajo Tigre, Santa Cruz Province, Argentina.

DESCRIPTION. Seed-bearing structures, all of one kind, are very abundant in the bed where *Ginkgoites tigrensis* occurs. Very few other plant remains are present in association, all of which are rare : two ferns, one referred to *Cladophlebis* and the other to *Sphenopteris*, and a conifer with long linear leaves. This conifer becomes more abundant in an upper bed and is known to occur with male and female cones organically attached to the branches. *G. tigrensis* and *Karkenia incurva* are not only abundant fossils in this bed but are always found in close association.

Many of the fructifications are found entire or slightly broken, but with the ovules still attached to the main axis. Detached or shed seeds are also very abundant and they clearly show an egg-shaped stone, finely striated in surface view, with a marked acuminate apex. The stone is surrounded by the remnants of the outer fleshy layer about 1 mm. thick. The size of the ovules and the seeds is similar. There is no trace of the peduncle when the seeds are found isolated, except an occasional slight thickening at the hilum area.

Several transfers of these fructifications have been prepared. All show the irregular insertion of the ovules which have no definite phyllotaxis. The ovules face the axis of the fructifications with their micropylar end, or may be slightly turned from that position, but never erect. The peduncles are short, not much longer than the total length of the ovules. Ovules are crowded and compact, suggesting a cone-like structure. The peduncles are attached only to the hilum sector of the ovules, where a slight expansion may sometimes be seen ; for the rest they are free and easy to separate from the ovules. Therefore, the inverted position of the ovules corresponds to an atropous incurved type. No bracts or laminar appendages were observed in relation to the ovules or the peduncles. *Karkenia* may be defined as having a central axis bearing pedunculate, naked and inverted

ovules. I suggest that the peduncle-ovule structure is morphologically a lateral branch of the main central axis, being analogous but not homologous to the megasporangiophores of other groups. There is no specialization of the peduncles, which are merely lateral appendages of the central axis.

As for the cutinized membranes of the ovules, there is no doubt about the shape and size of the megaspore. The nucellus, closely attached to the megaspore and sometimes to the inner layer of the integument, is also cutinized down to near the base of the seed. The micropylar projection is seen as a very short apical extension of the nucellus and is also cutinized. The micropylar canal was not clearly seen and no pollen was found in connection. There is doubt about the structure and extent of the inner lining of the integument. It is a structureless membrane, sometimes showing very faint marks which may be cell outlines, but this is not sure. Granules are clearly seen. Also, there is doubt about the structure of the external surface of the integument, although some cells have been observed. It is similar to the inner lining of the integument but thicker. Granules and some papillae were also seen, but there are no stomata. Between these two membranes round bodies are found isolated or in large groups of 20–30 or more. They may well be resin bodies, which are more likely to be preserved than the mucilage cavities present in the Recent *Ginkgo biloba*. I believe these round bodies are natural features of the seeds, because they are constant in all the specimens observed and are of the same type ; often, when detached, they leave a round impression on the integument membrane.

Associated dwarf-shoots and roots. In close association with *Karkenia* and *Ginkgoites* I have found small, short branches which are probably dwarf-shoots of the same plant. One of these specimens shows a shoot, 3·3 cm. long by 5 mm. wide, bearing three dwarf-shoots at intervals of about 0·8 cm. The largest dwarf-shoot is 1·5 cm. long by 4 mm. wide. The widest seen was 1 cm. Each of these shoots is crowded with spirally disposed rhomboidal scars, their longest axis being horizontal. The width of these scars is 1–2 mm. and corresponds to the size of the main axis of the female structures and the petioles of the leaves. In the middle of these cushions one or two (?) small circular scars are seen. They may correspond to the vascular bundles. In its distal part one of these dwarf-shoots shows the remnants of an axis and a few ovules of the type described for *Karkenia*. The organic attachment between shoot, axis and ovules may be inferred from the continuous brown colour which is clearly different from the adjacent light colour of the matrix (Pl. 2, fig. 12).

In close association with the previously described material, many fragments of roots occur (Pl. 2, figs. 15, 17). Some of them cross the sedimentary layers obliquely, while others are lying in the sedimentary planes, which, however, are not clearly defined.

The *Ginkgoites* leaves, complete *Karkenia* structures, dwarf-shoots and the roots, are situated in the boundary of two different sediments ; the lower sector, bearing most of the organic remains, is a pale brown, fine-grained rock succeeded

by a white coarse-grained sediment. The plants were found in abundance only a few millimetres above and below this boundary plane. On top of this sector, only detached Ginkgoalian leaves and fragmentary conifers are present. The presence of roots may well indicate that the most productive part of the plant bed was deposited *in situ*, and therefore the plants included have not suffered a long transport.

The roots are composed of a main root about 0·4 cm. wide, giving off secondary roots, irregularly disposed, at acute or right angles. These secondary roots give rise to delicate rootlets which are typically crowded with round bodies, 1–2 mm. in diameter, irregularly situated. No organic remains were found except for a few carbonized fragments which dissolved completely under maceration. These round bodies may well belong to some type of mycorrhiza.

