

A NEW MESOZOIC FLORA FROM TICÓ,
SANTA CRUZ PROVINCE, ARGENTINA

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A NEW MESOZOIC FLORA FROM TICÓ, SANTA CRUZ PROVINCE, ARGENTINA

By SERGIO ARCHANGELSKY

SYNOPSIS

The present paper is the first contribution to our knowledge of the newly discovered Ticó flora from Santa Cruz Province, Argentina. Six fern-like fronds and a small fruit are referred to five new genera, *Ticoa*, *Rufloflinia*, *Mesodescolea*, *Mesosingeria* and *Ktalenia*. The conifers consist of four new species of *Brachyphyllum* (*B. brettii*, *B. mucronatum*, *B. irregulare* and *B. mirandai*) the last-named species being associated with small male cones probably belonging to the Araucariaceae. The cuticle of *Athrotaxis ungeri* (Halle) is described for the first time and a new genus, *Tomaxellia*, with a single species, *T. degiustoi*, is based on sterile cutinized twigs of uncertain systematic position. The age of the flora is probably Upper Jurassic or Lower Cretaceous.

I. INTRODUCTION

DURING the 1957 Palaeobotanical Expedition to Patagonia, sponsored by the Lillo Institute, Dr. J. M. de Giusto (geologist of the YPF National Oil Company) conducted Mr. R. Herbst and the writer to a recently discovered fossiliferous locality in the centre of Santa Cruz Province, Argentina. The main exposures occur in the Magdalena Estancia in a semicircular cliff (*barranca* in Spanish) and it is here proposed to include all the exposures which belong to a uniform group of sediments, probably of fluvial origin, under the name Ticó Amphitheatre.

Only a few specimens of fossil plants were collected from two fossiliferous beds during this first short visit. The specimens were subsequently found to be very well preserved compressions and a further expedition was undertaken during the summer of 1958 when a more thorough survey was made and at least a dozen new fossiliferous beds were discovered in the Amphitheatre. Towards the north, the same formation was found to constitute the main exposure in an area covering many square miles. To the east it was possible to trace a lateral correlation with the lowermost part of the Baqueró Formation, in the classical area of Punta del Barco and Cerro Cuadrado, composed of white tuffs with good impressions of *Hausmannia*, *Gleichenites*, *Cladophlebis* etc. There is little doubt that a vast sedimentary basin exists in this part of Santa Cruz Province and it is hoped that a thorough study of the fossil flora will help to determine its age. Present incomplete evidence points to its being between Upper Jurassic (and very likely post-Kimmeridgian) and Lower Cretaceous. The complete absence of Angiosperms tells against an Upper Cretaceous age.

The first part of this paper deals with a small group of gymnospermous plants and the second part with Conifers. Dr. C. A. Menéndez (Buenos Aires) is presently studying the Bennettitales from the same flora with a view to publication in the near future.

II. SYSTEMATIC DESCRIPTIONS

Gymnospermae

The species described below may well have been placed in form-genera such as *Sphenopteris* and *Pecopteris*, at least in the comprehensive way in which they were once used. But as much more information than the shape of the pinnules is available in the present material, the fact that they are gymnospermous leaves can be clearly demonstrated and a whole series of new genera is needed for them. Their affinities are most likely to be with the Cycads in the strict sense or with the Pteridosperms.

It is interesting to note that some of the genera described (e.g. *Ticoa*, *Mesodescolea*) possess stomata very similar to those of Recent Cycadales. *Ktalenia circularis* gen. et sp. n., a fructification, is included below because it is closely associated with *Ruflorinia sierra* gen. et sp. n., and was seen only where this plant occurs.

Genus *TICOA* nov.

DIAGNOSIS.—Leaf large, up to tripinnate with robust main rachis. Primary and secondary pinnae laterally attached at angle of 45°. No pinnules between pinnae on primary rachis. Pinnules of pecopteroid type, slightly decurrent, usually concrescent at their base, sometimes overlapping. One vein entering each pinnule, in large pinnules giving off lateral veinlets and in small pinnules forking once at an acute angle.

Cuticle varying in thickness from 2.5 to 8 μ (measured in folds); upper cuticle usually thicker than lower. Stomata few or absent on upper cuticle. All cells elongated on upper cuticle; lower cuticle with elongated cells on margins and on veins, more or less elongated cells between the veins, becoming isodiametric or wedge-shaped around the stomata. Cell walls straight, not interrupted by pits. Cell surface normally flat. Cells on rachises markedly elongated. Trichomes and papillae may be present.

Stomata mainly on lower cuticle with few on the upper; those on lower cuticle avoiding veins and margins; concentration in intermediate areas 9–30 per sq. mm. Guard cells rather large (50 μ long) orientated with longitudinal axis parallel with veins, sunken in a large pit; pit oval or round, formed by subsidiary cells and one or more series of encircling cells. Mouth of pit formed by 8–14 outer encircling cells.

DISCUSSION.—The genus *Ticoa* is based on two species found in different beds of the Ticó Amphitheatre. Both species possess well-preserved cuticles. *T. harrissii* is an important constituent of the floral assemblage in Ticó and is dominant in one bed together with *Ruflorinia sierra*.

If form and venation alone were considered the leaves could have been included in *Pecopteris* (or *Cladophlebis*), but the facts provided by the cuticles warrant more precise taxonomic treatment. The polycyclic stomata with large round pits are more like those of such Cycadales as *Cycas revoluta* or *Dioon edule* than any other living or fossil plants, and *Ticoa* is here classified provisionally as near the Cycadales in the strict sense. It has rather different stomata from certain other living Cycads and the presumed fossil ones such as *Ctenis* and *Pseudoctenis*. It must also be admitted that the distinction between "presumed fossil Cycads" and "presumed Mesozoic Pteridosperms" is vague but *Ticoa* has no close resemblance in stomata to any "presumed Pteridosperm" yet described.

TYPE SPECIES.—*Ticoa harrisii* sp. n.

***Ticoa harrisii* sp. n.**

(Pl. 1, figs. 2, 5 ; Pl. 2, fig. 7 ; Pl. 4, figs. 15, 16, 20 ; Text-figs. 1, 2, 9–13)

DIAGNOSIS.—In part of leaf known, leaf tripinnate, up to 16 cm. wide. Main rachis 8 mm. wide with slight longitudinal striae. Primary pinnae laterally inserted at an angle of 45°, subopposite, separate or slightly overlapping, over 10 cm. long, 2 cm. wide, linear lanceolate ; rachises 2 mm. wide, bearing two distinct flanges on the upper surface near the edges. Secondary pinnae typically 15 mm. long, 5–6 mm. wide, inserted at an angle of 45°, alternate ; the first arises near the main axis on the catadromic side. Secondary pinnae as a whole lanceolate, slightly overlapping adjacent pinnae ; secondary pinnae ending in an acute pinnule. Pinnules up to 3 mm. × 1.6 mm., slightly decurrent, lanceolate with broad base. Those towards distal part of pinnae rather acute. Those towards proximal part of pinnae (near rachis) broader, having alternate, slightly marked lobes. Each pinnule with a single vein ; vein simple or forked once at an acute angle. No small pinnules occurring on the main primary rachises.

Upper cuticle, 3.5 μ, slightly thicker than lower (2.5 μ measured in folds) having almost no stomata but numerous trichomes ; cells elongated, parallel to the margins. Lower cuticle with elongated cells near margins and on veins, somewhat isodiametric or wedge-shaped near stomata and trichomes, slightly elongated on rest of lamina ; cells often placed in groups side by side, showing late division. Surface of cells normally flat but a very few bearing an inconspicuous median papilla. Cuticle of rachises with very long cells and abundant trichomes, smaller than in lamina with few markedly elongated stomata. Small round papillae may be present. Cell walls of both cuticles conspicuous, straight, not interrupted by pits ; cell surface flat, without any visible markings.

Stomata dicyclic, usually avoiding veins and margins, orientated with long axis parallel to veins and margins, 25–30 per sq. mm. Guard cells strongly sunken in round or oval pit, 15–30 μ deep, formed by subsidiary cells and encircling cells. Encircling cells usually 8–10, conspicuous, forming sides of pit typically 40–50 μ wide and mouth of pit typically 30–40 μ wide. Mouth of pit round or irregular, situated at same level as epidermis ; subsidiary cells small and inconspicuous at bottom of pit ; guard cells typically 50 μ long, with small area of cutinised surface



Ticoa harrisii gen. et sp. n.

- FIG. 1. General aspect of the holotype. LIL 2538. $\times 1$.
 FIG. 2. Normal pinna of same. $\times 2.5$.

Ticoa magnipinnulata sp. n.

- FIG. 3. Portion of pinna from holotype. LIL 2540. $\times 1$.
 FIG. 4. Apical part of pinna. LIL 2541. $\times 1$.
 FIGS. 5, 6. Portions of pinnae. LIL 2540. $\times 2.5$.

near aperture and at poles. Trichomes single, sometimes in pairs, 45–55 per sq. mm., consisting of basal granulate cell, 25 μ wide in exposed part, but with inwardly extending cutinised walls enlarging to 35–40 μ wide, surrounded by about 5 ordinary epidermal cells. Free part only known as a short tube of cuticle about 20 μ wide.

HOLOTYPE.—LIL PB n. 2538.

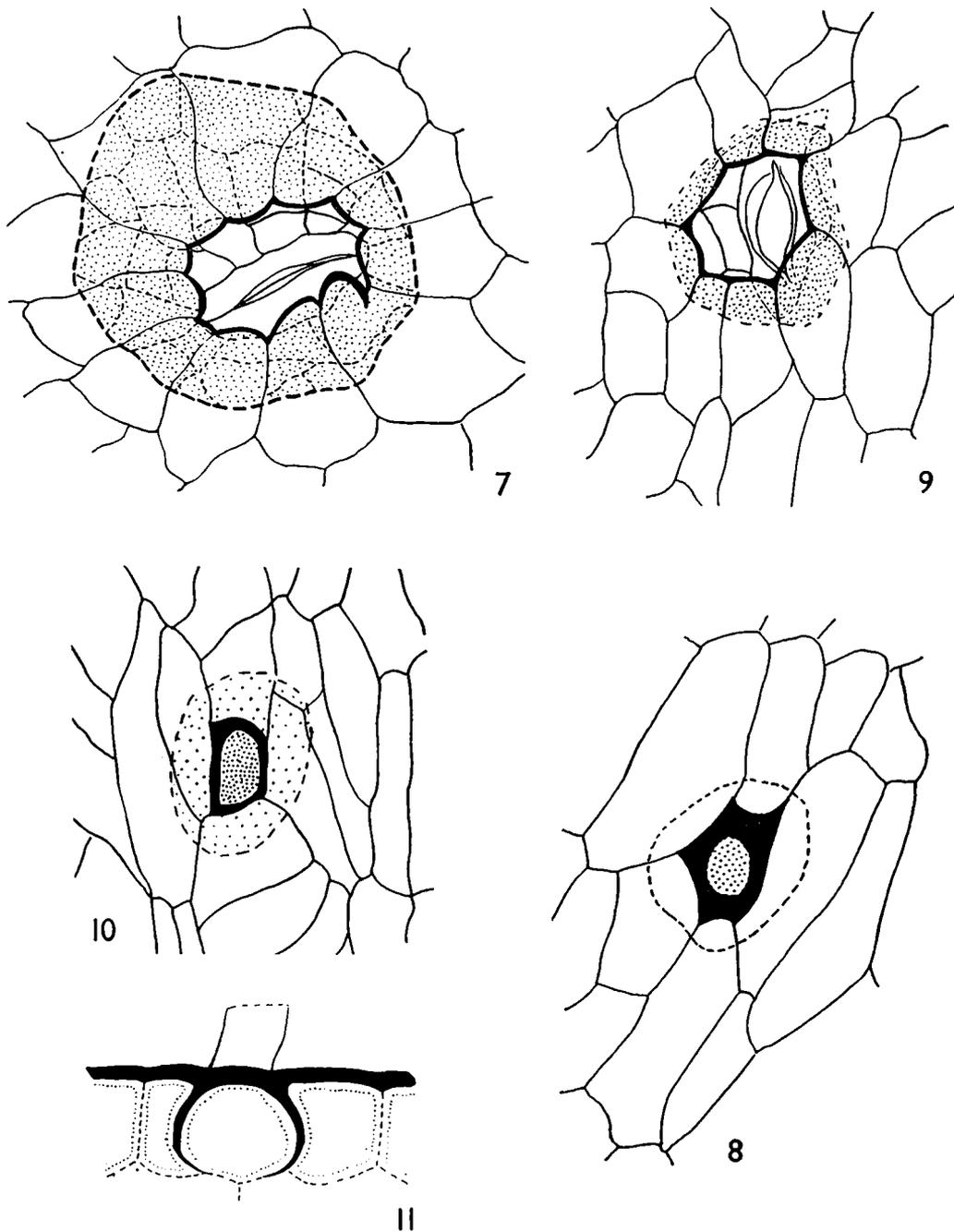
MATERIAL.—In addition to the holotype, LIL PB n. 2539; Brit. Mus. (Nat. Hist.) Palaeontological Dept., no. V. 44660. Slides: LIL 160–164; V. 44659.

DESCRIPTION.—The best available specimen is shown in Text-fig. 1 but there are many other fragments and it is one of the commonest species. Well preserved cuticles alone remain as a pale yellow film, the whole interior substance having almost disappeared. The cuticle of the main rachis has fallen off. The veins of the pinnules can only be seen with certainty on the lower cuticle where elongated epidermal cells and the almost complete absence of stomata are the main diagnostic features. Forking of the veins is rarely seen. The upper cuticle is thicker than the lower and in stained preparations this difference in thickness is clearly seen. The lower cuticle shows that on the margins of the pinnules there is a conspicuous zone, devoid of stomata, with elongated cells attaining more than $100 \times 15 \mu$, in up to 10 definite rows. This tendency for elongation in the epidermal cells is noteworthy, for only in areas around the stomata or trichomes can more or less isodiametric cells, about 20–40 μ in diameter, be found. The cell walls are straight, 1 μ thick, and no sinuosities have been seen. The depth of the stomatal pits mentioned in the diagnosis can be seen in occasional stomata which have been compressed laterally. It is interesting to note that the mouth of the stoma is usually open. The trichome bases are abundant and remains of trichomes have occasionally been observed. The cell lying under the trichome is always cutinised, but not completely (Text-fig. 11). The anticlinal walls of these cells project inwards at least 10 μ , the extent of this projection being clearly seen in obliquely compressed specimens. There is a marked tendency for the bases to unite in pairs or groups of three. Occasionally small papillae may be seen. The two flanges found on the rachises attain up to 0.4 mm. in width on a rachis 2 mm. wide. They are always folded towards the edges.

DISCUSSION.—The stomata of *Ticoa* look remarkably like those of *Cycas revoluta*. However, in *Cycas* the pore formed by the encircling cells is raised, while in *Ticoa* it is on the same level as the rest of the cuticle. The same difference applies to *Dioon edule* which also has a markedly raised pore. In *Cycas revoluta* and *Ticoa harrisii* there is a conspicuous line dividing the guard cell from the subsidiary cells. The depth of this line is slightly less than that of the aperture of the guard cell. In *Cycas* this line is known to be a sharp fold and looks as if it were a hinge assisting stomatal movement. I have made full use of the stomata of *Cycas revoluta* in my reconstruction of that of *Ticoa harrisii*.

Pseudoctenis lanei Thomas, as figured by Harris (1932 : 89, text-fig. 36, I) sometimes has a dicyclic stomatiferous apparatus, being quite similar to *T. harrisii* in this respect. The pit in *P. lanei*, however, is much smaller and the shape of the leaves does not correspond to that of *Ticoa*.

The species is dedicated to Professor T. M. Harris of Reading University.



Ticoa magnipinnulata sp. n.

FIG. 7. Stoma. FIG. 8. Base of trichome. Both from V.44658.

Ticoa harrisii gen. et sp. n.

FIG. 9. Stoma. FIGS. 10, 11. Bases of trichomes. Slide LIL 161.
All $\times 500$.

Ticoa magnipinnulata sp. n.

(Pl. 1, figs. 1, 3, 4; Pl. 2, fig. 6; Pl. 4, figs. 17-19; Text-figs. 3-8, 14-16)

DIAGNOSIS.—(Leaf known from very small fragments only). Pinnae up to 2 cm. wide; rachis 1 mm. wide, flat. Pinnules subopposite, of pectopteroid form; shape oblong, typically 10 mm. long \times 4 mm. wide, margins entire, apex rounded or obtuse, occasionally acute, base broad, lower margin decurrent, angle of insertion 65° ; smaller pinnules relatively shorter, united with their neighbours for about 1 mm. near the base. A midrib arises near lower margin and curves outwards and then remains straight to pinnule apex; lateral veins simple, alternate, first vein on catadromic side arises close to pinna rachis; lateral veins forming angle of 35° with midvein. No small pinnules on primary rachises.

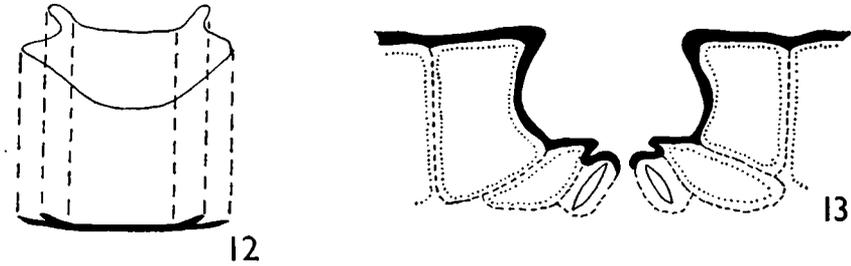
Cuticle of upper side very thick, up to $8\ \mu$, having a darker colour than lower one, bearing numerous trichomes but no stomata. Cells on upper cuticle uniformly elongated, except around trichomes where they are isodiametric. Cells of lower cuticle markedly elongated on margins and on veins, slightly elongated on rest of lamina, more or less isodiametric around stomata; cells sometimes placed in groups side by side, showing late division. Cells on rachis cuticle markedly elongated, having numerous trichomes and few long stomata. Cell walls on both cuticles conspicuous, straight, not interrupted by pits; cell surface flat, without any visible markings.