MATERIAL. Dwarf-shoots : LP 5587–88, 5642, 5643*b*, 5644*b*, 5645–46 ; British Museum (Nat. Hist.), V.51575. Roots : LP 5575–79, 5593*b*, 5594*b*, 5598*b* ; British Museum (Nat. Hist.), V.51504–05.

DISCUSSION. *Ginkgoites tigrensis*, *Karkenia incurva* and the dwarf-shoots described may belong to the same plant. The close association and the absence of other forms which could possibly bear female structures are the only arguments to suggest this identity.

Comparisons of *Karkenia incurva* can only be made with the Recent *Ginkgo biloba* and with *Trichopitys heteromorpha* Saporta, a Permian Ginkgoalean plant whose female structures are inadequately known.

Trichopitys heteromorpha Saporta as described by Florin (1949) has in common with *Karkenia incurva* the irregular distribution of the ovules on a main axis, and their inverted position. The number of the ovules is, however, smaller, but the size is similar. The pedicels which bear the ovules and the main axis are wider in *Trichopitys*, and the whole fructification may be longer. Also, the ovules of the Permian genus are separated and do not form a compact structure as in *Karkenia*. The leaves of *Trichopitys* are very different, not having a developed lamina. No dwarf-shoots are known to occur. Neither in *Trichopitys* nor in *Karkenia* is there a collar at the base of the ovule.

Ginkgo biloba has a female structure composed of one long stalk bearing two terminal ovules, one of which usually aborts. At the base of the ovules there is a cup-like structure known as a collar. The stalks are spirally disposed on short branches (dwarf-shoots) in the axils of young leaves. Abnormal cases do occur ; one of them shows several ovules irregularly disposed on a main axis. These ovules have long pedicels but are not inverted. This case suggests, as stated by Florin (1949), that the ancestors of the group must have been multiovulate structures, like *Trichopitys* and *Karkenia*. The main differences are the absence of a collar and the inverted position of the ovules, which *Karkenia* has probably retained from primitive forms.

The collar is considered by Florin (1949) as a secondary feature, related to the insertion of the erect ovules, and *Karkenia* (as well as *Trichopitys*) is in accordance because there is no collar but an inverted position of the ovules.

The absence of any laminar structure in direct relation to the ovules, suggests that the abnormal cases of leaves bearing ovules (found in the Recent *Ginkgo*) are secondary phenomena.

Karkenia may well be an intermediate type of female structure (" flower ") between *Trichopitys* and *Ginkgo*, having undergone some fusion and reduction processes since Permian times, but still retaining some primitive features.

It is difficult to establish the degree of relationship between *Trichopitys* and *Karkenia*. Possibly each of the " sporangial trusses " of *Trichopitys* can be homologous with the single ovule and its peduncle of *Karkenia*. In such a case, the " sporangial trusses " must have fused to form a compact structure, while the main axis was strongly reduced. The leaves (sterile telomes) of such branches became reduced and further disappeared, while they persisted on the entirely sterile branches. During all these changes, probably the " short shoot " habit was attained, with sterile and fertile telomes clearly differentiated. There is no information about all these possible intermediate types (Permian—Lower Cretaceous).

It is perhaps easier to understand the processes which followed in order to reach the *Ginkgo* type of flower. Every compact structure of *Karkenia* may be homologous with the *Ginkgo* peduncle and ovules. This state was attained by reduction of *Karkenia* peduncles, and fusion of its ovules, followed by their erection (forming a collar as a secondary feature). It may be suspected that the erect position of the ovules and the formation of the collar, is probably a rather recent phenomenon, possibly post-Neocomian, when the Angiosperms began to dominate.

Text-fig. 19 is a reconstruction of *Karkenia* borne on dwarf-shoots, together with *Ginkgoites tigrensis* leaves.

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PLATE 1

Ginkgoites tigrensis sp. n.

FIGS. 1–3. Different leaves showing variation in size, shape and lobation of the segments. Fig. 1 (LP 5807) ×1·2 ; Fig. 2 (LP 5824) ×2 ; Fig. 3 (B.M.N.H. V.51571) counterpart of holotype, ×1·1.

FIG. 4. Leaf with long petiole. LP 5552, ×1.

Ginkgoites ticoensis sp. n.

FIG. 5. Holotype (LP 5800) ×1·5. Fragments of *Brachyphyllum mirandai* Arch. and *Ruflorinia sierra* Arch. are also seen.

FIG. 6. Fragmentary leaf to show venation. LP 5801, ×1·5.

Allicospermum patagonicum sp. n.

FIGS. 7, 8. Isolated seeds showing carbonized remains of the outer fleshy integument adhering to the main body. Fig. 7, LP 5804, ×8 ; Fig. 8, LP 5822, ×8.

FIG. 9. Several seeds in different positions. LP 5821, ×1·5.

Karkenia incurva gen. et sp. n.

FIG. 10. An almost complete fertile structure (left) together with a leaf of *Ginkgoites tigrensis*. B.M.N.H. V.51582, ×1·1.

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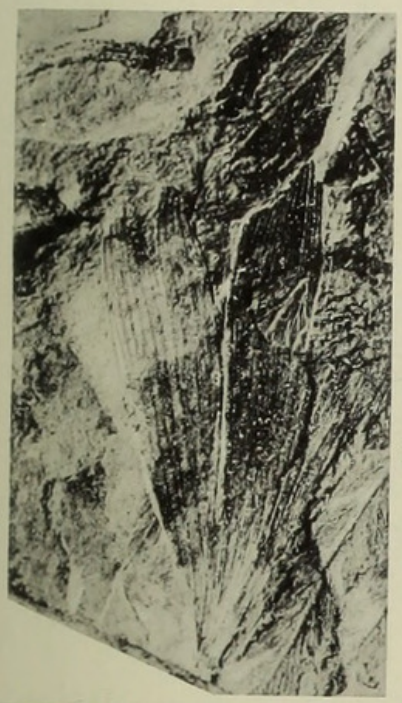

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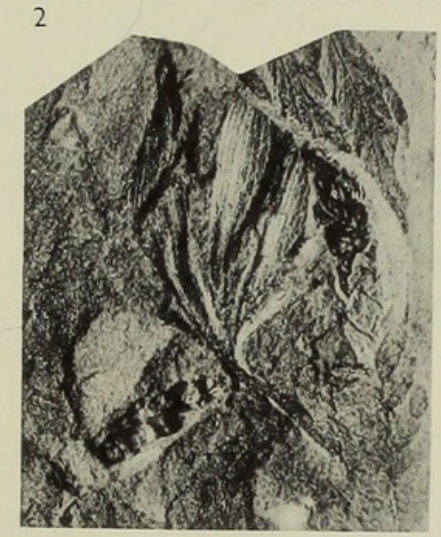

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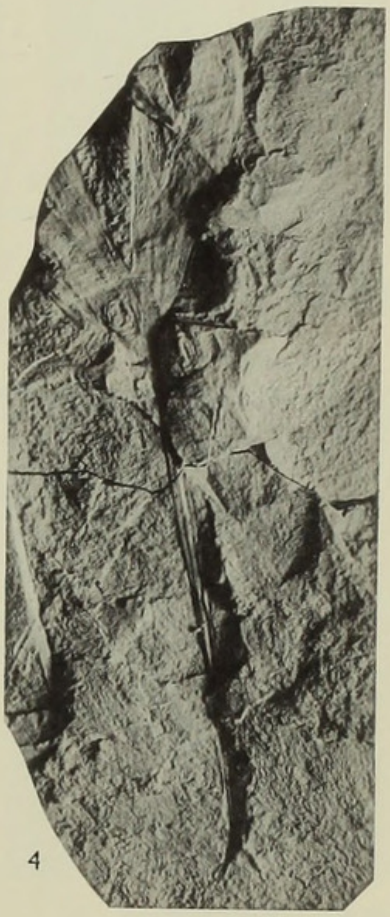

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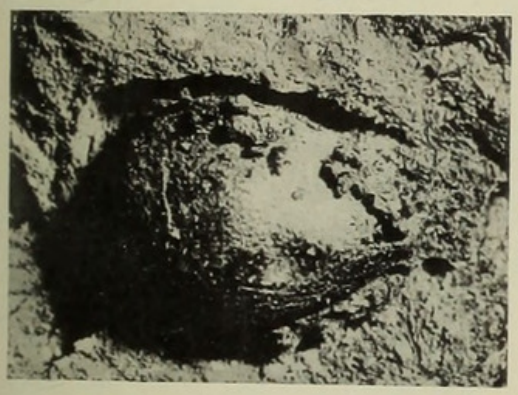

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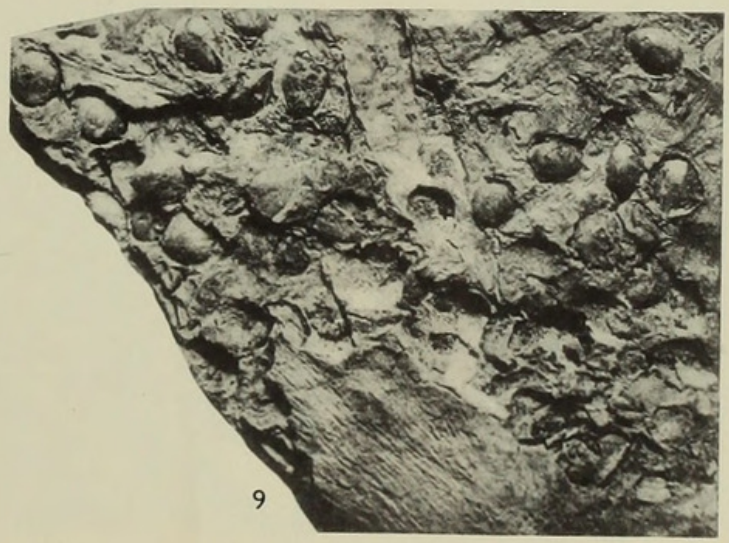