Stomata confined to lower cuticle, polycyclic, avoiding veins and margins, round or oval with long axis parallel to veins, 9-13 per sq. mm. Guard cells strongly sunken in oval or round pit formed by subsidiary cells, inner encircling cells and one or two series of outer encircling cells. Outermost encircling cells sometimes markedly thickened near mouth of pit, projecting as large inwardly pointing hollow papillae. Mouth of pit typically $50\ \mu$ long \times $30\ \mu$ wide, slightly raised over epidermis, formed by typically 12-14 encircling cells. Subsidiary cells small and inconspicuous at bottom of pit, surrounded by ring of similar encircling cells surrounded by at least one other series of cells, forming the sides of the pit, typically $100\ \mu$ long \times $80\ \mu$ wide, together with outermost encircling cells. Guard cells typically $50\ \mu$ long \times $10\ \mu$ wide. Trichomes single, sometimes in pairs, 20-40 per sq. mm., consisting of a basal granulated cell, $15\ \mu$ wide in exposed parts, but with inwardly extending cutinised walls enlarging to a width of $40\ \mu$, surrounded by 5-6 epidermal cells. Sometimes groups of cells on lower cuticle forming oval structures up to $100\ \mu$ long \times $60\ \mu$ wide, slightly sunken in a pit.

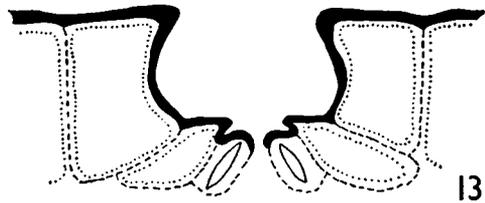
HOLOTYPE.—LIL PB 2540.

MATERIAL.—In addition to the holotype, LIL PB 2541; Brit. Mus. (Nat. Hist.) no. V.44657. Slides: LIL 165-169; V.44658.

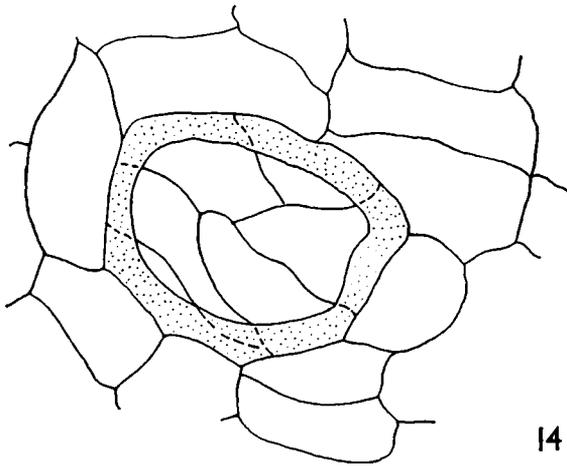
DESCRIPTION.—The few specimens referred to this species were found in a different bed from that in which *Ticoa harrisii* occurs. The cuticles are equally well preserved and similar in colour to those of *T. harrisii*. In the few pinnules preserved the veinlets can be clearly seen in translucent preparations but only very obscurely on the rock. They have a typical monopodial arrangement. The specimens of *T. magnipinnulata* agree in their form and cuticle, but one specimen is distinguished



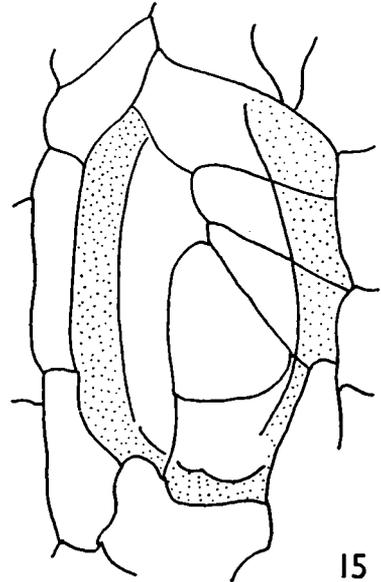
12



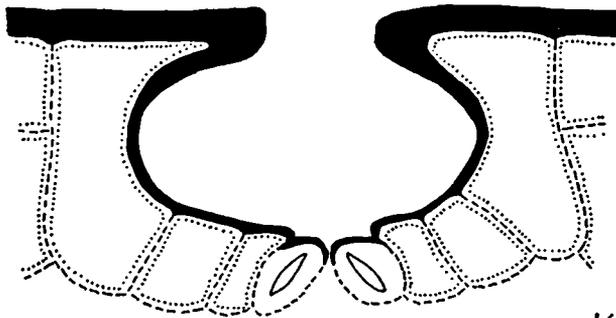
13



14



15



16

Ticoa harrisii gen. et sp. n.

FIG. 12. Compression of the two rachis flanges. $\times 10$.

FIG. 13. Section of stoma. $\times 500$.

Ticoa magnipinnulata sp. n.

FIGS. 14, 15. Oval structures on lower cuticle, slightly sunken in a pit.

V.44658. $\times 500$.

FIG. 16. Section of stoma. $\times 500$.

from the others by its more acute pinnules and rather fewer stomata and trichomes. They all agree in having no stomata on the upper side and that even the smallest stomata are polycyclic. Certain laterally compressed stomata show the guard cells to be sunken 40μ below the general surface level. The trichomes are remarkably small, compared with the size of the stomata, and quite often the inward extension of the cutinised basal cell does not widen very much. Very few groups of two trichomes were seen, most trichomes occurring singly. In one specimen the lower cuticle shows groups of cells of variable size and shape, usually the same size as stomata and forming an oval structure sunken in a pit and sometimes even having a rim of cutin around the large mouth of the pit. The function of these structures is unknown (Text-figs. 14, 15).

DISCUSSION.—*Ticoa magnipinnulata* looks very like *T. harrisii* and the cuticles of both species are also similar, but there are some real differences which are set out below.

	<i>Ticoa harrisii</i>	<i>Ticoa magnipinnulata</i>
Flanges on upper side of rachis	Present	Absent
Pinnules	Lanceolate with broad base. Larger ones concrescent. 3 mm. long \times 1.5 mm. wide.	Oblong with broad base. Larger ones separated. 10 mm. long \times 4 mm. wide.
Cuticles .	Up to 9.5μ thick. Upper with a few stoma. Stomata dicyclic. 25–30 stomata per sq. mm. Mouth of pit 30–40 μ . Same level with epidermis. Encircling cells 8–10. Sides of pit 40–50 μ . Trichomes 45–55 per sq. mm. Basal cell 25 μ (nearly as large as stoma).	Up to 8 μ thick. Upper non-stomatiferous. Stomata polycyclic. 10–13 stomata per sq. mm. Mouth of pit 50–30 μ . Slightly raised. (Outer) encircling cells 12–14. Sides of pit 100–80 μ . Trichomes 30–40 per sq. mm. Basal cell 15 μ (much smaller than in stoma).

Genus *RUFHORINIA* nov.

DIAGNOSIS.—As for the only species, *Rufhorinia sierra* sp. n.

Rufhorinia sierra gen. et sp. n.

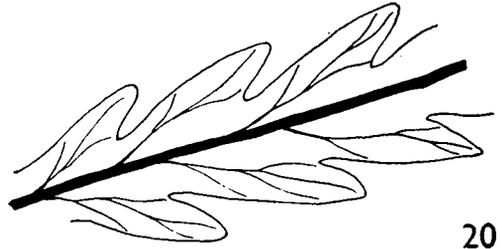
(Pl. 2, figs. 8, 9 ; Pl. 5, fig. 21 ; Text-figs. 17–20, 24)

DIAGNOSIS.—(For purposes of description leaf assumed to be tripinnate).

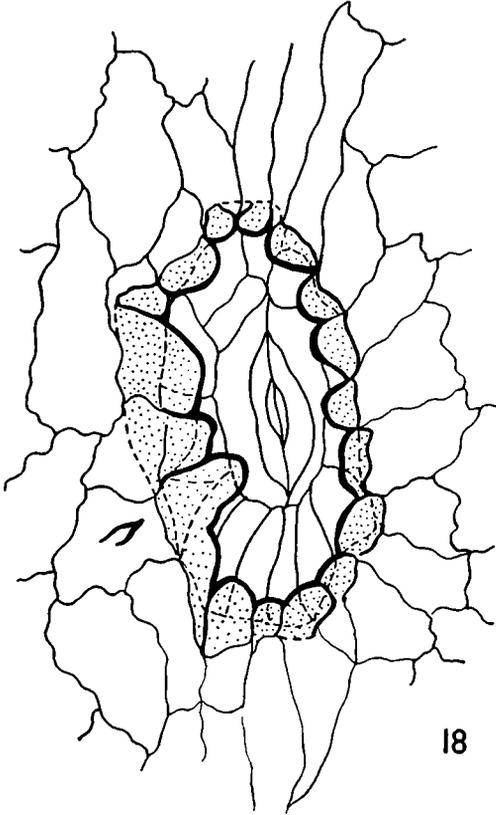
Primary pinna at least 8 cm. long, 4 cm. broad. Rachis of primary pinna 2 mm. wide with median groove on upper side with flanges of decurrent, lamina 0.3 mm. wide. Secondary pinnae alternate to subopposite, decurrent, insertion angle 45° , linear, with acute apex, up to 45 mm. long \times 4–5 mm. wide ; lamina of one pinna separated from next by narrow gap ; pinna rachis with slight median longitudinal



17



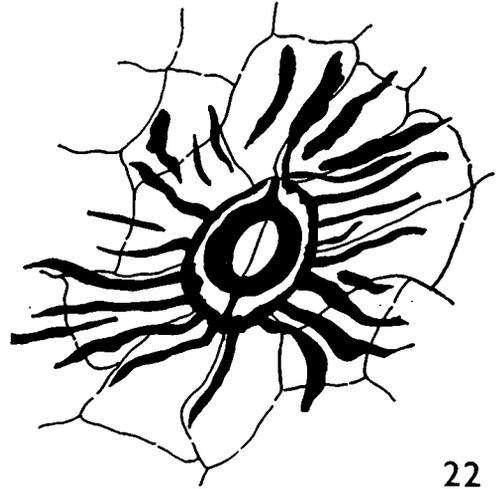
20



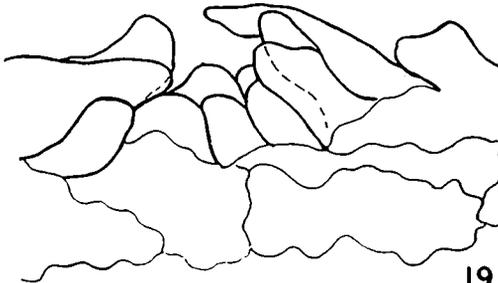
18



21



22



19



23

Ruflorinia sierra gen. et sp. n.

FIG. 17. Section of stoma. $\times 450$.

FIG. 18. Stoma. Slide LIL 170. $\times 450$.

FIG. 19. Lateral view of compressed stoma, showing papilla-like projections of the subsidiary cells. Slide LIL 171. $\times 500$.

FIG. 20. Details of pinna, showing venation. LIL 2565. $\times 5$.

Mesodescotea plicata gen. et sp. n.

FIG. 21. Section of stoma. $\times 500$.

FIGS. 22, 23. Stomata showing cuticular ridges. Slide LIL 177. $\times 500$.

groove and laminate margin. Pinnules concrescent at their base or up to half their length, with lanceolate acute apex, inserted at an angle of about 25° , measuring up to 4 mm. long \times 1.5 mm. wide. A single vein enters the pinnules, forking once near base at acute angle, and again, sometimes twice, near middle of lamina. No small pinnules on primary rachises.

Upper and lower cuticle same thickness, 1–2 μ ; upper cuticle devoid of stomata. Cell walls sinuous on both cuticles, sharply marked, not interrupted by pits, cells on margins and veins elongated, near stomata somewhat isodiametric. On rachises and main veins, cells very long, narrow, rectangular, having less sinuosities. Cell surface normally flat; cells with occasional hollow papillae only found around stomal region.

Stomata dicyclic or polycyclic, avoiding veins and margins, disposed in marked longitudinal rows, usually occurring in small groups, with long axis orientated in long axis of pinnules; about 10 stomata per sq. mm. Guard cells on same level as epidermis or slightly sunken in round or oval pit formed by numerous subsidiary and encircling cells. Subsidiary cells rather small, forming bottom of pit; polar subsidiary cells often elongated and narrow. Inner encircling cells (if present) small, forming sides of pit typically 75 μ in diameter when round. Outer encircling cells, typically 14–18 in number, forming sides and top of round or oval pit, often extending onto epidermal surface; cuticle becoming thickened in part near stoma and raised to form large hollow papilla; papillae often completely united to sides of adjacent papilla so that whole set of papillae form a raised rim overhanging stomatal pit; opening between papillae often narrow. Polar encircling cells often long and narrow. Guard cells typically 50 μ long, with oval thickened area round mouth of stoma, up to 40 μ long \times 5 μ broad.

HOLOTYPE.—LIL PB 2542 (a).

MATERIAL.—In addition to the holotype, LIL PB 2544, 2545, 2549, 2550(a), 2551, 2552, 2554–56, 2565(b), 2567(b), 2570(b), 2575(b); Brit. Mus. (Nat. Hist.) nos. V.44676–77, V.44686, V.44681–82. Slides: LIL 170–172; V.44678–80.

DESCRIPTION.—*Ruflorinia sierra* is found in close association with *Ticoa harrisii*. It is, however, easily distinguishable from this species by the different shape of the pinnules and thinner cuticle. The cuticle is brownish yellow and when detached leaves a brown impression on the matrix. The details of such impressions are usually better preserved than those of *T. harrisii*. Being much thinner, the cuticle is not as well preserved as that of *T. harrisii*, but reasonably good preparations can be made without much difficulty. The leaf was probably tripinnate but the present material studied does not provide conclusive evidence that this was so.

The concrescence of the pinnules is noteworthy and in distal parts of the pinnae only their apices are separated; the shape then suggests that of a saw (*sierra* in Spanish). The veins often bifurcate three times and the ultimate veinlets can reach the apex or lateral margins of the pinnules. The absence of stomata on the upper cuticle and on the rachises is consistent. On the lower cuticle the stomata are usually present in quite definite rows, tending to form groups or patches composed of up to 5–6 stomata together. Large areas of the lamina are devoid of stomata and so it is not easy to establish with accuracy their number per sq. mm. which in any case is

extremely low. The stomata vary greatly in size from moderate to extremely large, and the mouth of the pit is closed in some but wide open in others. There are a

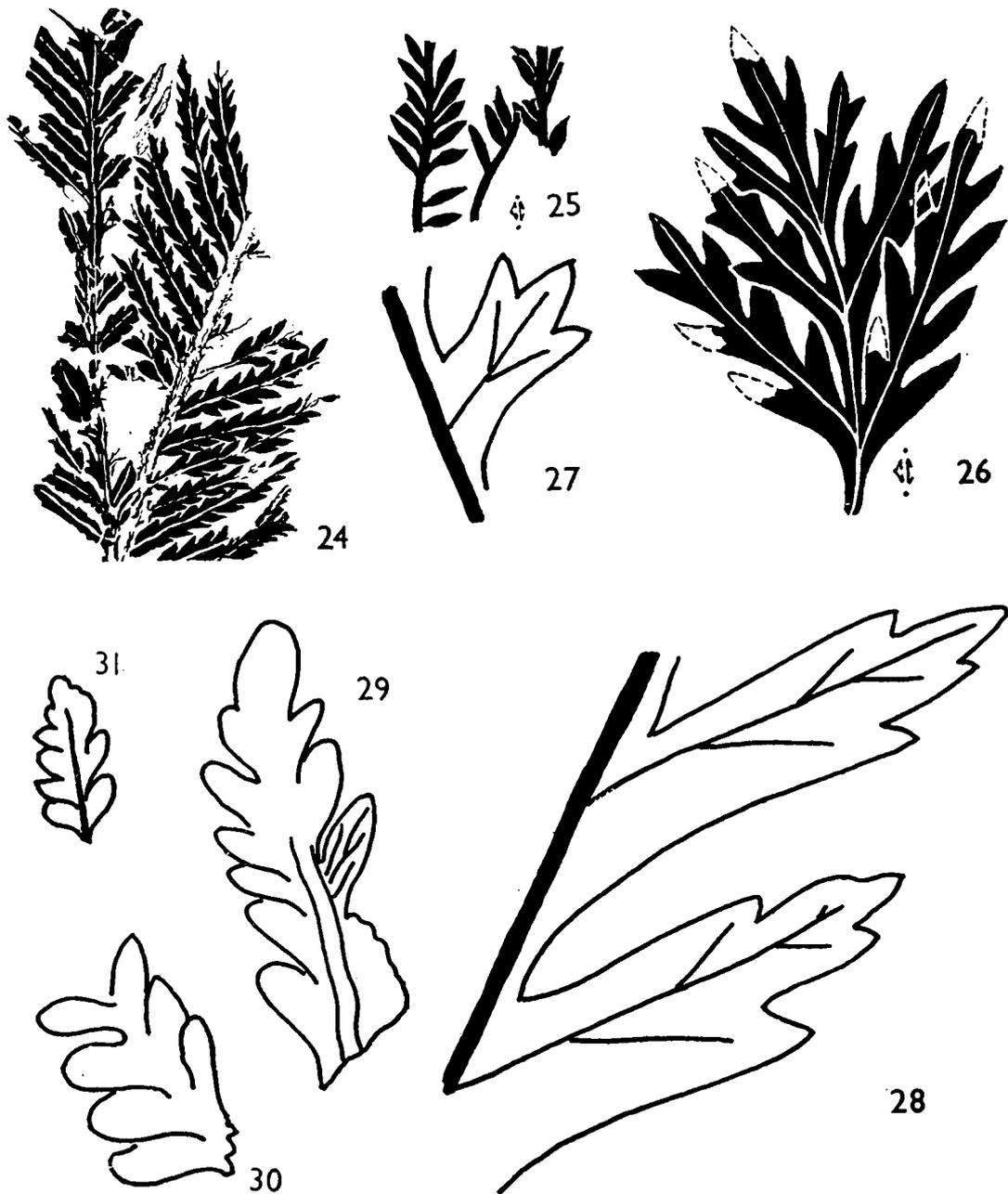


FIG. 24. *Ruflorinia sierra* gen. et sp. n. General aspect of the holotype. LIL 2542. $\times 1$.