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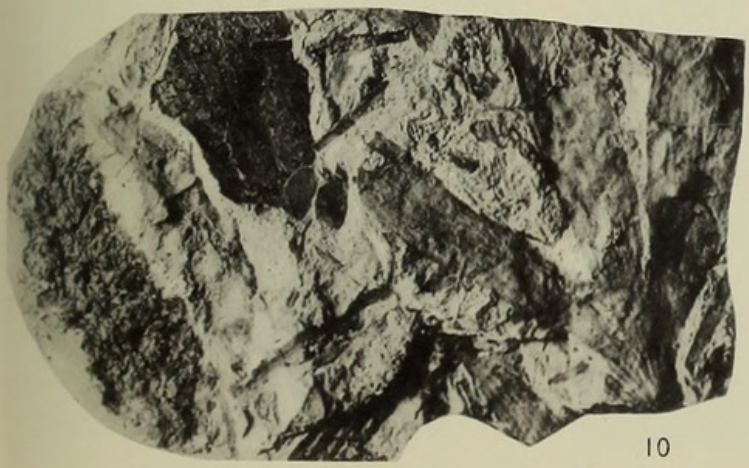

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PLATE 2

Karkenia incurva gen. et sp. n.

FIG. 11. Enlarged fragment of a female structure, showing main axis (bottom) and several ovules (some are inverted). LP 5817, ×4·5.

FIG. 14. Several fragments of female structures and part of a *Ginkgoites tigrensis* leaf. LP 5816, ×1.

FIG. 16. Fragments of female structures. Towards the left, a small fragmentary pinna of *Cladophlebis* sp. is also seen. LP 5815, ×1.

FIG. 18. Two isolated seeds. LP 5818, ×1·5.

DWARF SHOOTS

FIG. 12. Enlarged fragment showing at the top two seeds of *Karkenia incurva*. LP 5645, ×8.

FIG. 13. An almost complete branch showing rhomboidal scars. LP 5643, ×4.

ROOTS

FIG. 15. Enlarged rootlets showing round bodies attached. LP 5598, ×8.

FIG. 17. A root (white arrow) traversing the sediment. LP 5593, ×1.

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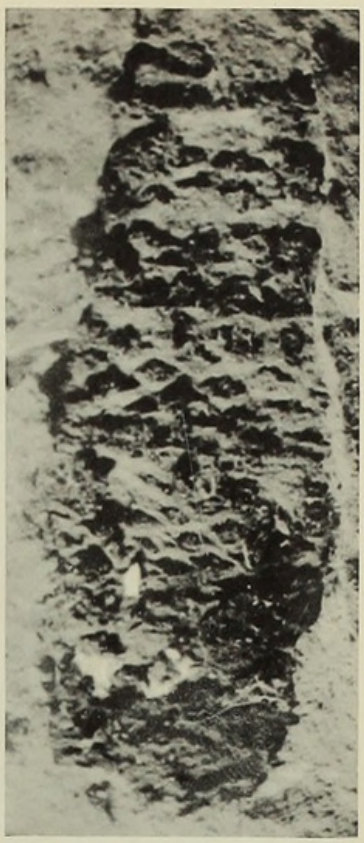

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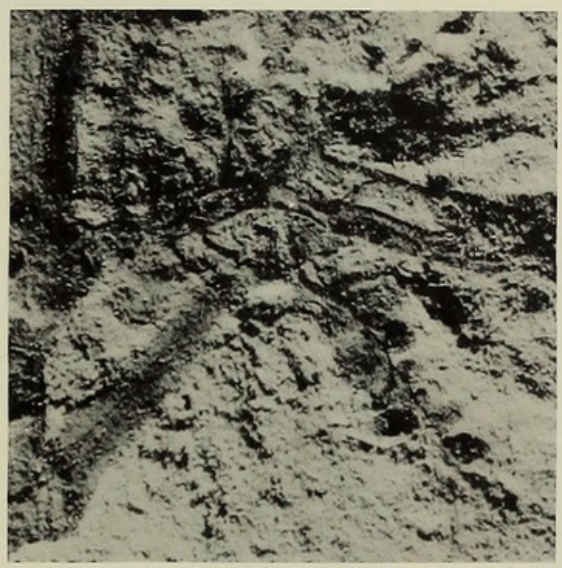

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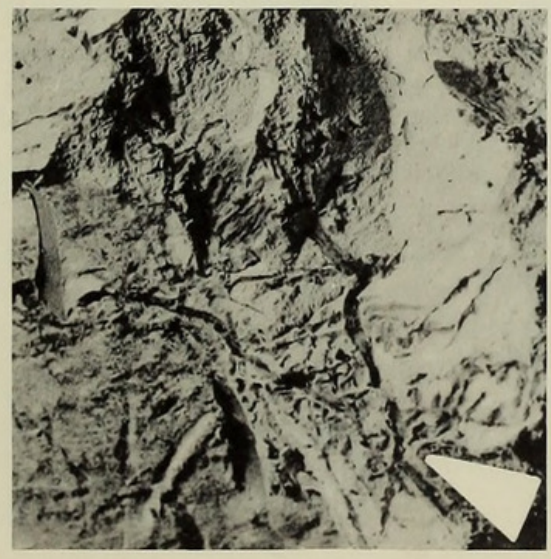

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PLATE 3

Ginkgoites ticoensis sp. n.

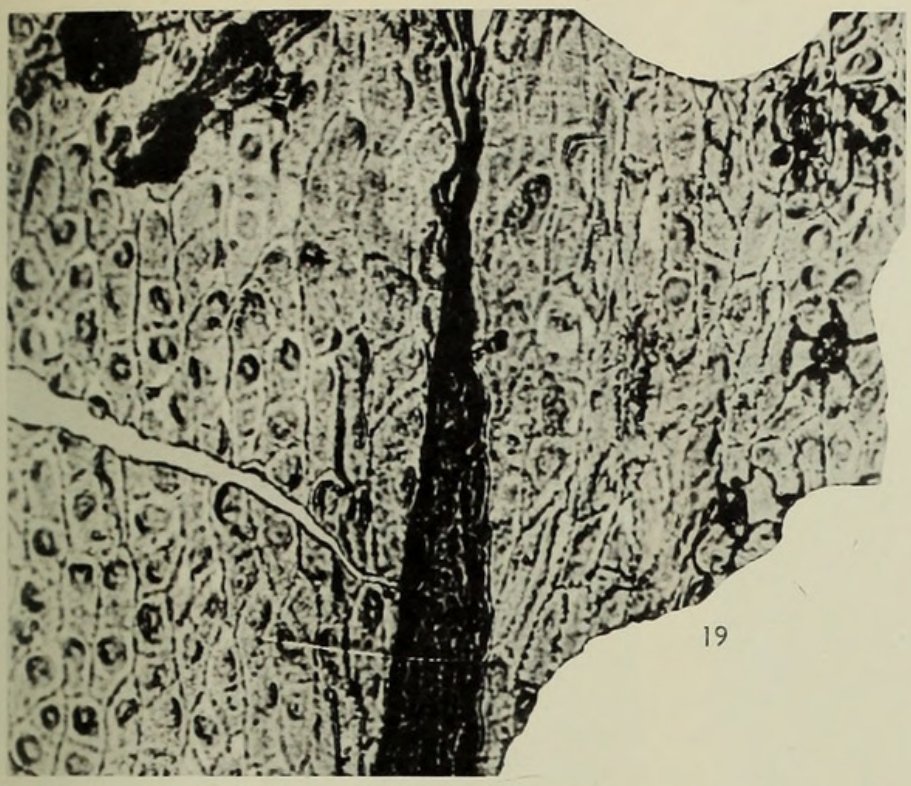
FIG. 19. General aspect of both cuticles (the lower towards the right). Slide LP 24, ×180.

FIG. 20. Lower cuticle. Sector between veins showing distribution of stomata. Slide LP 25, ×180.

FIG. 21. Two stomata showing strong thickenings overhanging mouth of pit. Slide LP 25, ×800.

Ginkgoites tigrensis sp. n.

FIG. 22. Fragment of leaf segment showing three resin bodies near left margin. Slide LP 30, ×40.