FIG. 25. *Mesosingeria herbstii* sp. n. Holotype. LIL 2546. $\times 1$.

FIGS. 26-28. *Mesodescolea plicata* gen. et sp. n. 26, Holotype. LIL 2548. $\times 1$. 27, 28, Non-differentiated pinnae. $\times 2.5$.

FIGS. 29-31. *Mesosingeria coriacea* gen. et sp. n. 29, 30, Fragments of the holotype. LIL 2547. $\times 1$. 31, Another fragmentary pinna. LIL 2558. $\times 1$.

few stomata in which the whole apparatus is 110μ long, which is rather exceptional in plants of any family. The walls of the subsidiary and encircling cells form a complex network around the guard cells. A very constant feature is the tendency for the polar subsidiary and encircling cells to be elongated in the longitudinal axis of the pinnules. There may be one, or sometimes two, subsidiary cells approximately opposite each pole of the guard cell, but a single polar encircling cell is found opposite the pair if there are two. This indicates a late radially orientated division in the polar subsidiary cell.

DISCUSSION.—*Ruflofloria* has remarkable characters which clearly distinguish it even from genera of rather similar habit. *Ticoa* is the most similar genus in being repeatedly pinnate and having polycyclic stomata. *Ruflofloria*, however, differs in its sinuous cell walls, the grouping of stomata in patches and in the papillae of the outer encircling cells which project over the mouth of the pit.

The genus is dedicated to Professor Rudolf Florin, Stockholm, Sweden.

Genus *MESODESCOLEA* nov.

DIAGNOSIS.—As for the only species, *Mesodescolea plicata* sp. n.

Mesodescolea plicata gen. et sp. n.

(Pl. 3, figs. 12–14, Pl. 5, figs. 24, 25 ; Text-figs. 21–23, 26–28)

DIAGNOSIS.—Leaf bipinnate, oblong, typically 6 cm. long \times 4 cm. wide. Leaf rachis less than 1 mm. wide with deep longitudinal midfurrow. Pinnae opposite, decurrent, arising at 30° to rachis, lanceolate, with rather narrow base, up to 4–5 cm. long \times 1.5 cm. wide near middle and ending with single acute pinnule. Pinna rachis with pronounced midfurrow. Pinnules subopposite to alternate, arising at 30° to pinna rachis ; pinnules with broad base and acute apex, up to 15 mm. long \times 3 mm. wide, margins entire ; lower margin markedly decurrent and connecting with upper margin of pinnule below. An unbranched midrib enters pinnules and extends to near apex.

Upper cuticle without stomata. Cells polygonal, square or rectangular, up to 40μ long \times 30μ wide. Anticlinal walls usually pitted, up to 3μ thick. Cell surface usually with ridges having no definite orientation. Cuticle of lower surface having stomata except on veins. Cells on veins elongated, with conspicuous longitudinal ridges. Cells on lamina of irregular shape, usually with rounded contours ; anticlinal walls about 2μ thick, pitted. Cell surface with irregular ridges. Specialised small cells (trichome bases) present, surrounded by conspicuous series of radiating ridges which cross up to several rows of surrounding cells. Ridges at right angles or parallel to long axis of stomata, also conspicuous.

Stomata on lower cuticle typically monocyclic, oval or nearly round, with no definite orientation, typically 23–35 μ long, 45–60 per sq. mm. Guard cells little or not at all sunken. Subsidiary cells not specialised, from 5–8, usually bearing

ridges which can be normal or parallel to long axis of stoma. Guard cells with a conspicuous and constant rim surrounding mouth, sometimes interrupted at poles. Contact of guard cells and subsidiary cells generally covered by strong ridge reproducing roughly the outlines of guard cells.

HOLOTYPE.—LIL PB n. 2548.

MATERIAL.—In addition to the holotype, LIL PB 2550(b); Brit. Mus. (Nat. Hist.) no. V.44682-83. Slides: LIL 177-180; V.44684-85.

DESCRIPTION.—This species is associated with *Ticoa harrisii* and *Ruflorenia sierra*. It is generally found in fragments which leave only a faint impression on the rock, but the rachis impression is distinct and marked with strong furrows. The cuticle although well preserved is difficult to prepare in large pieces. The lower cuticle is yellowish while the upper is darker and brownish in colour.

On the same block containing the holotype, near the base of the leaf, a cutinised rachis is preserved and although there is no definite evidence of actual connection it may well belong to *Mesodescolea*. The rachis is 5 mm. wide, having a thick cuticle with elongated cells; the cell walls are pitted and 4 μ thick. The cell surface is covered with conspicuous longitudinal ridges.

The difference in the shape of the cells on the upper and lower cuticles is evident, as is the lack of stomata or trichomes on the upper cuticle. However, both cuticles bear conspicuous ridges which are a constant feature of the species.

The guard cells of the stomata always have the rim of thickened cutin surrounding the mouth. Usually, a ridge is present on the edge of the guard cell, and sometimes there is another longitudinal ridge in between the two thickened zones. No trichomes or hairs have been seen, but the specialized small cells with concentric radiating ridges, occupying large areas of the lamina are presumably the bases of trichomes.

Certain leaf fragments were also found that might well be small undifferentiated pinnae or rather large pinnules with three apical horns.

DISCUSSION.—*Mesodescolea plicata* is a remarkable fossil. The leaf somewhat resembles certain species of *Pachypteris* in shape, for instance *P. dalmatica* Kern (see Carpentier, 1927, pl. 12, figs. 13, 14). Certain Angiosperms too have leaves of similar outline, although quite a different type of venation. The cuticle has some features in common with the living Cycad *Stangeria*, in particular, the surface striation or ridges, but these are stronger in *Mesodescolea* (cf. Thomas & Bancroft, 1913, pl. 17, fig. 2). The stomata in both plants are unspecialized, the guard cells being on the same level with the epidermis or a little sunken. The thickenings round the aperture of the guard cells as well as the polar and lateral ridges on the margins of the guard cells are comparable; in *Mesodescolea* these ridges are generally fused to form a continuous rim of cutin and are also stronger than in *Stangeria*. The cells of the lower and upper cuticles of *Stangeria* have sinuous walls and no pits. The cells on the veins of both plants are also comparable; they are elongated and have strong longitudinal ridges. In spite of all these similarities, however, there is considerable difference in branching and venation, and while one may provisionally classify *Mesodescolea* in or near the Cycadales it can only be with reservation. This is equally true of the relation between *Ticoa* and *Cycas* or *Dioon*.

There are certain similarities with *Ctenis minuta* Florin (1933, text-fig. 22, c; pl. II, fig. 5) in the cuticular ridges and the radiating striae from trichome bases. *C. kaneharai* Yokoyama, however, bears the greatest resemblance to *Mesodescolea* as far as the cuticular structure is concerned. This species was first described from the Upper Cretaceous of Japan, but neither Yokoyama nor Oishi gave any description of the cuticle. Harris (1950) described some specimens from the Jurassic of Yorkshire with cuticles preserved and I was able to compare the Yorkshire cuticles with that of *Mesodescolea*. The Yorkshire cuticle is intensely marked with ridges as in the Ticó specimens (more than in *Stangeria*), there are similar trichome bases and the stomata are present only on the lower cuticle. In *C. kaneharai*, however, the stomatal apparatus is more protected and somewhat sunken in an oval pit. The guard cells have no thickenings and the stomata of *Mesodescolea*, in this respect, are closer to those of *Stangeria*.

As in the case of *Ticoa*, one can assume that *Mesodescolea* also is a Gymnospermous plant, having certain features in common with the living *Stangeria paradoxa* on the one hand, and with some fossil *Ctenis* species on the other. *Mesodescolea* probably belongs to a stock of plants with cycadean affinities, which existed in Patagonia during Upper Mesozoic times, before the appearance of a true angiospermous flora.

The genus *Mesodescolea* is dedicated to Dr. Horacio Descole, Tucumán, Argentina.

Genus *MESOSINGERIA* nov.

DIAGNOSIS.—Leaf bipinnate. Pinnæ ovate or lanceolate ending with a single pinnule. Pinna rachis flat. Pinnules oblong to lanceolate, margins entire, angle of insertion 45° – 50° , alternate; base narrower than middle of lamina and lower margin slightly decurrent. One or more veins enter pinnule, each forking once or twice at acute angle, all branches going straight up to near apex.

Cuticle thick. Stomata present on both cuticles, more frequent on lower. Epidermal cells on both cuticles typically isodiametric, slightly elongated on margins. Cells on rachises rectangular or square. Veins not distinguishable on either cuticle. Cell walls strongly marked, straight, with visible middle lamella and border. Cell surface flat, finely granular.

Stomata monocyclic, often with longitudinal orientation. Guard cells strongly sunken in round or oval pit formed by typically 5–8 unspecialised subsidiary cells. Mouth of pit raised over surface of epidermis, constricted by more or less continuous rim of cutin. Trichome bases present.

TYPE SPECIES.—*Mesosingeria coriacea* sp. n.

DISCUSSION.—This genus is based on two species, rather incompletely preserved, but sufficiently well to make a clear generic separation from other fossil leaves known at present.

Mesosingeria differs from the fern-like leaves described above as *Ticoa*, *Ruflofloria*, and *Mesodescolea*. In the general shape of the leaves and in the thick cuticle, *Mesosingeria* can be compared with *Pachypteris* and *Pachydermophyllum*, the cuticles of which are rather similar, having more or less isodiametric epidermal cells, thick walls and sunken guard cells. But in *Mesosingeria* the subsidiary cells

do not project over the mouth of the pit like papillae (Thomas & Bose, 1955, text-fig. 3, E). Instead there is a more or less continuous round rim of cutin raised over the general surface of the lamina. This peculiar feature is also found in species of *Ctenozamites* (cf. *Ctenopteris*) such as *C. leckenbyi* or *C. cycadea* (Harris, 1961, text-fig. 2, B). However, there are other features which do not agree with *Mesosingeria*. In *Ctenozamites* the veins are distinct on both lower and upper cuticles and the stomata are usually confined to the lower side; also, the epidermal cells are not as isodiametric as in *Mesosingeria*. In *Pachypteris* and *Ctenozamites* there are pinnules on the main rachis, between the pinnae, while they are absent in *Mesosingeria*.

It seems probable that *Mesosingeria* is related to *Pachydermophyllum-Pachypteris* and belongs to the Mesozoic Gymnosperms, probably Pteridosperms (*sensu lato*).

Another similar plant is Saporta's *Scleropteris* (1873: 364). I have examined specimens in the Paris Museum but could not find any evidence of cuticle and the question of any relationship between *Mesosingeria* and *Scleropteris* must therefore remain unanswered.

The genus is dedicated to Professor Rolf Singer, Buenos Aires, Argentina.

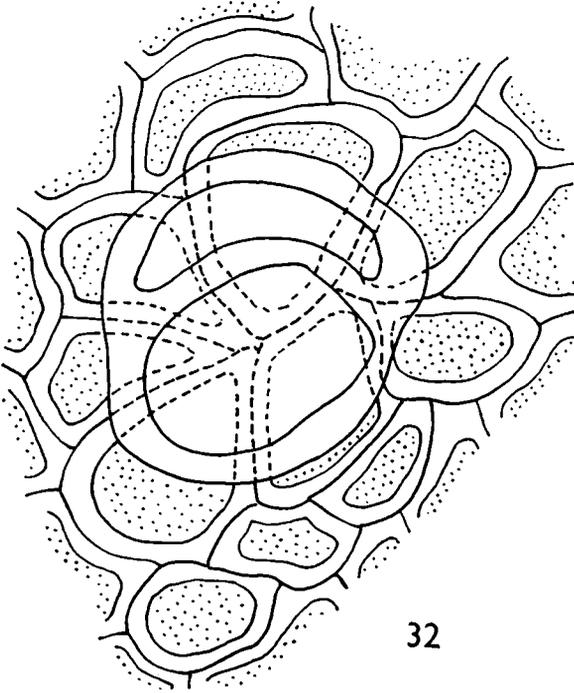
Mesosingeria coriacea gen. et sp. n.

(Pl. 3, fig. 10; Pl. 5, figs. 22, 23; Text-figs. 29-33, 37, 38)

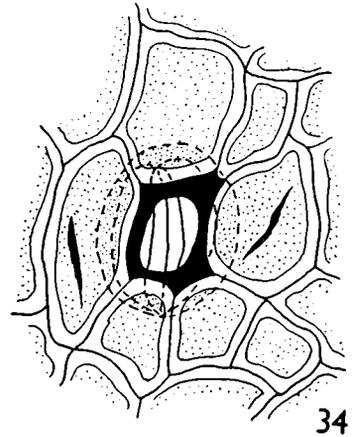
DIAGNOSIS.—(For purposes of description, leaf assumed to be bipinnate). Pinnae up to 4 cm. long \times 1.5 cm. wide, ending with single obtuse pinnule; pinna rachis flat, up to 2.5 mm. wide. Pinnae apparently overlapping. Pinnules oblong with rounded apex, touching each other, inserted at an angle of 45° to pinna rachis, alternate, typically 1 cm. long \times 0.4 cm. wide with margin entire; base narrower than middle of lamina; upper margin contracted and lower margin slightly decurrent. One or more veins enter the pinnule, each forking once or twice at very acute angle, all branches going straight up to near apex; all veins of same thickness. Margins quite flat.

Cuticles on both sides thick, up to 7 μ . Stomata present on both cuticles but more abundant on lower. Cells on both cuticles isodiametric or slightly elongated, typically 40 μ in diameter; cells on margins rather elongated; cells on rachis rectangular or square. Veins not distinguishable on either cuticle. Cell walls very strongly marked, consisting of a cutinised middle lamella (anticlinal walls) extending up to 50 μ inwards. At surface, middle lamella accompanied by strongly marked border about 8 μ wide. Surface of cell (periclinal walls) flat, finely granular.

Stomata typically 60-70 per sq. mm. on lower cuticle, and less than 5 per sq. mm. on upper. Stomata monocyclic, nearly all with longitudinal orientation on lower side, but varied on the upper. Guard cells sunken strongly in a pit; pit up to 60 μ in diameter with thickly cutinised walls, often constricted by typically 5-7 un-specialised subsidiary cells. Mouth of pit rounded or elongated, up to 50 μ wide, raised over surface of lamina. Mouth of pit further constricted by very delicate, more or less continuous projection of cutin, pierced by a round hole. Hole with distinct border. Guard cells moderately cutinised, typically 90 μ long \times 30 μ wide. Hypo-



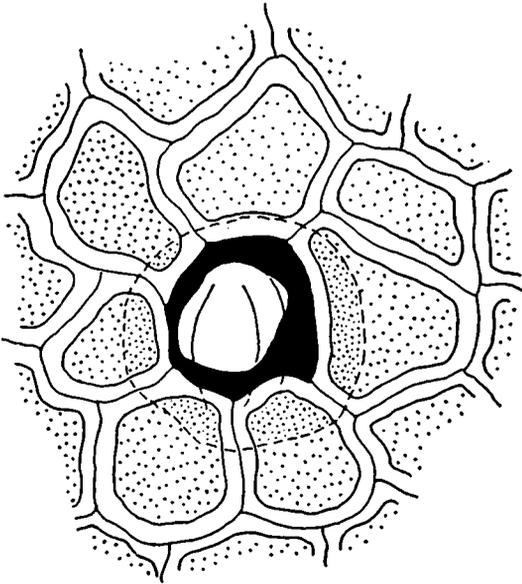
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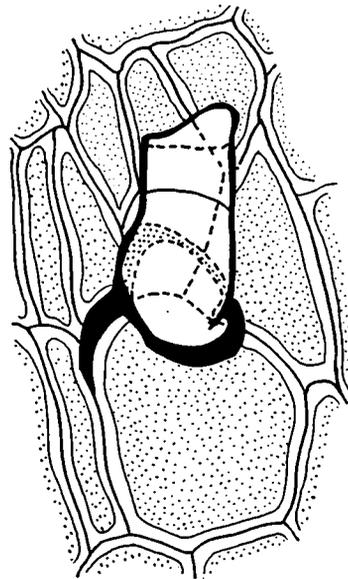
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36

Mesosingeria coriacea gen. et sp. n.

FIG. 32. Base of hair. Slide LIL 173.

FIG. 33. Stoma with rim of cutin round the mouth of the pit. Slide LIL 173.