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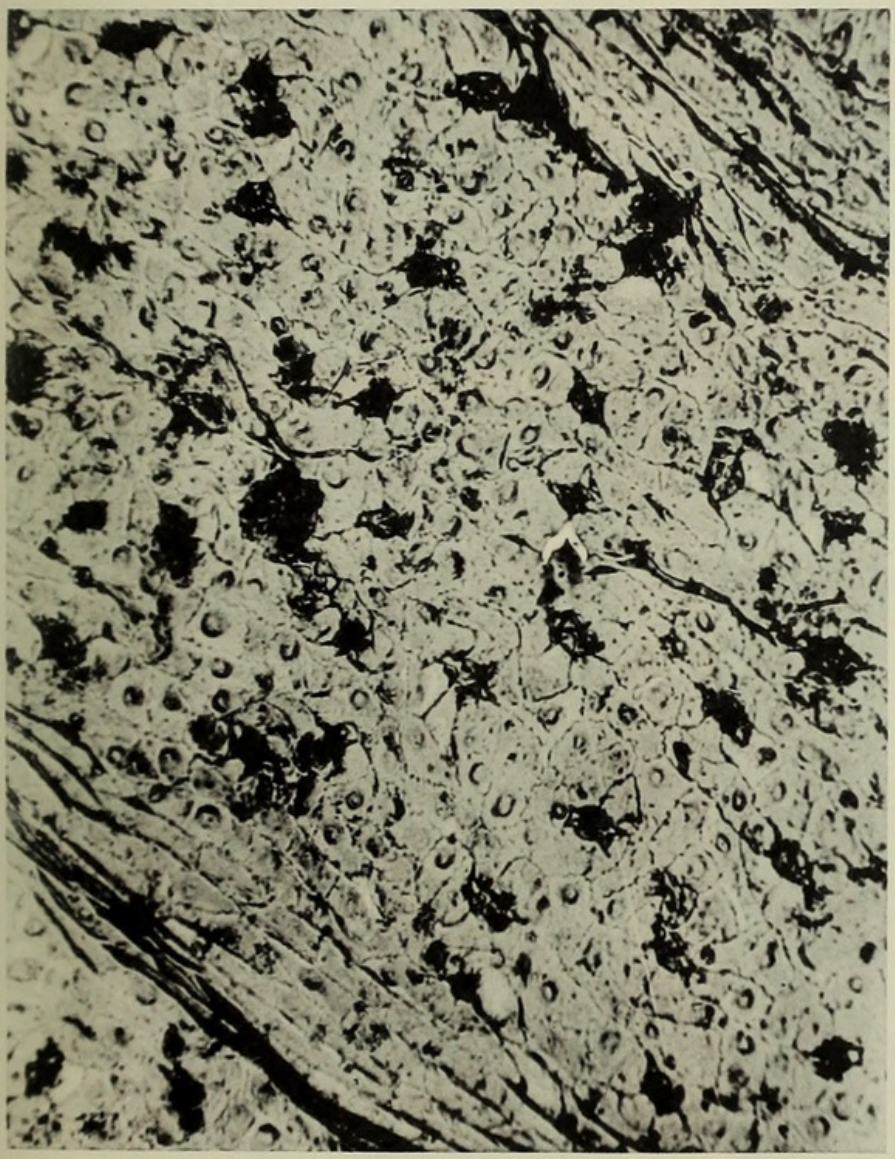

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PLATE 4

Ginkgoites tigrensis sp. n.

FIG. 23. Fragment of upper cuticle showing few scattered stomata. Slide LP 30, ×180.

FIG. 24. Fragment of upper cuticle showing elongated cells on veins and a sector between veins, almost devoid of stomata. Slide LP 40, ×180.

FIG. 25. Stoma showing an almost continuous rim of cutin overhanging mouth of pit. Slide LP 40, ×850.

Fig. 26. Stoma. Slide LP 30, × 800.

Ginkgoites ticoensis sp. n.

FIG. 27. Stoma showing guard cells slightly cutinized. Slide LP 22, ×800.

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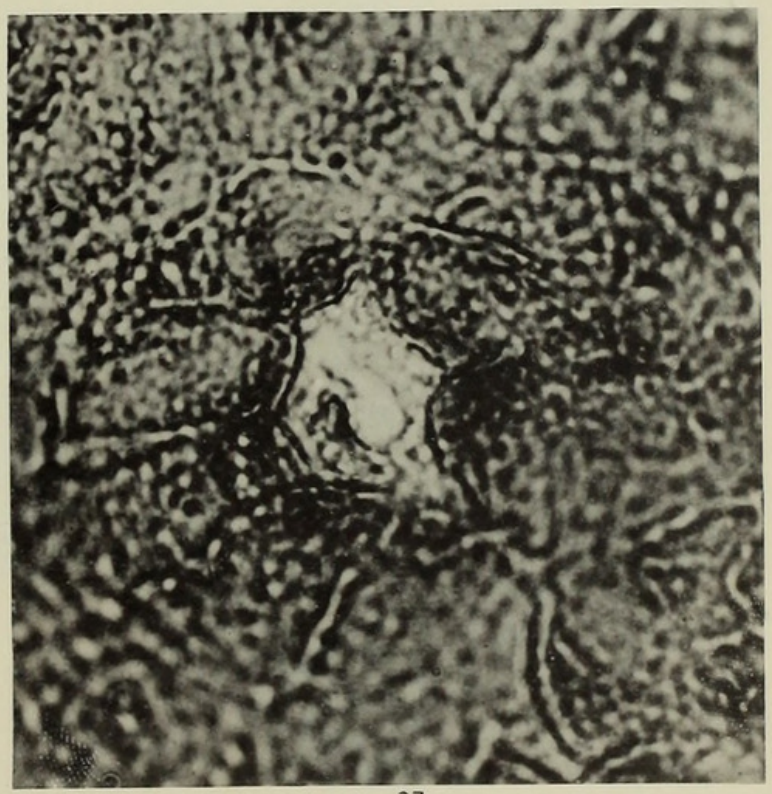

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PLATE 5

Allicospermum patagonicum sp. n.

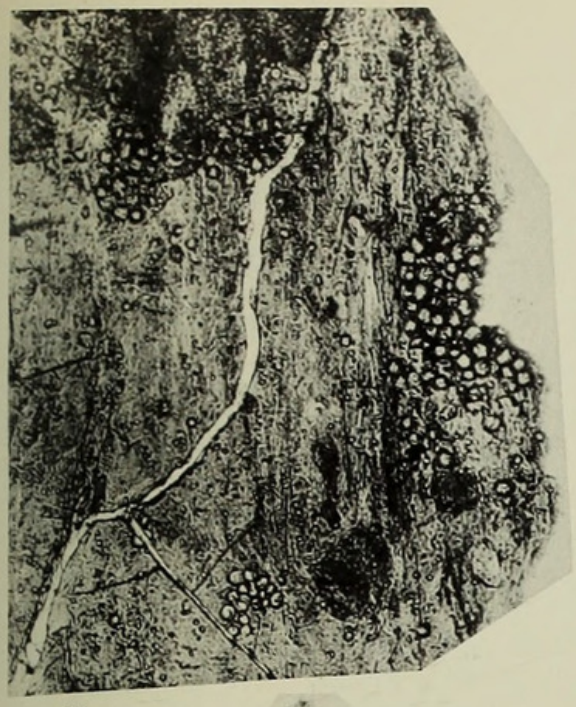
FIG. 28. Nucellus membrane (left) and megaspore membrane (right). Slide LP 51, ×175.

Karkenia incurva gen. et sp. n.

FIG. 29. Part of a seed showing groups of resin (?) bodies. Slide LP 139, ×60.

FIGS. 30. 31. Two apical portions of nucelli. Fig. 30, Slide LP 47, ×175 ; Fig. 31, Slide LP 42, ×60.

FIG. 32. Megaspore membrane. Slide LP 45, ×175.



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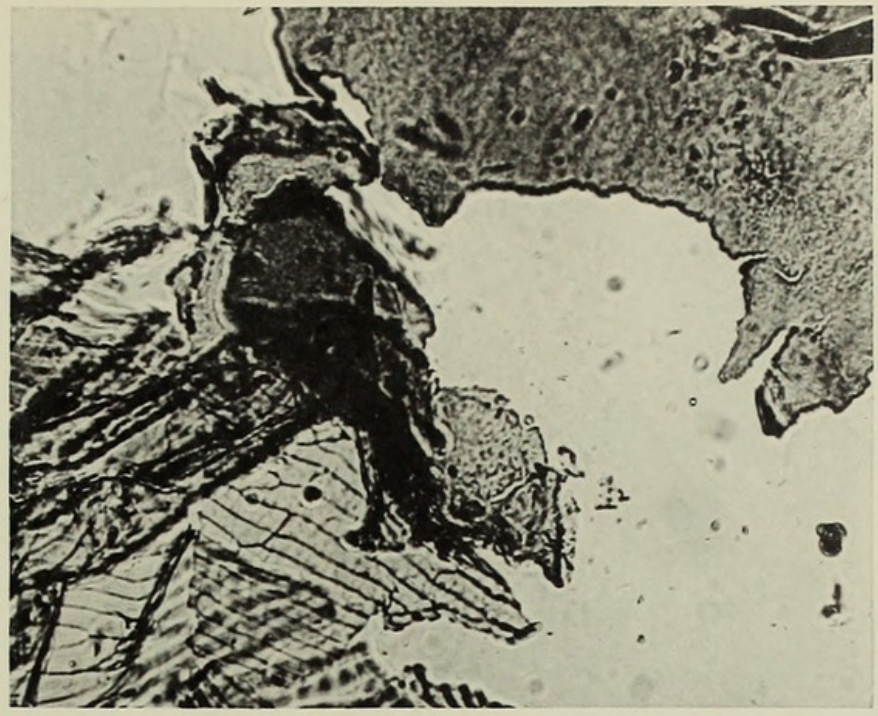