Mesosingeria herbstii sp. n.

FIG. 34. Stoma without projecting rim of cutin. Slide LIL 175.

FIG. 35. Section of stoma.

FIG. 36. Bicellular hair. Slide LIL 175. All $\times 500$.

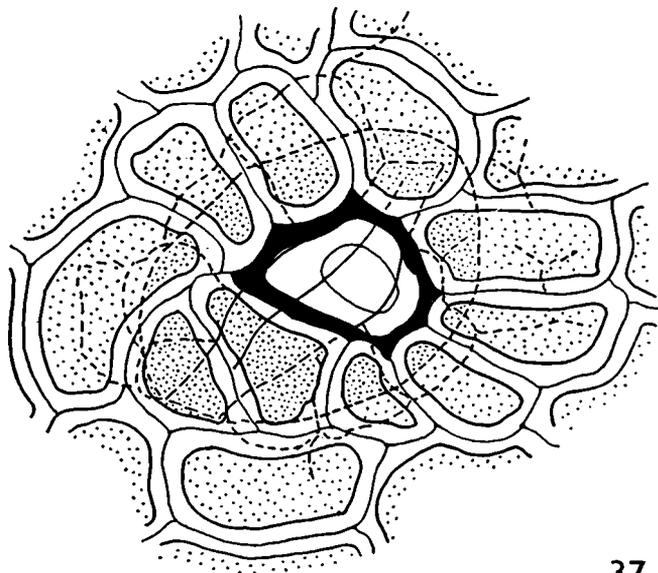
dermal cells often cutinised, in contact with guard cells of stomata, smaller than epidermal cells.

Trichome bases present in small numbers on both sides, consisting of a round cell about 50–60 μ in diameter on top of normal epidermal cells; trichome bases sometimes consisting of two cells sharing a thin area. Free part of trichome missing.

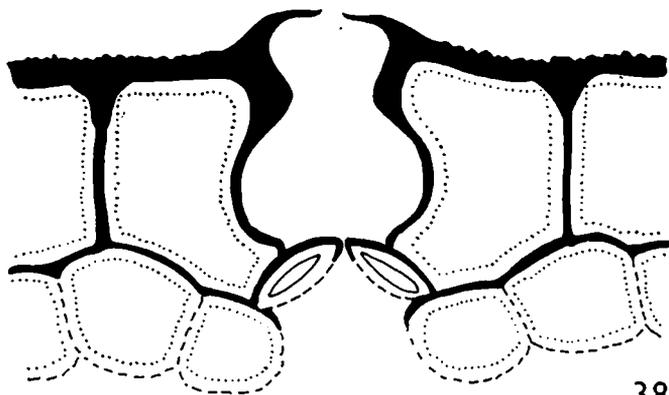
HOLOTYPE.—LIL PB n. 2547.

MATERIAL.—In addition to the holotype, LIL PB 2558. Slides: LIL 173, 174; Brit. Mus. (Nat. Hist.) nos. V. 44665–66.

DESCRIPTION.—This species is found in the same bed with *Ticoa magnipinnulata* and *Mesosingeria herbstii*. The dark-brown cuticles are very well preserved. The largest specimens required much longer maceration than the rest of the material



37



38

Mesosingeria coriacea gen. et sp. n.

FIG. 37. Stoma showing sunken guard cells. Slide LIL 173. $\times 500$.

FIG. 38. Section of stoma showing projecting rim of cutin over the mouth of the pit and cutinized hypodermal cells. $\times 500$.

hitherto studied. The impressions show generally clear contours with marked veins. Although the holotype is fragmentary, several pinnae having a parallel course appear to originate from a common rachis. It is for this reason that the leaf is assumed to be at least bipinnate.

With a hand lens the cell contours and the anticlinal cutinised walls are clearly seen. The smaller specimens have a thinner cuticle which needs less maceration, although it is dark brown in colour. The shape of the pinnules and the angle of insertion is the same as in the larger specimens but the pinnules of the smaller ones tend to be more united at the base. Numerous misshapen or crushed cells with dark contents can be seen. They are perhaps pathological.

DISCUSSION.—This species resembles *Pachydermophyllum papillosum* more than the other species described below. Comparison between two specimens, one of *P. papillosum* and the other of *M. coriacea* shows a resemblance in the shape of the pinnules and in the thickness of the cuticle. *Pachydermophyllum*, however, has a single midvein in each pinna (as does *Pachypteris* in each pinnule, except for the terminal lobe where there are a few main veins, representing suppressed pinnules).

Mesosingeria herbstii sp. n.

(Pl. 3, fig. 11; Pl. 5, figs. 26, 27; Pl. 6, fig. 36; Text-figs. 25, 34–36)

DIAGNOSIS. (Leaf only known from fragments). Pinnae up to 1 cm. wide; rachis flat, 1.5 mm. wide, with fine striae. Pinnules lanceolate, separated, alternate, typically 7 mm. long \times 1.5 mm. wide; margins entire with definite flange; apex acute, base narrower than middle of lamina; lower margins slightly decurrent, angle of insertion about 40°.

Upper cuticle, 4 μ , thicker than lower cuticle. Stomata present on both cuticles, more abundant on lower one. Cells on both cuticles isodiametric, typically 20–25 μ in diameter, slightly elongated on margins. Veins not distinguishable on either cuticle. Cells on rachis elongated rectangular, having several hairs and papillae. Cell walls straight, strongly marked, projecting slightly outwards and more strongly inwards, inward part occasionally interrupted by pits. Cell surface normally flat, very finely granular, showing several obscure striae. Occasional cells bearing hollow papilla; some cells, especially near margins, bearing hairs of 1–2 cells, strongly cutinised for whole length, 60 μ long \times 20 μ wide. Cells on smargin and apex strongly cutinised and often projecting as small tooth. Stomata on upper cuticle about 40 per sq. mm., on lower cuticle about 110 per sq. mm., often with longitudinal orientation, not forming rows. Stomata typically monocyclic with guard cells sunken in round pit, typically 30 μ wide, formed by 6–8 unspecialised subsidiary cells. Mouth of pit rounded or oval, 8–10 μ wide, constricted by continuous rim of cuticle extending from inner edges of subsidiary cells. Guard cells feebly cutinised, about 30 μ long \times 15 μ wide.

HOLOTYPE.—LIL PB n. 2546.

MATERIAL.—In addition to the holotype, slides LIL 175, 176; Brit. Mus. (Nat. Hist.) no. V.44664.

DESCRIPTION.—The specimens described here were found in the same bed as *Ticoa magnipinnulata*. The cuticles are well preserved and light yellow in colour. The impressions, although showing clear contours, do not show any trace of veins. In one instance, however, a trace of the midvein appears to be present. The apical parts of the pinnules have conspicuous longitudinal wrinkles or folds in their cutinised surface which suggest veins, but there is no other evidence to confirm that the veins run in this direction. The flanges on the margins are clearly seen and are probably due to the abundant papillae and hairs. The insertion of the pinnules is not exactly lateral, one row seems to overlap slightly onto the rachis.

The lower cuticle is thinner, 2.5μ , and stains strongly with safranine. The guard cells can be seen only in stomata in which the round rim of strongly cutinised matter is either missing or has fallen off. The guard cells are feebly cutinised and their contours cannot always be made out. The pit is usually a little expanded, but in some cases the lateral walls of the subsidiary cells descend almost vertically.

DISCUSSION.—This species differs from *M. coriacea* in the shape of its smaller pinnules which are more lanceolate and in the colour and thickness of cuticle. The size and shape of the pinnules of the two species can be compared in Text-figs. 25, 29–31. The frequency of stomata on both upper and lower cuticles is higher in *M. herbstii*. All the epidermal features such as cells, stomata and hair bases are also smaller in this species. The numerous hairs present in the marginal regions also constitute a conspicuous character, whereas they are absent in *M. coriacea*, which has no marginal concentration of hairs but only a few trichome bases scattered over the lamina.

Some figured specimens of *Pachypteris lanceolata* Brongniart are similar to this species. Thomas (1954 : 320, text-figs. 1, 2) figures some specimens from Yorkshire which are similar in shape but larger than *M. herbstii*. Vachrameev & Samilina (1958, text-figs. 1, 2) also figure specimens of *Pachypteris* from the Jurassic of Russia which resemble *M. herbstii* although the pinnules are rather broader in the Russian material. The epidermal structure of these leaves, which I have studied from preparations of the Yorkshire material, presents some small differences when compared with that of *M. herbstii*, such as the presence of a definite midrib seen on the lower cuticle, and the dicyclic condition seen in some stomata. On the upper cuticle of *P. lanceolata* there are almost no stomata.

Mesosingeria herbstii shows some resemblance, as far as the external morphology of fronds is concerned, to some species of the genus *Scleropteris*. In the Paris Museum I was able to examine specimens of *S. pomelii* and *S. compacta*. *S. pomelii* (no. 11549 and no. 11555) is only a faint impression with no cuticle or organic matter remaining. The holotype of *S. compacta* Saporta (no. 11507) still retains some organic matter, but it was impossible to make a cuticle preparation. This species has much smaller pinnules than *M. herbstii*. Another species, *S. laevigata*, is missing from the collections. The following species of *Scleropteris* are more or less comparable to *M. herbstii* : *S. phillipsii* (Saporta, 1873, pl. 45, figs. 2, 3) and *S. laevigata* (pl. 46, fig. 3), but in the absence of cuticular structure a reliable comparison cannot be made.

The species is dedicated to Mr. R. Herbst, Tucumán, Argentina.

Genus *KTALENIA* nov.

DIAGNOSIS.—As for the only species, *Ktalenia circularis* sp. n.

The generic name has been taken from the word *Ktalenk*, which in the language of the Tehuelche Indians (Patagonia) means "little".

Ktalenia circularis gen. et sp. n.

(Pl. 6, figs. 28–33; Text-figs. 39–43)

DIAGNOSIS.—Fruit circular (originally globular), typically 3–4 mm. wide. Surface smooth. (Stalk and pollination opening not distinguished.)

Fruit wall strongly cutinised. Cuticle typically $5\ \mu$ thick, but thinner in some areas. Stomata absent. Surface flat, anticlinal cell walls straight, entire, sometimes pitted, cutinised down to hypodermis. Periclinal walls smooth or having granules and reticulation. Cells typically isodiametric, $15\text{--}20\ \mu$ wide, often elongated, having no definite orientation. Sometimes elongated cells converging radially to a centre occupied by one or two more or less isodiametric cells. Circular bases of trichomes present, usually sited over three or four cells at their corners. Hypodermal cells cutinised, larger than epidermal cells.

One or two seeds enclosed in the fruit. Seeds orthotropous. Integument, nucellus and megaspore membrane cutinised.

Cuticle of integument very delicate, extending from micropylar canal over nucellus, down to base of seed. Cell outlines very feebly marked. Cells somewhat rectangular. One or more small papillae present on cell surface.

Nucellus free, cutinised down to base. Cuticle of nucellus less than $1\ \mu$ thick. Largest seeds with nucellus 1.5 mm. long, smallest 0.8 mm. long. Cells of nucellus large, rectangular, typically $100\ \mu \times 30\text{--}40\ \mu$, becoming small and isodiametric at base of micropylar canal. Cell walls on micropylar canal more strongly cutinised than cells of nucellus, rectangular, with somewhat sinuous walls. Cells near chalaza becoming narrower. Micropylar canal in large seeds (occurring single in a fruit) about $250\ \mu$ long $\times 140\ \mu$ at base, becoming narrower towards top. At base, a round hole, about $150\ \mu$ wide, represents the insertion point of nucellus in chalaza.

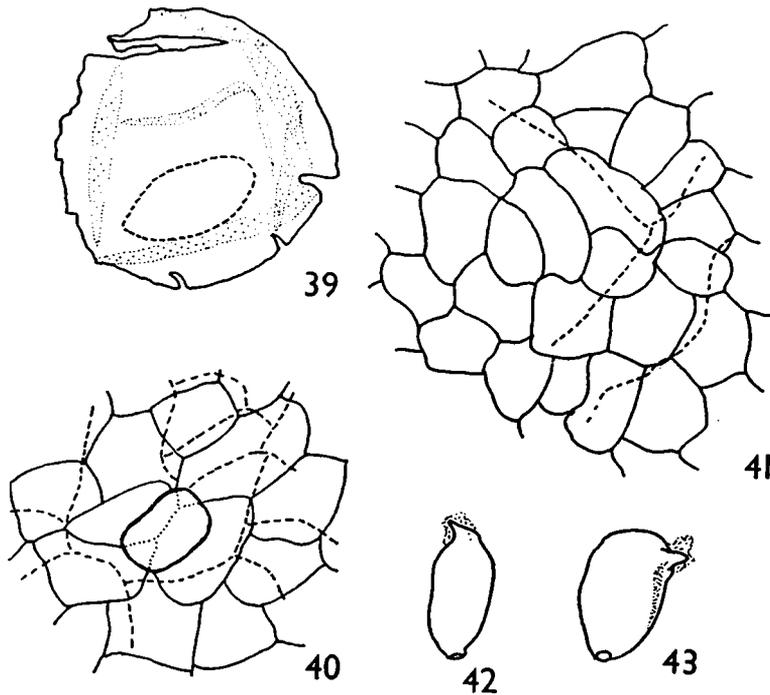
Megaspore membrane usually present, without any definite indication of cells, but a finely granular texture. Numerous round dark brown bodies, about $30\text{--}40\ \mu$ wide, are enclosed in megaspore membrane. They may correspond to an oily endosperm.

HOLOTYPE.—Slide LIL 181.

MATERIAL.—In addition to the holotype, slides: LIL 181–184; Brit. Mus. (Nat. Hist.) nos. V.44687–89.

DESCRIPTION.—*Ktalenia circularis* is an abundant fossil in the *Ticoa harrisii* bed. Often it is found in association with *Ruflovinia sierra*. It is preserved in two different ways in the same bed. The most complete type of preservation consists of a disc of cuticle enclosing the one or two seeds and a very little coaly matter. In these specimens the seeds do not form any visible bulge on the outside of the fossil. The other form, which is rather commoner, consists of half-fruits. Here, only one

surface shows the fruit cuticle, and the other, the internal surface, shows a hollow which is filled with rock matrix. The hollow is round or slightly oval in shape. These specimens are considered to be the same as the complete ones, because they are of the same size and the cuticles are exactly similar; no seeds have been found in these half-fruit. Between the hollow and the cuticle there is a thick carbonaceous layer, probably corresponding to the stony layer of the fruit wall.



Ktalenia circularis gen. et sp. n.

FIG. 39. General aspect of the fruit wall cuticle, showing a single seed inside (broken line). Slide LIL 181, holotype. $\times 10$.

FIG. 40. Cuticle of the fruit wall to show base of a trichome. Slide LIL 182. $\times 500$.

FIG. 41. Fruit wall cuticle showing a group of recently divided cells in the centre. Slide LIL 182. $\times 500$.

FIGS. 42, 43. Schematic drawings of two seeds, showing the cuticle of the nucellus; at the base the circular chalazal insertion, and at the top (dots) remains of the integument around micropylar canal. $\times 10$.

I have so far been unable to discover the stalk or the pollination opening of the fruits, although occasionally fragments of integument cuticle containing circular holes were observed.

The cuticle of the nucellus, when preserved, is easy to prepare. It is more difficult to deal with the integument cuticle. The micropylar canal is not always preserved, probably being broken off during maceration. The megaspore membrane and the endosperm substance are usually but not always preserved. With regard to the origin of the round bodies inside the megaspore membrane, I assume these are the remains of oil reserves which hardened during fossilisation. Their nature could be

similar to the aleurones of *Caytonia* and some other seeds. They are probably preserved because of the protection afforded by the thick cuticle of the fruit wall and the two other cuticles, the integument and nucellus, which are almost closed.

No pollen grains have been seen in the micropylar canal, although some are occasionally present in the preparations, sticking to the cuticles. They are of different types and no attempt has been made to correlate them with the fruits.

DISCUSSION.—For the purpose of description I have assumed these round bodies to be fruits and as more than one seed has been found inside them they may well be true fruits. In this respect the terminology is like that used for the fruit of *Caytonia* or the Angiosperms, but this is not meant to imply close affinities. At present we lack much important data.

It is unfortunate that nothing can be said about the attachment of these fruits, nor about the opening which permitted pollination or fertilization. Clearly both must have existed, but as far as present evidence goes, the cuticle of the fruit forms an almost continuous sac. Some specimens do show small gaps which I believe to be original features, but these gaps cannot be related to one another.

Among Mesozoic seeds which have been described in detail, only *Caytonia* possesses features similar to *Ktalenia* but there are some differences. In *Caytonia* there are usually more than two seeds in the fruit, rarely two. In *Ktalenia* the micropylar canal is directly opposite the top of the nucellus (probably they are fused) as in *Caytonia*. The cuticle of the nucellus of both genera is thicker than that of the outer integument, and there is no evidence of inner integument. The megaspore membrane, present in *Ktalenia*, is missing in *Caytonia* (Harris, 1958).

CONIFERALES

Halle (1913) described, among other fossil plants, some Mesozoic conifers from Patagonia, preserved as impressions. Subsequently petrified cones from what is now known as the Matilda Formation (Middle to Upper Jurassic) were described by several authors in successive contributions (Spegazzini, 1924 ; Gothan, 1925 ; Calder, 1953). Apart from these there are only a few scattered references to Mesozoic coniferous shoots including Menéndez (1956) who described two shoots with poorly preserved cuticle. In the Tertiary, however, several interesting species are known (Florin, 1948).