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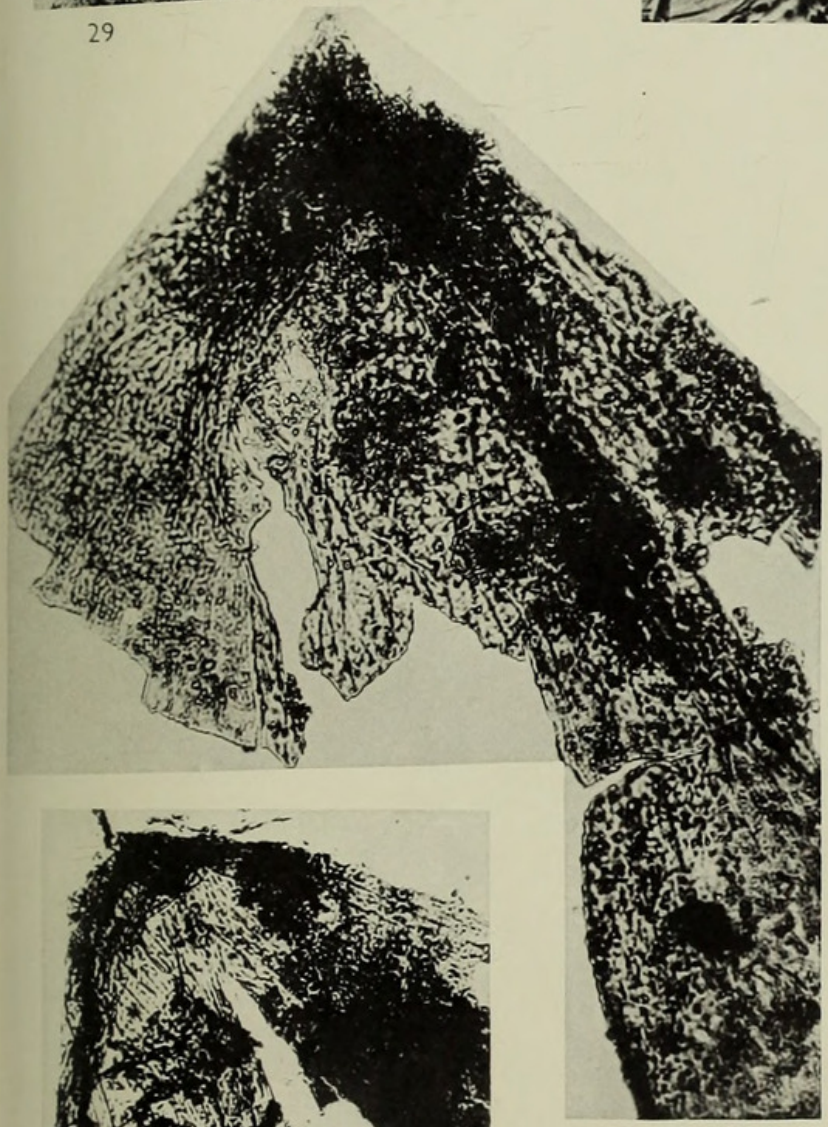

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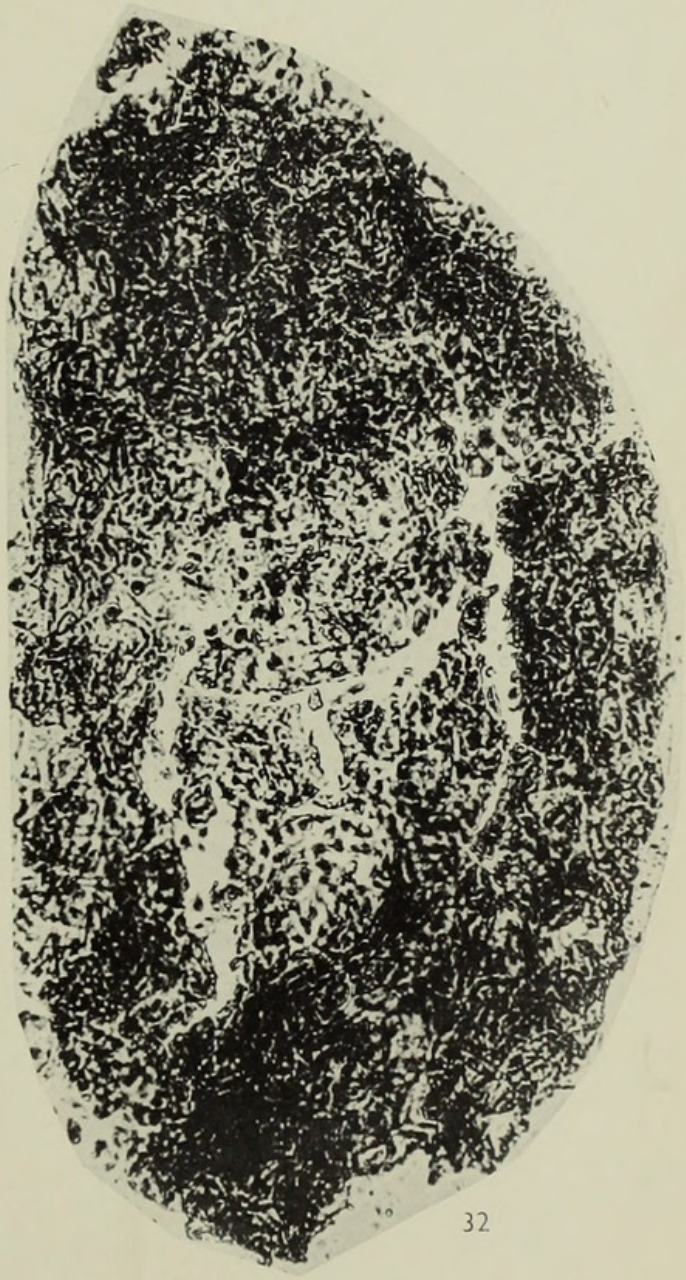

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