The specimens described below are compressions in which cuticles are well preserved but almost all the internal coaly matter has disappeared. The cuticles are easily prepared by maceration in HNO₃ plus KClO₃ for a few hours, followed by dilute ammonia.

The present evidence is consistent with the view expressed by Florin (1940) that all known Argentinian Mesozoic Conifers belong to the families Taxodiaceae, Araucariaceae and possibly Podocarpaceae, the last two being represented in the flora today.

Genus *BRACHYPHYLLUM* Brongniart

The four species described below agree generically with the emended diagnosis of

Brachyphyllum given by Kendall (1947) and accepted by Wesley (1956), but the species differ from those of the Northern Hemisphere.

Brachyphyllum is certainly an unnatural assemblage. One species, *B. mamillare* has Araucarian reproductive organs, whilst another, *B. expansum*, has a cone which does not appear to be Araucarian (Kendall, 1949). The foliage of *Cheirolepis muensteri*, if considered alone, would certainly be placed in the genus *Brachyphyllum* but its cones are very different from those of *Araucaria*. It is interesting that a male cone resembling *Araucaria* is associated with *Brachyphyllum mirandai* sp. n., but there is not yet sufficient evidence to relate the cone and the shoots as organs of one species.

Three of the species described here are very similar, and quite probably they belong to one natural genus. There is doubt about the position of the other species, *B. irregulare*, which differs markedly in some diagnostic characters.

Brachyphyllum brettii sp. n.

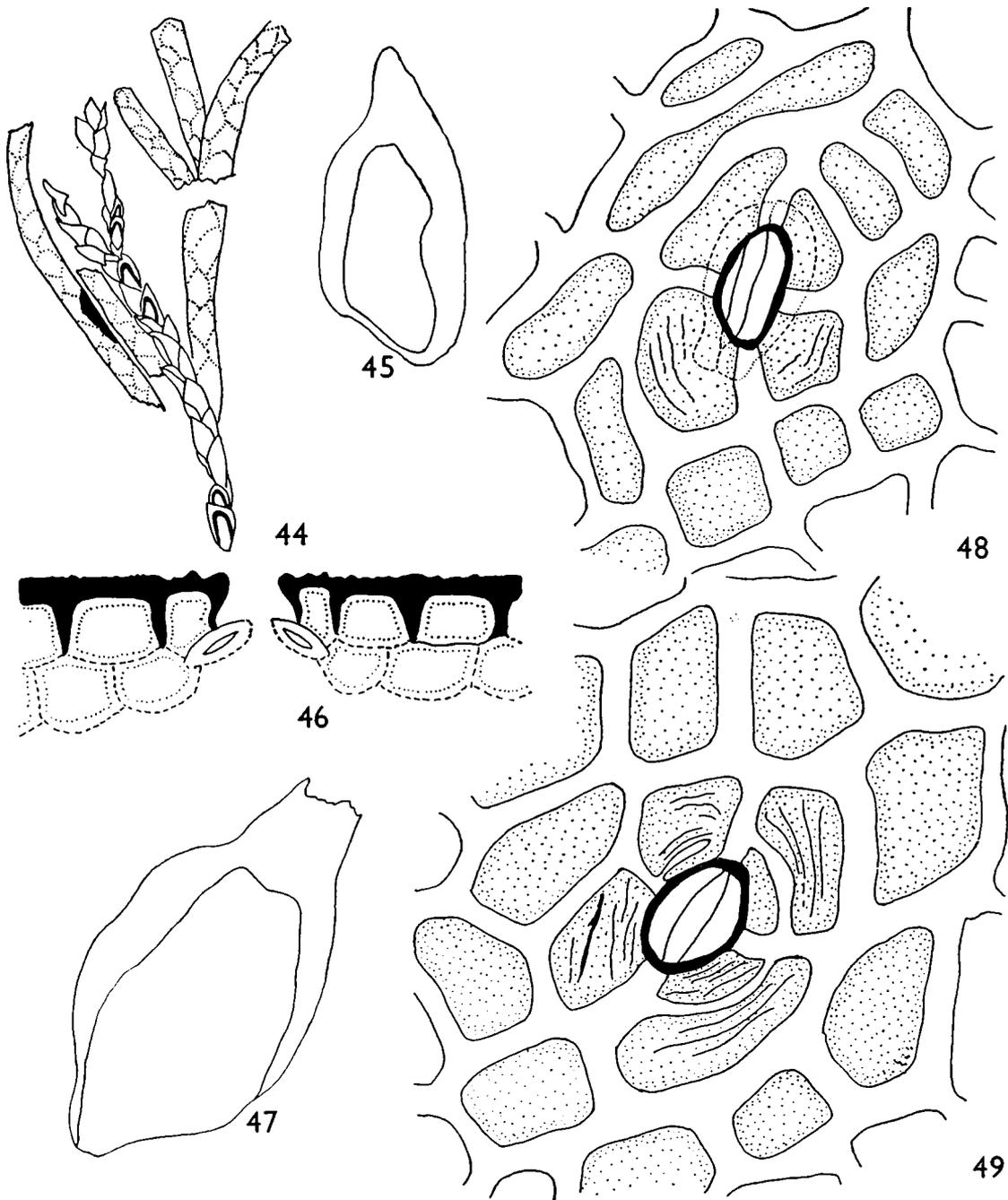
(Pl. 7, figs. 37, 38; Pl. 8, figs. 47–50; Pl. 9, figs. 63, 64; Pl. 12, fig. 74; Text-figs. 44–49)

DIAGNOSIS. Larger shoots 10 mm. in diameter, branching at an acute angle in one or more planes to give off branchlets typically 2 mm. in diameter. Leaves spirally attached to rhomboidal or somewhat oval leaf base cushion, large leaf with cushion typically 7.5 mm. long \times 3.5 mm. broad; normal size 3–4 mm. long \times 1.5–1.75 mm. broad; length usually about twice breadth. Free part of leaves (upper side) $\frac{1}{3}$ to $\frac{1}{4}$ of total length. Leaves with rounded or acute apex. Venation not seen. Thickness of lamina up to 0.8 mm. measured in laterally compressed specimens.

Cuticle thick, up to 3 μ , lower slightly thicker than upper. Margins of leaves entire with distinct projection of marginal cells, transversely elongated, up to 100 μ long, appearing serrate where both cuticles join. Stomata present on both cuticles, numerous, tending to form longitudinal rows, particularly in central part of lamina. Stomata usually absent near apices of leaves on lower cuticle, and present near margins and base. Stomata on both cuticles variably orientated; in some rows tending to be transverse. Stomata of a row often with subsidiary cells in contact, but usually separated by one or more epidermal cells. Stomata rarely sharing a subsidiary cell. Stomatal rows separated by 2–4 rows of square or rectangular epidermal cells.

Epidermal cells located on same rows as stomata, usually isodiametric, occasionally transversely elongated, typically 20–25 μ . Epidermal cells between rows of stomata usually square or rectangular, 20–30 μ , rarely elongated up to 100 μ . Epidermal cells on margins and apex square or rectangular. Epidermal cells on base typically isodiametric. Periclinal cell walls straight, unpitted, with distinct border, up to 5–7 μ broad (including two borders and middle lamella). Anticlinal walls cutinized. Cell surface generally flat with round or elongated irregular granules, sometimes forming compact ring near border of walls. Striae and ridges present, sometimes anastomosing to form a reticulum.

Stomata similar on both cuticles, typically monocyclic, rarely imperfectly dicyclic. Stomatal apparatus usually oval but occasionally circular. Guard cells slightly sunken in oval or round pit, feebly cutinized, 40–50 μ long \times 30 μ wide (both)



Brachyphyllum brettii sp. n.

- FIG. 44. General aspect of the holotype, showing branching. LIL 2565. $\times 2$.
 FIG. 45. Small leaf. Slide V.44671. $\times 15$.
 FIG. 46. Section of stoma. $\times 500$.
 FIG. 47. Leaf of a normal size. V.44673. $\times 15$.
 FIG. 48. Stoma showing sunken guard cells (broken lines) and a few striae on subsidiary cells. Slide LIL 196. $\times 500$.
 FIG. 49. Stoma showing numerous striae on subsidiary cells. Slide LIL 194. $\times 500$.

surrounded by typically 4-5 subsidiary cells. Polar and lateral subsidiary cells usually not differentiated. When two cycles of subsidiary cells are present, the inner cells are narrow and curved following the edge of mouth of pit. Encircling cells larger. Mouth of pit marked by more or less continuous rim of cutin, formed by fusion of subsidiary cells. Occasionally, subsidiary cells with 1 or 2 ridges parallel to mouth of pit.

Hypodermal cells sometimes cutinized, markedly elongated.

HOLOTYPE. LIL PB n. 2565.

MATERIAL. In addition to the holotype, LIL PB 2570(a), 2567(a), 2571-72, 2575(a); Brit. Mus. (Nat. Hist.) nos. V.44670, V.44676. Slides: LIL 185-199; V.44671-75.

DESCRIPTION. This species is common in the *Ticoa harrisii* bed. One specimen has a large branch, 1 cm. wide, with leaves still attached. The leaves are more or less separated.

Some of the shoots definitely branch in more than one plane. The cuticle is very well preserved and easy to prepare. The lower cuticle is thicker than the upper, which stains more strongly with safranin. The natural colour of the cuticle is brown.

The lamina substance (mesophyll) is often carbonized. These fragments when treated with dilute ammonia rapidly dissolve leaving no definite trace of tissues.

On the lower cuticle there is sometimes a longitudinal median area, about 10 cells wide, devoid of stomata. The stomatal pits are clearly seen, but the guard cells are sometimes absent. The hypodermal cells are very seldom visible.

The branchlets of *Brachyphyllum brettii* are given off at a more acute angle than those of *B. mucronatum*. The ratio of length and breadth of the leaves in these two species, as well as the natural colour of the cuticle is also different. The marginal cells of the leaves forming serrate projections are more obvious in *B. brettii* and are present on the apical part of the leaf. This character, shared by all the Ticó specimens, is met with in some Northern specimens of related genera such as *Pagiophyllum magnipapillare* Wesley (1956, text-fig. 18, G) and *Cheirolepis muensteri* Schenk (Lewarne & Pallot, 1957, text-fig. 2, B). The epidermal cells in *B. brettii* tend to be isodiametric, while in *B. mucronatum* they are usually rectangular, especially between rows of stomata. The cell surface is much more sculptured than in *B. mucronatum*, resembling in this respect the sculpturing in *B. mirandai*. *B. brettii* differs from *B. mirandai* in the length of the free part of the leaf (upper cuticle) and in the thickness of the lamina substance (mesophyll). In *B. mirandai* the epidermal cells are usually larger, the periclinal cell walls are much thicker and the hypodermal cells are much more strongly cutinized than in *B. brettii*. For comparison with species from other countries, see p. 76.

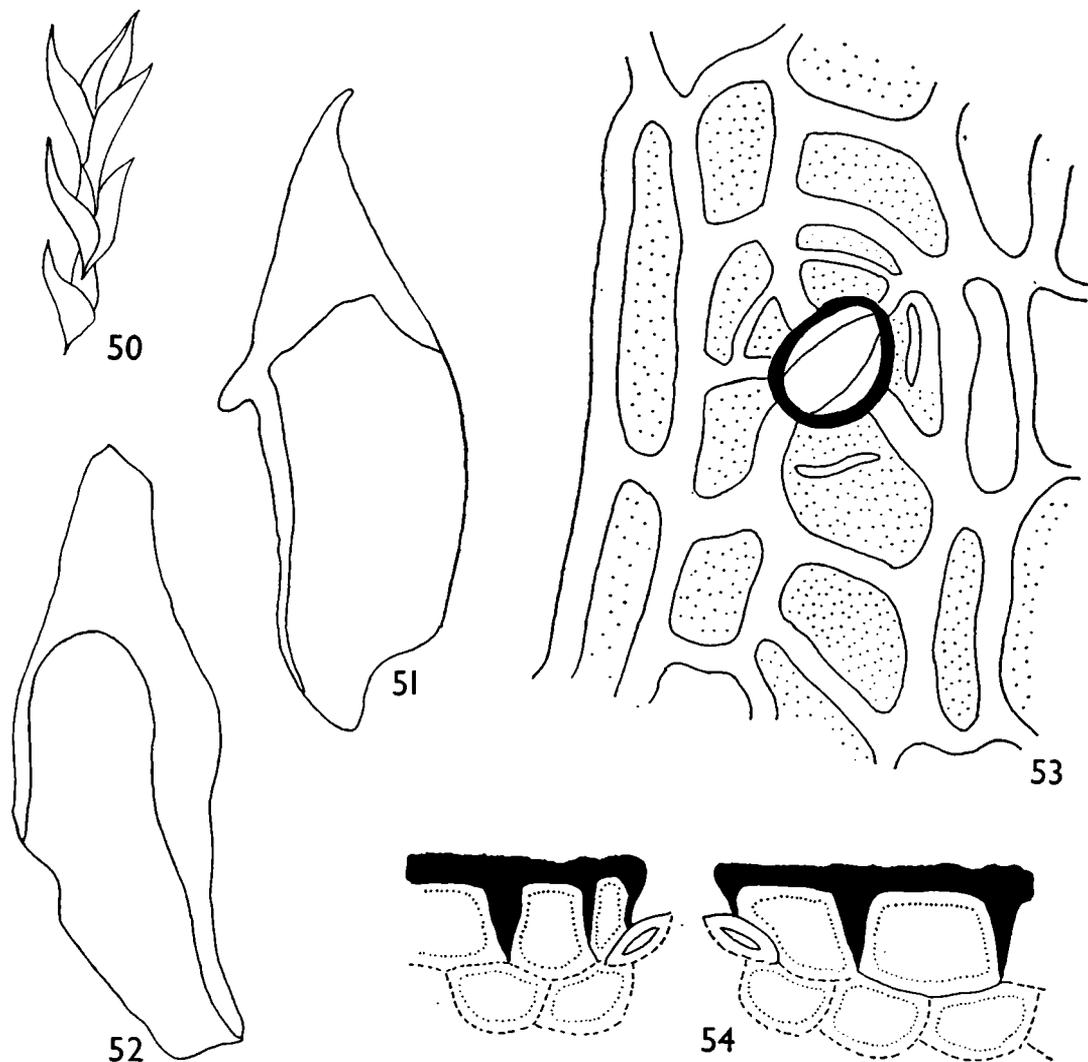
The species has been named after Donald W. Brett, Botany Department, The University, Glasgow.

Brachyphyllum mucronatum sp. n.

(Pl. 7, fig. 43; Pl. 8, figs. 51, 52; Pl. 10, fig. 66; Pl. 12, fig. 75; Text-figs. 50-54)

DIAGNOSIS. Largest branch known 3 mm. in diameter, giving off lateral branch-

lets, 1.5 mm. diameter, at an acute angle of approximately 45° . Branching in one or more planes. Leaves attached spirally to oval leaf base cushion, largest known 5 mm. long \times 1.5-1.7 mm. broad. Ratio between breadth and length 1 : 2, 3-1 : 3.



Brachyphyllum mucronatum sp. n.

FIG. 50. Fragmentary branchlet showing a few spirally attached leaves. V.44670. $\times 4$.

FIGS. 51, 52. Leaves of normal size. Slides LIL 200, 201. $\times 15$.

FIG. 53. Stoma showing two ridges on subsidiary cells. Slide LIL 201. $\times 500$.

FIG. 54. Section of stoma. $\times 500$.

Free part of leaves typically $\frac{1}{3}$ of total length. Leaves usually with acute apex, often projecting towards branch axis and mucronate. Venation not seen.

Cuticle thick. Apical part of leaves with sharp margin formed by layer of transversely projecting cells up to 50μ long, edge microscopically serrate. Stomata occurring on both sides of lamina and on cushions; on adaxial side of leaf generally

distributed, on abaxial side distributed over basal cushions and margins but usually absent near leaf apex. Stomata forming short rows, rows ill-defined but more definite near midline of lamina, stomatal orientation varied, but frequently longitudinal. Stomata of a row sometimes with subsidiary cells in contact but usually separated by one or more epidermal cells. Stomata very rarely sharing a subsidiary cell. Stomatal rows typically separated by 2-4 files of rectangular elongated epidermal cells.

Epidermal cells located on same rows as stomata, usually isodiametric, 25-40 μ , sometimes transversely elongated. Epidermal cells between stomatal rows typically rectangular, 60-70 μ long \times 10-15 μ broad, rarely up to 100 μ long. Epidermal cells at base typically isodiametric, sometimes bearing a single round papilla. Epidermal cells on margins rectangular or slightly elongated. Epidermal cells near apex rectangular, tending to be isodiametric near apical margin. On upper cuticle, epidermal cells rectangular or isodiametric. Periclinal walls straight, unpitted, with distinct border, up to 5-6 μ broad (including 2 borders and middle lamella). Anticlinal walls cutinized. Cell surface flat. Delicate striae parallel to border of cells. Basal cells often with delicate granules, rarely conspicuous ones.

Stomata similar on both cuticles, typically monocyclic, sometimes imperfectly dicyclic. Stomatal apparatus usually oval but occasionally circular. Guard cells slightly sunken in oval or round pit, feebly cutinized, about 50 μ long, surrounded by typically 4-5 subsidiary cells. Polar and lateral subsidiary cells usually not differentiated, sometimes with anticlinal walls extending to hypodermis. Mouth of pit marked by more or less continuous rim of cutin, formed by fusion of subsidiary cells. Subsidiary cells usually with a ridge parallel to mouth of pit, ridges sometimes united to form a ring.

Hypodermal cells sometimes feebly cutinized, markedly elongated.

HOLOTYPE. LIL PB n. 2569.

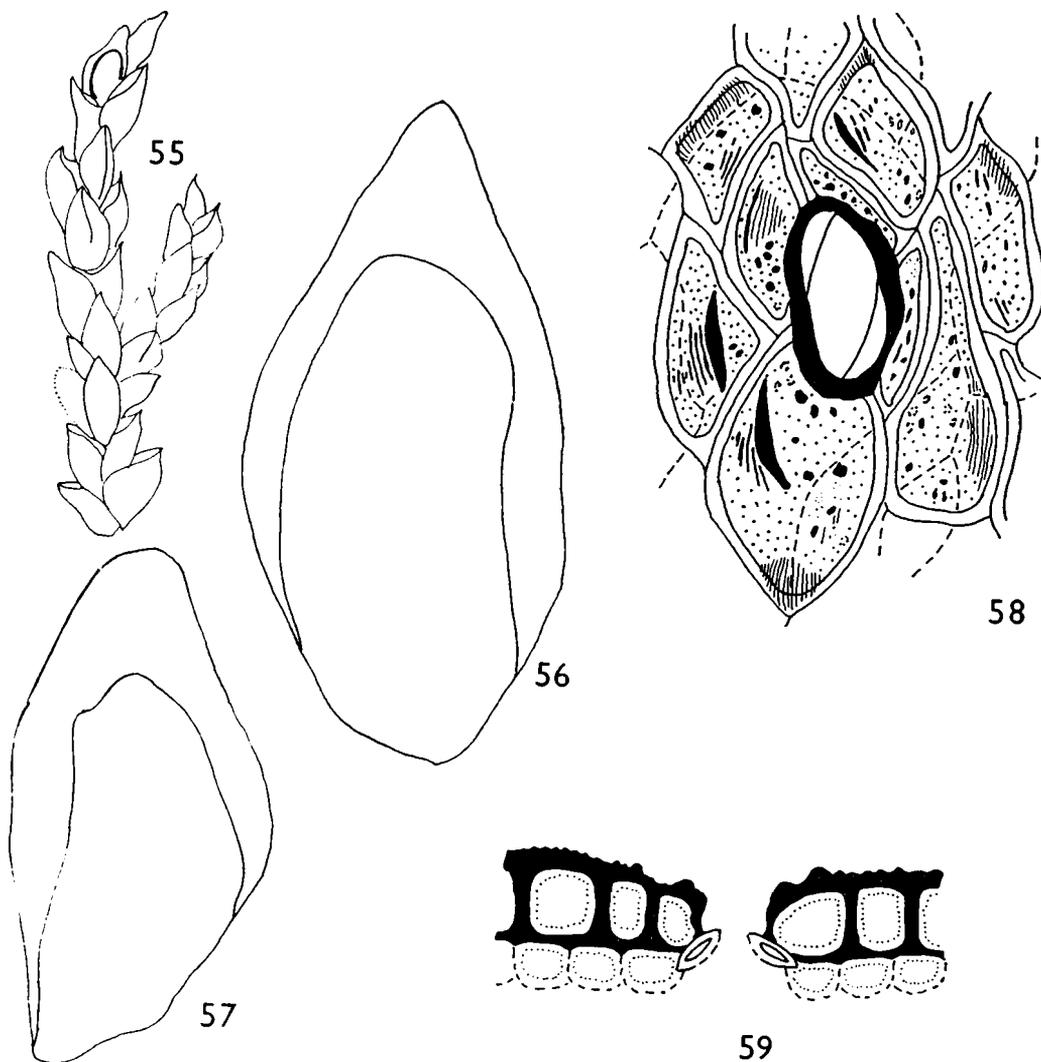
MATERIAL. In addition to the holotype LIL PB n. 2573; Brit. Mus. (Nat. Hist.) no. V.44670. Slides: LIL 200-214; V.44669.

DESCRIPTION. This species is present in the *Ticoa harrisii* bed, and is as abundant as *Brachyphyllum brettii*. Branchlets of *B. mucronatum* are often found mixed with twigs of *B. brettii*. They can be distinguished macroscopically by the lighter colour of the cuticle of *B. mucronatum* (yellowish-brown) and by their leaves which are more acute, but the two species can only be separated with certainty by the microscopical characters of their cuticles.

Brachyphyllum mucronatum differs from *B. mirandai* as follows:

In *B. mucronatum* the leaf is relatively narrower (1.5 mm. as against 4 mm.) and the free part of the leaf is a longer portion of the whole ($\frac{1}{3}$ as against $\frac{1}{4}$). The cuticle is paler, thinner and less prominently sculptured than in *B. mirandai* and its hypodermal cells are less cutinized. The apex of the leaf is more acute in *B. mucronatum* than in *B. mirandai* or indeed in any other species described here, and there is a tendency for it to curve further inwards towards the branch axis.

The narrowness of the leaves of *B. mucronatum* may be compared with some Northern species of *Pagiophyllum* but the free part of the leaf is always much shorter than the length of the leaf base cushion.



Brachyphyllum mirandai sp. n.

FIG. 55. Fragment of the holotype showing branching. LIL 2560. $\times 2$.

FIGS. 56, 57. Normal and small leaves. Slide LIL 215. $\times 15$.

FIG. 58. Stoma showing abundant granules, striae and ridges on subsidiary cells. (Hypodermal cells with broken lines). Slide LIL 216. $\times 500$.

FIG. 59. Section of stoma. $\times 500$.

Brachyphyllum mirandai sp. n.

(Pl. 7, fig. 41; Pl. 8, figs. 53-55; Pl. 9, figs. 61, 62; Pl. 12, fig. 76; Text-figs. 55-59)

DIAGNOSIS. Larger branch, 4 mm. in diameter, giving off smaller lateral branchlets at acute angle. Leaves spirally attached to rhomboidal or rounded leaf base cushion; largest leaves 7 mm. long \times 4 mm. broad; normal size 4-5 mm. long \times 2-2.5 mm. broad. Free part of leaf about $\frac{1}{4}$ of total length. Apex rounded or acute. Sub-

stance of lamina up to 1.2 mm. thick, measured in laterally compressed leaves. Venation not seen. Median keel sometimes seen on abaxial surface of leaves.

Cuticle thick. Sharp margins formed by layer of transversely projecting cells up to 70μ long, edge microscopically serrate. Stomata numerous, present on both sides of free part of leaves and on leaf cushion, usually absent near apex. Stomata normally scattered but sometimes forming short ill-defined longitudinal rows. Stomata usually orientated longitudinally, often obliquely, rarely transversely; lateral subsidiary cells of neighbouring stomata in contact; rarely two stomata sharing a lateral subsidiary cell.

Epidermal cells usually slightly elongated, rectangular, polygonal, sometimes square. Rectangular cells typically $80-100 \mu$ long \times $35-45 \mu$ broad. Typical isodiametric cells on lamina and margins about 50μ in diameter. Periclinal walls straight, about 10μ thick, rarely pitted, with a distinct border. Anticlinal walls cutinized down to hypodermis. Surface flat with irregularly distributed striae, granules or occasional reticulations. Occasionally one or more very small papillae present near marginal cells.

Stomata similar on both cuticles, typically monocyclic or imperfectly dicyclic. Guard cells typically 60μ long \times 40μ wide (when open) sunken in oval or round pit, feebly cutinized, surrounded by typically 4-5 subsidiary cells, not well differentiated into polar and lateral. Mouth of pit sometimes marked by rim of cutin formed by fusion of borders of subsidiary cells. Subsidiary cells with usually one, sometimes two strong ridges parallel to mouth of pit. Numerous distinct striae and granules of varying size present on subsidiary cells. Encircling cells, when present, also with ridges, numerous striae and granules.

Hypodermal cells cutinized on same level as guard cells, markedly elongate.

HOLOTYPE. LIL PB n. 2560.

MATERIAL. In addition to the holotype, LIL PB n. 2559, 2561; Brit. Mus. (Nat. Hist.) no. V.44668. Slides: LIL 215-217.

DESCRIPTION. This conifer was found in a new bed in which it is the dominant element. The matrix of the rock is thin, much more compact than in the *Ticoa harrisii* bed, and darker (brown) in colour. The cuticles also look much darker.

The branching of the specimens is imperfectly known, the material being too fragmentary. However, in a few specimens that show branching it seems to be in more than one plane.

The stomatal apparatus usually stains more strongly with safranin than the rest of the epidermis and it can be clearly seen that the strongly sculptured outer (periclinal) walls of the subsidiary and encircling cells obscure the vertical (anticlinal) walls of these cells.

DISCUSSION. *Brachyphyllum mirandai* is distinguished from all other species of *Brachyphyllum* more readily than *B. brettii* because of the unique surface sculpture of its subsidiary cells. However, *Pagiophyllum peregrinum* (L. & H.) from the Lower Lias of Lyme Regis, Dorset has rather similar striae (Kendall, 1948: 83) but no granules or reticulations. Furthermore the stomata of *P. peregrinum* are arranged in longitudinal rows and are usually transversely orientated, features which do not occur in *B. mirandai*. The encircling cells of the European species seem to

form a more constantly differentiated ring than in *B. mirandai*. The epidermal cells of *P. peregrinum* are smaller and trichomes have been observed. The cell walls, however, are sometimes pitted as in *B. mirandai*. Finally, twigs of *P. peregrinum* are usually broader than those of *B. mirandai*.

A cuticle has been described by Hörhammer (1933) from vegetative shoots of *Cheirolepis muensteri* Schenk which resembles in every respect the cuticle of *Brachyphyllum*. The leaves figured by him (1933, pl. 1, figs. 9, 9a, 9b) have somewhat dentate margins and a markedly acute apex. The stomata are arranged in definite longitudinal rows and the epidermis appears to be granulated. The subsidiary cells of the stomata in *C. muensteri* are more markedly striated and the cells between the stomatal rows are more elongated than in *B. mirandai*.

Lewarne & Pallot (1957) describe *C. muensteri* from the Rhaeto-Liassic of South Wales. The leaves are generally smaller than those of *B. mirandai*, but the shape is similar. The adaxial cuticle is much smaller in relation to the abaxial one, than in *B. mirandai* but the subsidiary cells of the stomata have a rather prominent ridge running parallel with the pit which is similar to that described in all our species of *Brachyphyllum*. Furthermore, the leaf margins, especially near the apex, are specialized, with a distinct cuticular projection as shown in Text-fig. 2, B. This is also comparable with our species.

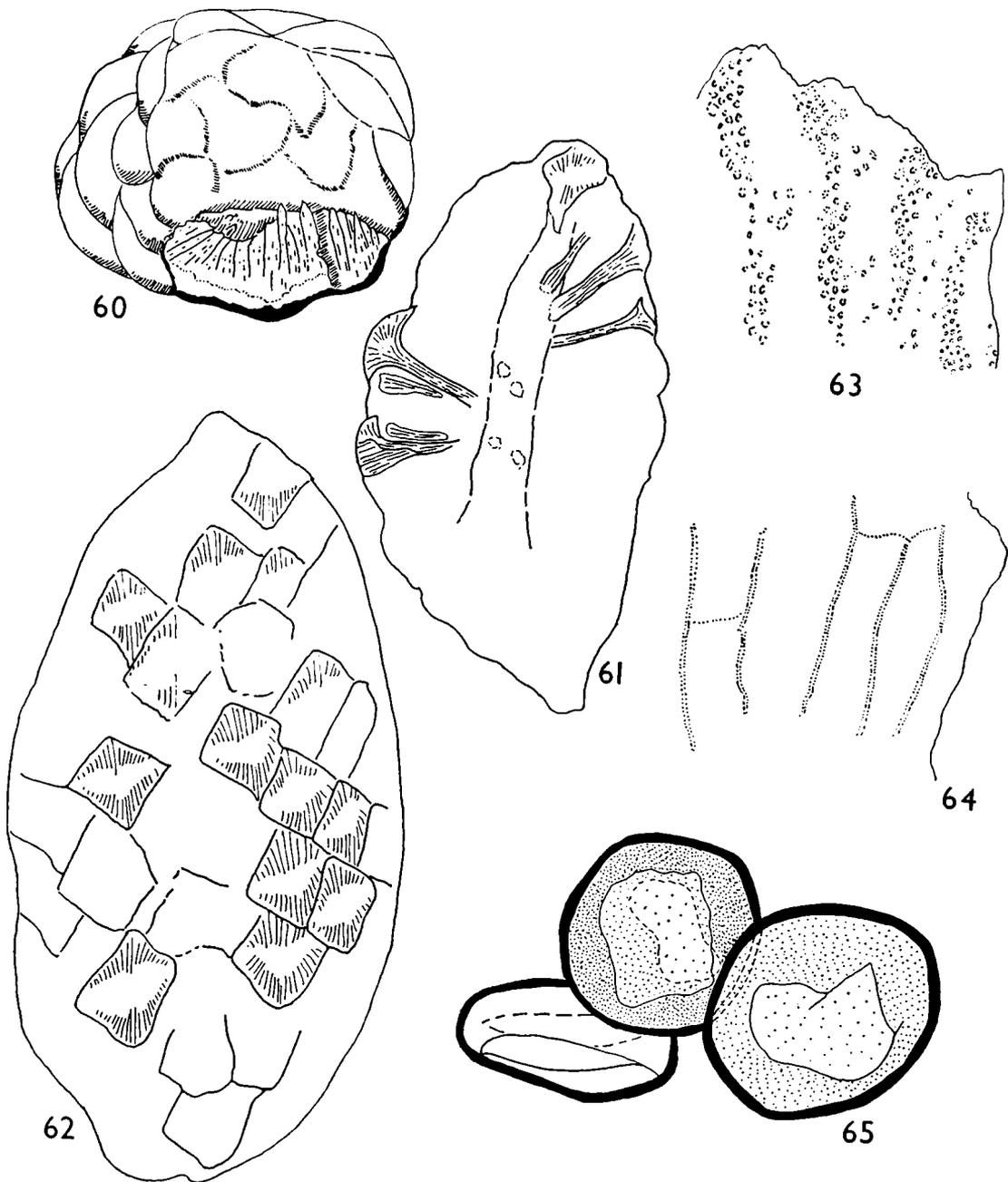
The species is named after Mr. H. Miranda who was the first to discover the plant bed with cutinized specimens in the Ticó Amphitheatre in 1957.

Male cones associated with *Brachyphyllum mirandai* sp. n.

(Pl. 7, figs. 45, 46 ; Text-figs. 60-65)

Several small cones were found in the bed containing the sterile twigs of *B. mirandai*. Some are compressed vertically and others longitudinally. None of them has a stalk (LIL PB 2561-62). The shape of these cones is elliptical. One specimen, compressed vertically, has a width of 4 mm. Impressions of the heads of the microsporophylls are clearly seen and they are more or less rhomboidal in shape. In one corner, a thick layer of strongly compressed tissue was found. After maceration this tissue proved to be composed of compressed cuticles of microsporophylls with their pollen sacs ; all details of their original shape have been obliterated. The pollen sacs could be seen on the actual specimen projecting inwards as sharp teeth, but it is not possible to determine their number. The cuticles are unsatisfactorily preserved but two kinds were noted. One, possibly belonging to the microsporophyll or the outside of the pollen sac, shows dark elongated cells 10 μ wide and is not granular. The other, the lining of the pollen sac, also shows elongated cells 10 μ wide but is covered with prominent granules, typically 1-2 μ wide. These granules are detachable and also adhere to the pollen grains.

Another cone, longitudinally compressed, measures 8 mm. long \times 4 mm. wide. The median axis is seen, its width being about 0.8 mm. Round scars, corresponding to the insertion of vertically compressed microsporophylls, can be seen arranged in a spiral on the main axis of the cone. The microsporophylls are about 1.5 mm. long and are inserted at right angles or slightly obliquely to the main axis. The stalk is straight and at the end expands in a wide head which is transversely elongated to the



Male cone associated with *Brachyphyllum mirandai* sp. n.

- FIG. 60. Vertical compression showing some pollen sacs. LIL 2561. $\times 10$.
 FIG. 61. Lateral compression showing some stalks and heads of microsporophylls still attached to the cone axis. LIL 2562. $\times 10$.
 FIG. 62. Lateral compression showing rhomboidal heads of sporophylls. LIL 2562. $\times 10$.
 FIG. 63. Granulose membrane. Slide LIL 224. $\times 500$.
 FIG. 64. Smooth membrane showing cellular outlines. Slide LIL 224. $\times 500$.
 FIG. 65. Pollen grains. Slide LIL 221. $\times 500$.

stalk of the microsporophylls. Two (or more?) pollen sacs are attached in the inner part of the head and extend towards the main axis of the cone. The pollen sacs are long, somewhat fusiform and have longitudinal striations. After macerating the microsporophylls of this cone the same two types of cutinized membranes were seen, one with dark elongated cells and the other, thinner, with prominent granules. The pollen is rare but similar to that found in the previous cone. No other type of pollen was seen.

A third specimen, also a longitudinally compressed male cone, is oval in shape and measures 1 cm. in length and 0.5 cm. in breadth. Although the innermost part of the cone has disappeared, the external prints of the heads of the microsporophylls are clearly seen. They are perfectly rhomboidal and arranged in a spiral. Each head measures about 1 mm. \times 1 mm. Fine striations are given off from the central part of the heads.

A constant feature of these cones is that they are always found without stalk or sterile foliage at their base.

Pollen. The pollen grains are alike in the two cones which have been macerated. The sporangia have dehisced and shed nearly all their pollen, but a few grains, all of one type, remain on the granulose membrane. Most of the pollen grains are circular, 50–55 μ wide, with an exine 3 μ thick. There are no wings. The surface is almost smooth but may be very faintly granular. Most grains show some irregularly orientated folds which are probably due to compression. Other folds are usually arranged in a circular manner, surrounding a middle pale area which is here presumed to be the sulcus. These circular folds may be the original edges of the sulcus which was concave. A few of the grains are oval and these are regarded as having been laterally compressed; their folds are entirely consistent with the idea that the pale area is a sulcus. The grains thus, may have been flattened discs with one concave side.

One grain shows a separate round body, 30 μ wide, with a well-developed wall. This body is present on the other side of the disc and could have been another concave or flat circular area. This feature has not been seen in any of the other specimens, and its nature is unknown.

The combined data available from these cones give a fairly complete picture of their structure. Unfortunately the important information regarding the number and position of pollen sacs is lacking. The definition of these male cones is as follows:

Male cones elliptical, found always detached from the shoots, without stalk, typically 8–10 mm. long \times 4–5 mm. wide. Microsporophylls arranged spirally, inserted to one main central axis about 0.8 mm. wide, in a perpendicular or slightly oblique manner. Heads of sporophylls typically rhomboidal, crowded, forming a close structure. Two cuticles are seen. One, probably of the microsporophyll, is thick, with dark elongated cells about 10 μ wide. The other, thinner, also with elongated cells about 10 μ wide, is crowded with prominent granules typically 1–2 μ wide. Pollen sacs elongated. Pollen grains (when compressed) circular and flattened, typically 50–55 μ wide. Exine 3 μ thick. No wings present, surface smooth. A middle thinner area is seen, probably corresponding to the sulcus.

DISCUSSION. These three male cones are considered to belong to the same species, because they are found in the same bed, they are approximately the same size and their pollen and cutinized membranes are similar. They may belong to the same plant as the foliage *Brachyphyllum mirandai* sp. n. which so far is the only conifer foliage that has been found in the same bed.

This type of cone and the pollen it bears is different from all Taxopsida and from most of the Pinaceae, Cupressaceae and Podocarpaceae. Similar cones are found in the Araucariaceae and Taxodiaceae, mainly in the genera *Araucaria*, *Agathis*, *Cryptomeria* and *Sciadopitys*. If we accept the evidence of their close association as an indication that the cones and foliage belong to the same plant, *B. mirandai* may then be compared closely with the Araucariaceae; but this has still to be proved.

The pollen grains of *Cheirolepis muensteri*, although similar in shape, are smaller than those described above (20–30 μ), and have a thickened exine in the equatorial region. There is a similarity in shape with pollen grains of *Classopollis torosus* (Reissinger) type and the range in size coincides with our material (up to 46 μ). Couper (1958) believes that *C. torosus* grains are similar to those found in male cones of *Pagiophyllum connivens*. However, I could not see the characteristic equatorial thickenings of *C. torosus* in our pollen. Couper points out that none of the Recent conifers possesses pollen of this type.

Harris (1957) described carbonized fragments of *C. muensteri* from Wales. The fragments of male cones yielded supplementary information about the nature of the microsporophylls which are inserted spirally on the main axis, as in the Ticó specimens, but the heads of the sporophylls seem to be larger. The number of microsporophylls in the cones was probably smaller in *Cheirolepis* than in the Patagonian specimens. Unfortunately it has not been possible to compare the number and size of the pollen sacs owing to the fragmentary nature of our material. The shape of the pollen grains of the Welsh material is similar, but the grains are smaller and the tuberculate equatorial area figured by Harris (1957, text-fig. 5, A–C) is not evident in the Patagonian specimens.

The compressed material described by Hörhammer (1933, pl. 4, figs. 27, 27A) looks rather different from our specimens.

Some male cones found in association with *Brachyphyllum* and *Pagiophyllum* can be compared with the present specimens. Kendall (1952) described male cones associated with *Pagiophyllum connivens* from the Jurassic of Yorkshire. They are wider than the Patagonian cones, having a diameter of 7 mm. The pollen grains are much smaller (20–30 μ) but the exine has the same thickness. Other microstrobili have been found attached to *Brachyphyllum mamillare* and have been described by Kendall (1949). The diameter of these cones is somewhat smaller than the previous species mentioned, and are thus more comparable to ours. The pollen grains have more or less the same size and have no marked sculpturing on the exine.

I can make no comparison with the presumed male cones found associated with *Athrotaxis ungeri* (Halle, 1913, pl. 3, fig. 21) described from the Upper Mesozoic

strata of Río de los Fósiles, Argentina. The cone is longitudinally compressed and has lost all traces of organic matter; there is no information about the cuticles or pollen grains.

Brachyphyllum irregulare sp. n.

(Pl. 7, fig. 44; Pl. 8, figs. 56, 57; Pl. 10, fig. 65; Pl. 12, fig. 77; Text-figs. 66-71)

DIAGNOSIS. Largest branches known, 2 mm. in diameter, giving off lateral branchlets, about 1 mm. in diameter, at an acute angle. Leaves spirally attached to an oval leaf base cushion on branchlets typically 3 mm. long \times 2 mm. wide with rounded apex. Leaves on largest branches up to 6 mm. long \times 3 mm. wide, usually with acute apex. Free part of leaves typically $\frac{1}{3}$ of total length. Ratio between length and breadth 1.5 : 1-2 : 1. Venation not seen.

Cuticle thick. Sharp margins formed by layer of transversely projecting cells up to 80 μ long, edge microscopically serrate. Stomata present on both cuticles and leaf cushion but becoming less numerous near leaf apex, on both sides. Stomata placed irregularly, typically not forming rows, rarely forming short, ill-defined rows of not more than 3-4 stomata long; orientation varied but with slight tendency to be longitudinal. Stomata sometimes with subsidiary cells in contact, rarely sharing one.

Epidermal cells usually isodiametric, 35-50 μ , often somewhat rectangular, longitudinally elongated, rarely up to 100 μ long. Epidermal cells on both cuticles similar on margins, base, apex and lamina. Periclinal walls straight, sometimes pitted, with distinct border, up to 5-7 μ wide (including 2 borders and middle lamella). Anticlinal walls cutinized. Cell surface flat, very finely granular.

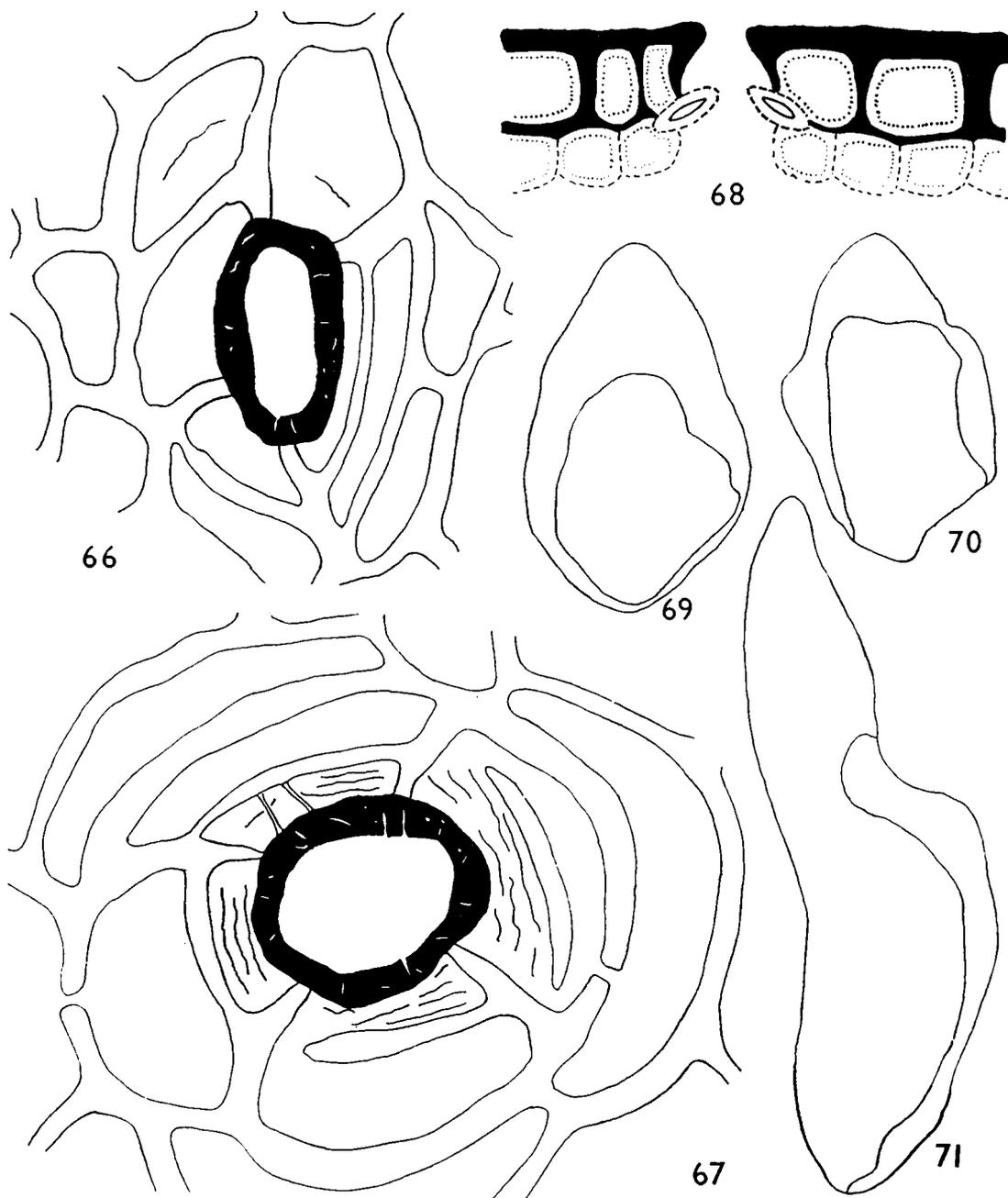
Stomata similar on both cuticles, typically monocyclic or imperfectly dicyclic. Dicyclic stomata sometimes seen on upper cuticle. Stomatal apparatus usually oval but sometimes circular. Guard cells not cutinized, surrounded by typically 4-5 subsidiary cells. Polar and lateral subsidiary cells usually not differentiated. Mouth of pit marked by more or less continuous rim of cutin which stains less strongly with safranin and has irregular striae. Subsidiary cells usually with ridge parallel to mouth of pit. Ridges of adjacent cells sometimes united to form a ring. Rarely, on surface of subsidiary cells there are perpendicular ridges to mouth of pit. Pitting in anticlinal walls of subsidiary cells to stomatal pit.

Hypodermal cells cutinized, narrow and markedly elongate.

HOLOTYPE. LIL PB n. 2576.

MATERIAL. In addition to the holotype, LIL PB n. 2577-79, 2582; Brit. Mus. (Nat. Hist.) no. V.44667. Slides: LIL 255, 233.

DESCRIPTION. *Brachyphyllum irregulare* was found in a new bed where it is abundant with *Cladophlebis*. Its cuticle is brown in colour. The rim of cutin surrounding the mouth of pit stains less strongly with safranin than does the rest of the cuticle and hence appears light in colour. The numerous pits which appear to traverse the anticlinal walls of the subsidiary cells bordering the stomatal pit are a constant feature.



Brachyphyllum irregulare sp. n.

FIG. 66. Stoma on lower cuticle. Slide LIL 225. $\times 500$.

FIG. 67. Stoma on upper cuticle showing some striae and ridges. Slide LIL 225. $\times 500$.

FIG. 68. Section of stoma. $\times 500$.

FIGS. 69, 70. Two leaves of normal size. Slide LIL 225. $\times 15$.

FIG. 71. A large leaf. Slide LIL 233. $\times 15$.

This species differs from all others of *Brachyphyllum* described in the present paper in the irregular distribution of stomata which do not form rows. The periclinal walls are pitted, as in *B. mirandai*, but the cell surface sculpturing is less conspicuous.

B. crucis Kendall from the Middle Jurassic of Yorkshire and Wiltshire is similar in that the stomata do not form definite rows. Its stomata are different, however, in having bulging subsidiary cells and hypodermal cells that are nearly isodiametric. In fact, *B. crucis* differs from typical *Brachyphyllum* species in the absence of definite longitudinal rows of stomata as does *B. irregulare*. In this respect, these two species are unlike any known Araucariaceae, living or fossil, but they resemble some Podocarpaceae such as *Podocarpus ustus* (Florin, 1933 : 270). Leaving our species in *Brachyphyllum* (an unnatural genus) I should stress the diagnostic feature of the stomata which usually tend to form, but sometimes do not form longitudinal rows. With this emendation the Patagonian species may be included in the genus *Brachyphyllum*.

Brachyphyllum expansum var. *indica* Sahní (1928) has a similar stomatal arrangement (not forming rows). The leaves are smaller, however, and there is no information about the stomata to make a clear comparison.

Athrotaxis ungeri (Halle)

(Pl. 6, fig. 35 ; Pl. 7, fig. 42 ; Pl. 10, figs. 67-69 ; Pl. 12, fig. 78 ; Text-figs. 75-79)

EMENDED DIAGNOSIS. Twigs branched. Largest branches 2-3 mm. wide. Branchlets given off at acute angle. Leaves spirally attached to rhomboidal leaf base cushion. Leaves small with acute apex and broad base, typically 2 mm. long \times 1.5 mm. broad. Free part of leaves (upper side) $\frac{1}{2}$ to $\frac{1}{3}$ of total length. Margins slightly dentate. Venation not seen. Leaves not spreading out but markedly adpressed to shoot, with apical part sometimes curved towards branch.

Lower cuticle, 7 μ thick, much thicker than upper cuticle. Stomata present on upper cuticle, very rarely at base of lower cuticle. Stomata not forming rows, variably orientated.

Epidermal cells on lower cuticle typically square or isodiametric, 30-40 μ wide, or rectangular, elongated, 50 μ long \times 20-25 μ wide, becoming markedly elongate towards margins. Cells forming definite longitudinal rows, one cell wide. Leaf margins marked by cells 60 μ long \times 20 μ wide which project outwards almost perpendicularly, with their apices free, as teeth. Anticlinal cell walls straight, cutinized down to hypodermis, sometimes pitted. Periclinal cell walls smooth, except for base of leaf where they are finely granulose with strongly marked round or slightly elongated single pinnae on almost every cell. Hypodermal cells cutinized, markedly elongated, much narrower than epidermal cells.

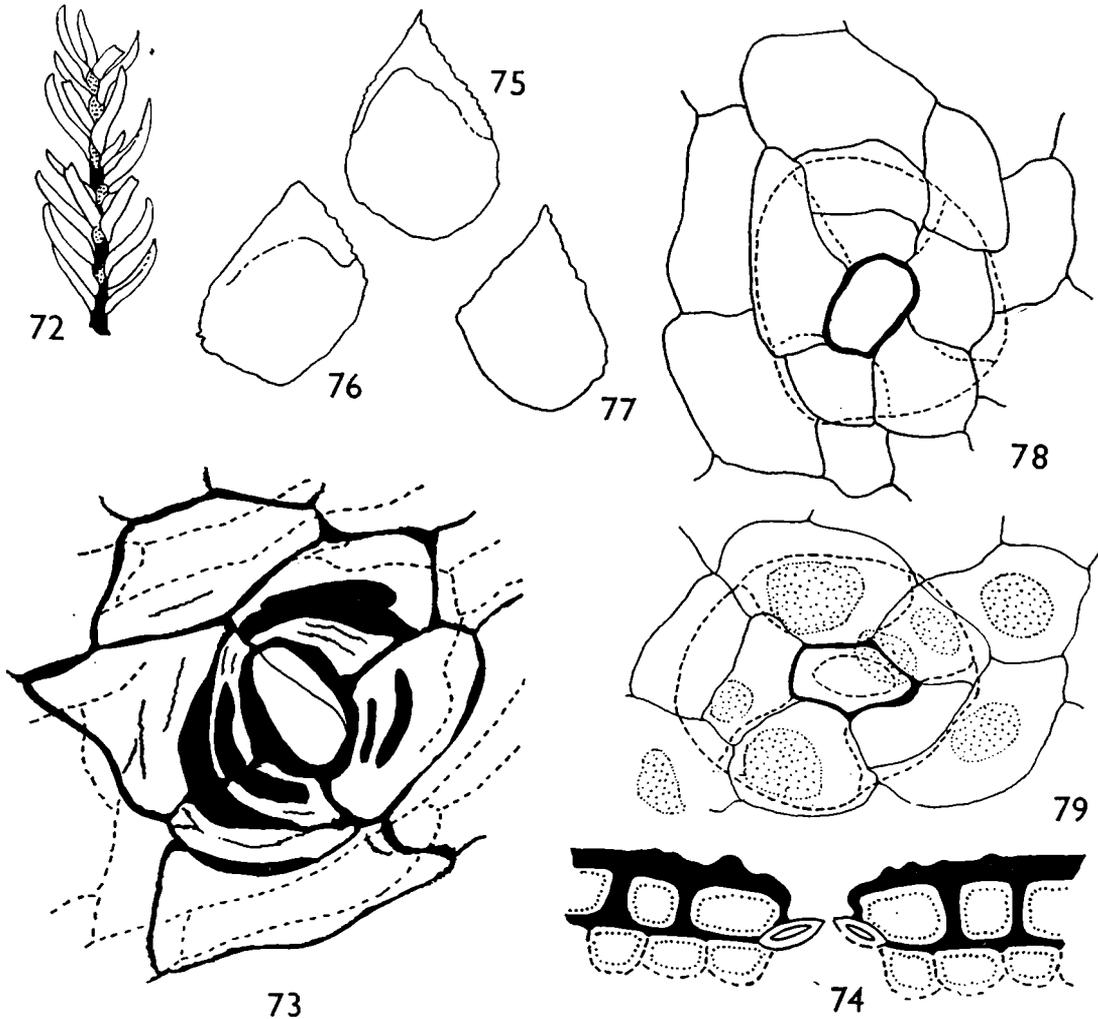
Epidermal cells on upper cuticle typically isodiametric with somewhat rounded contours, about 30-40 μ wide. Anticlinal cell walls not so strongly marked as on lower cuticle, straight, sometimes pitted. Periclinal cell walls finely granulose.

Stomata typically monocyclic, sometimes imperfectly dicyclic. Mouth of pit oval or sometimes polygonal, surrounded by typically 5 subsidiary cells. Guard cells sunken in pit, producing an oval or circular outline, underneath outer cuticle

of subsidiary cells. Stomata on base of lower epidermis of leaves with subsidiary cells bearing strong round papillae, sometimes projecting over mouth of pit.

MATERIAL. LIL PB n. 2563. Slides : LIL 226-228 ; Brit. Mus. (Nat. Hist.) nos. V.44662-63.

DESCRIPTION. This species was found in a new bed where Bennettitalean fronds are abundant. The branches are few, grouped together and perhaps belonging to a



Tomaxellia d. giustoi gen. et sp. n.

FIG. 72. Holotype. LIL 2542 (b). $\times 2$.

FIG. 73. Stoma showing strong ridges on subsidiary cells and cutinized hypodermal cells (broken lines). Slide LIL 229. $\times 500$.

FIG. 74. Section of stoma. $\times 500$.

Athrotaxis ungeri (Halle)

FIGS. 75-77. Leaves of normal size. V. 44662. $\times 15$.

FIGS. 78. Stoma on upper cuticle. Slide LIL 228. $\times 500$.

FIG. 79. Stoma on basal part of lower cuticle. Slide LIL 226. $\times 500$.

single tree; they are all fragmentary. The small leaves are markedly adpressed to the branches and their lower sides, almost devoid of stomata, must have been facing the sun.

The cuticle is very well preserved although the adaxial, because it is thin, is difficult to prepare. The abaxial cuticle consists of two distinct areas, the proximal being the third nearest the axis and the distal the remaining two-thirds. The proximal part is formed by cells with granular surface and bearing strong papillae, but the distal part shows cells with a smooth surface and no papillae at all. The adaxial cuticle shows no such division into areas, the outline of the cells being rounded. The margins of the whole leaf show tooth-like projections. The stomata on both cuticles are alike in structure and size, but those on the abaxial cuticle always have strong papillae on the subsidiary cells.

DISCUSSION. *Athrotaxis ungeri* differs from all other conifers described in this paper. It resembles *Brachyphyllum* in the shape of its leaves and in their spiral arrangement on the branch, but the leaves differ in size and the cuticular structure is quite different. This species cannot be included in the genus *Brachyphyllum* as modified by Kendall (1947), because the stomata never form rows and are almost completely absent from the abaxial cuticle.

A. ungeri can be compared with the living *Athrotaxis*. The leaves are the same shape and size as those of *A. cupressoides*, but they differ from the other two species of this genus. In this species, as in ours, the leaves are closely adpressed to the branches. The cuticular structure of *A. cupressoides* also has some similarities with that of *A. ungeri*: the lower cuticle is thicker than the upper and the epidermal cells are similar in shape. Furthermore, in the basal part of the leaf, each cell bears a single strongly marked papilla. The stomata never form longitudinal rows in either species and neither species has stomata on the abaxial sides of the distal $\frac{2}{3}$ of the leaf. The only difference between them is that while there are just a few stomata on the abaxial side of the proximal $\frac{1}{3}$ of the leaf in *A. ungeri*, there are a good many in *A. cupressoides*. The stomata of the two species appear to be very similar.

Many other conifers (*Juniperus chinensis*, *Cupressus sempervirens*, *Diselma archeri*, *Microbiota decussata* and *Chamaecyparis pisifera*) have a similar stomatal arrangement (few on the lower cuticle, mainly near the base). They all belong to the Cupressaceae which have a different leaf arrangement from that of *A. ungeri* (opposite, not spiral) and their stomatal apparatus is also rather different. *Microcachrys tetragona* (Podocarpaceae) should also be mentioned as having a similar arrangement of stomata but with a different leaf arrangement, stomatal apparatus and shape of epidermal cells.

Thus although various Recent conifers match the fossil in certain respects they differ in others, and *Athrotaxis cupressoides* is the only species that agrees in all respects—the arrangement and shape of the leaves and in the various features of the cuticles.

The present material agrees with that described by Halle (1913) from Río de los Fósiles, Santa Cruz Province, Argentina, of probable Lower Cretaceous age. The leaves are similar in arrangement, size and shape (the Ticó specimens are somewhat acute as in Halle's pl. 2, fig. 11, rather than as in some of his other figures). Un-

fortunately Halle's specimens have lost their cuticles, but they possess female cones similar to those of *A. cupressoides*. I was able to examine this material in the Stockholm Riksmuseum and I agree with Florin's interpretation, that it is closely similar to *A. cupressoides* (Florin, 1940).

The fossils from Lago San Martín are probably the same age as those from Ticó. The presence of the genus *Athrotaxis* in Upper Mesozoic floras of Patagonia, based on leaf cuticles, is another factor in favour of correlating both floras. The area between Lago San Martín and Ticó has not yet been thoroughly surveyed. There are some scattered references (Piatnitzky, 1938 : 64) about the finding of *Athrotaxis* near Lago Cardiel, but this should be verified by a more detailed survey of this extensive area.

Genus *TOMAXELLIA* nov.

DIAGNOSIS. Shoots of ultimate order bearing leaves spirally arranged, persistent, spreading, acicular, rhomboidal in section, acute at their apices, slightly decurrent at the base, amphistomatic, margins entire. Leaf cuticles thick. Cell walls straight, cell surface not papillose ; trichomes absent. Stomata widespread on abaxial cuticle, but avoiding margins, present on lower angle, not arranged in definite bands and forming ill-defined rows. Stomata on decurrent part of abaxial side irregularly distributed, not forming bands or rows. Stomata on adaxial cuticle, at base, forming ill-defined bands, then spread over whole surface, including median angle and lateral margins. Stomata present near apex, irregularly spaced, obliquely or longitudinally orientated, rarely transversely, sometimes side by side, never sharing subsidiary cells, haplocheilic and typically monocyclic or imperfectly dicyclic, with guard cells slightly sunken, surrounded by 4-5 subsidiary cells not well differentiated into polar and lateral. Subsidiary cells thickened near mouth of pit, with ridges parallel to margins of pit. Encircling cells sometimes with similar ridges. Anticlinal walls of subsidiary and encircling cells strongly cutinized. Hypodermal cells markedly elongated, cutinized.

TYPE SPECIES. *Tomaxellia degiustoi* sp. n.

DISCUSSION. *Tomaxellia* is a coniferous genus unrelated to the living and fossil Taxopsida. It can only be compared with some living genera belonging to the Podocarpaceae, Taxodiaceae, and in some degree to the Araucariaceae. It bears no relation or similarity to any other family of the Coniferales.

Similar genera belong to the Taxodiaceae, which have amphistomatic leaves, with four definite bands of stomata that are not arranged in definite rows but are indistinctly orientated. Some genera of this family have leaves similar in shape, size and insertion (*Cryptomeria* and *Athrotaxis*) but in these two genera the cuticular structure is rather different from that of *Tomaxellia*. On the other hand, some conifers having similarities with *Tomaxellia* in cuticular structure, have leaves of a different shape (*Taxodium*, *Sequoia sempervirens*). *Sequoia gigantea* (*Sequoiadendron*) has similar leaves, but the stomata, which agree in that they are arranged in definite rows and are widely scattered as in *Tomaxellia*, usually form rather definite bands. In this respect *Tomaxellia* also differs from *Araucaria*, in which the stomata are always aggregated in compact rows, but certain species of *Araucaria* have leaves

of similar shape as well as similar stomatal apparatus. *Agathis*, on the other hand, has leaves of a different shape and a different cuticular structure.

All genera in the family Podocarpaceae differ from *Tomaxellia* in the shape of their leaves, with the exception of some species of *Dacrydium* which agree with *Tomaxellia* in the size, shape and disposition of leaves on the branches. They differ, however, from *Tomaxellia* in that the stomata form definite bands and are often arranged in rows. The stomata are longitudinally orientated and their details are rather different.

Bellarinea Florin (1952 : 179) is a Jurassic genus from Australia which resembles some living *Podocarpus* of the section *Stachycarpus*. *Tomaxellia* differs from *Bellarinea* in many respects. Its leaves are spirally disposed but not expanded in one plane. In *Bellarinea* the leaves are hypostomatic while in *Tomaxellia* they are amphistomatic. The stomatiferous bands are much more marked in the Australian genus than in ours.

Of the fossil Taxodiaceae, *Elatides*, as defined by Harris (1953) is similar to *Tomaxellia* in leaf shape. The differences lie in the bands of stomata and in their orientation, usually transverse in this genus. Also, the pits of the stomata are rectangular in shape, while those in *Tomaxellia* are always oval.

Sphenolepis, another member of the fossil Taxodiaceae, differs from *Tomaxellia* in the shape of leaves (scale-like), in their hypostomatic condition, and in the stomata which do form bands, are transversely elongated and typically monocyclic.

The fossil genus *Elatocladus* is a comprehensive and unnatural one. It includes many species which differ from *Tomaxellia* in being mainly hypostomatic. The few amphistomatic species of *Elatocladus* are very different from *Tomaxellia* in their stomatal apparatus and general epidermal structure.

The only known Taxodiaceae from the Mesozoic floras of Patagonia (with the exception of *Athrotaxis ungeri*) is *Pararaucaria patagonica* Wieland from the Matilda Formation of Santa Cruz Province, the age of which is Middle to Upper Jurassic. It is based on a female cone related to *Cryptomeria* and *Taiwania* on the one hand, and the most typical Taxodiaceae on the other (Calder, 1953). It could well be that *Tomaxellia* is related to *Pararaucaria*; there is no great difference either in age or locality.

As far as I am aware, *Tomaxellia* differs from all other Jurassic or Lower Cretaceous conifer genera which have been described with their cuticles. On the evidence available no definite relationship between *Tomaxellia* and the Taxodiaceae, Podocarpaceae or Araucariaceae can be maintained.

The genus is dedicated to Professor Thomas Maxwell Harris of Reading University, England.

Tomaxellia degiustoi sp. n.

(Pl. 7, figs. 39, 40 ; Pl. 8, figs. 58-60 ; Pl. 11, Pl. 12, fig. 79 ; Text-figs. 72-74)

DIAGNOSIS (Plant known only from isolated and fragmentary branches). Ultimate (?) branches, 1-2 mm. in diameter, bearing spirally attached leaves of probably 2/5 phyllotaxis. Leaf cushions small, oval or rhomboidal, 2 mm. long \times 1 mm.

broad. Leaves long and narrow, slightly decurrent, almost acicular, typically 1 cm. long \times 1-1.5 mm. wide and 1.5 mm. thick, ending with acute apex, pointing forward and projecting towards the stem. Free part of leaf rhomboidal in transverse section but upper and lower angles somewhat rounded, and in middle region of leaf, lower angle bearing wide short papillae. Lateral angles sharp, entire.

Cuticle thick, up to 8 μ . Stomata present on both cuticles. On decurrent part, stomata irregularly distributed, not forming rows or bands. Towards the middle part of leaf, on abaxial cuticle, stomata forming irregular bands. On adaxial cuticle, irregular bands sometimes marked from the base. On lower cuticle, stomata markedly avoiding margins (lateral angles) leaving a non-stomatiferous band sometimes more than 10 cells wide. Median region (lower angle) with 2-3 narrow and markedly elongated rows of cells, sometimes with 1 or 2 bands of strongly cutinized cells which may bear short and round single papillae. When two of these bands are present, very elongated stomata can be found between (i.e. actually on the lower angle). On upper cuticle stomata indistinctly present near margins or median region. On apical part stomata becoming fewer but reaching apex. Bands ill-defined, sometimes marked up to near apex. Stomata typically obliquely or longitudinally orientated, sometimes transversely. Stomata in bands sometimes forming ill-defined rows separated by typically 2-4 rows of elongated rectangular cells. Stomata when in a row, usually separated, sometimes having their lateral encircling cells in contact (in oblique or transverse stomata) but never sharing subsidiary cells.

Epidermal cells located on same rows as stomata, usually elongated in longitudinal or transverse direction, rarely isodiametric. Epidermal cells between stomatiferous rows, bands and on margins, elongated, rectangular, typically 60-100 μ long \times 15 μ wide. Near leaf apex, epidermal cells unpitted, flat, but with low median ridge, sometimes with extensions towards corners of cells, and often with faint longitudinal striae. Lateral and end walls of cells straight, strongly marked, unpitted, without borders.

Stomata similar on both cuticles, typically monocyclic or imperfectly dicyclic, rarely perfectly dicyclic. Stomatal apparatus usually oval, rarely circular (never rectangular). Guard cells slightly sunken in oval pit, very feebly cutinized, surrounded by typically 4-5 subsidiary cells. Subsidiary cells small and inconspicuous in dicyclic stomata, larger in monocyclic, with their anticlinal walls strongly cutinized. Polar and lateral subsidiary cells not well differentiated. Mouth of pit oval. Subsidiary cells and sometimes encircling cells with one or more ridges parallel to mouth of pit.

Hypodermal cells cutinised, markedly elongated.

HOLOTYPE.—LIL PB n. 2542(b). The same specimen as *Rufloflorinia sierra*.

MATERIAL.—In addition to the holotype, Brit. Mus. (Nat. Hist.) no. V.44661. Slides: LIL 229-232.

DESCRIPTION.—This species comes from the *Ticoa harrisii* bed. It is not as common as the other two conifers described from the same bed (*Brachyphyllum brettii*, *B. mucronatum*). The two specimens so far available are fragmentary. In the matrix, however, detached leaves are often found. The leaves are long, almost acicular, somewhat falcate. The cuticle of the leaves is well preserved. The lower

cuticle is always wider than the upper, making the leaf kite-shaped in section. Both cuticles have a median longitudinal zone where they fold, having thus 4 definite areas. On the lower cuticle, this median fold is always marked by a band of strongly cutinized cells which do not occur on the upper cuticle. The shape of the leaf may have been somewhat similar to the living *Cryptomeria japonica*, *Araucaria columnaris*, *Dacrydium balansae* and *D. araucarioides*.

In no case was there any indication of a sharply marked stomatiferous band. On the upper cuticle the stomata are dispersed and very seldom form rows. On the lower cuticle the two non-stomatiferous bands are obvious near the margins. On the rest of the lamina the stomata have the same arrangement as on the upper cuticle.

The interpretation of the stomata is not easy, because there are numerous ridges on the subsidiary and encircling cells which can be confused with cell walls. However, using the phase contrast microscope, it was possible to distinguish between the true cell walls and the ridges. The anticlinal walls of subsidiary cells are strongly cutinized and often have the same thickness as the ridges present on the cell surface.

The leaves of *Tomaxellia degiustoi* are somewhat similar in shape and arrangement to those of some living Araucariaceae, Taxodiaceae and Podocarpaceae, for example *Araucaria columnaris* and *A. excelsa*. *Tomaxellia* differs from them, however, in the distribution of stomata. In *Araucaria* the stomata are not arranged in bands, they are crowded in definite rows.

The arrangement of stomata in 4 definite bands is characteristic of most Taxodiaceae; this feature is not shared by *Tomaxellia degiustoi* in which the stomatal rows are ill-defined. However, our genus is closer to the Taxodiaceae than to any other family, because in neither do the stomata form definite rows but are indefinitely orientated. In both Araucariaceae and Taxodiaceae the stomata tend to be crowded (dense), while in *Tomaxellia* they are markedly spaced.

In the Podocarpaceae, *Dacrydium balansae* and *D. araucarioides* from New Caledonia, are comparable to *Tomaxellia* in shape and size of leaves (the long leaved forms). The individual leaves are, however, somewhat more falcate. In both species, the leaves are amphistomatic, but in *D. araucarioides* the stomatiferous bands on the lower cuticle are ill- or not at all defined, and are only present on the decurrent part of the epidermis and a short way up the lamina. In addition the stomata are orientated longitudinally. In *Dacrydium gibbsiae* from Borneo, the stomata on the upper epidermis do not form bands, but longitudinal rows, reaching to the apical part of the leaf. On the lower epidermis stomata are present only on the basal part where they form short rows. All stomata are longitudinally orientated. The size and shape of leaves are comparable with *Tomaxellia* but they are more crowded on the branch.

The stomatal apparatus of *Tomaxellia* is comparable to some species of *Araucaria*, in being partially dicyclic; but the guard cells in *Araucaria* are usually more sunken. Strong ridges on subsidiary cells and encircling cells present in *Tomaxellia* are not common in *Araucaria*. In the Taxodiaceae, a comparable stomatal apparatus is found in *Sequoia sempervirens* and *S. gigantea* (*Sequoiadendron*) but with no marked

ridges on subsidiary cells as in *Tomaxellia*. The stomal apparatus of most *Dacrydium* species is rather different. There is a marked tendency for polar subsidiary cells to be differentiated from lateral ones and often the polar cells of two neighbouring stomata are in contact or are shared one per two adjacent stomata. In *Tomaxellia* the polar and lateral subsidiary cells of stomata are not differentiated. Furthermore, the ridges parallel to the pit are strongly developed. Such ridges do not appear to be present in the living species of *Dacrydium*.

As far as comparison with fossil genera goes, some features are shared with *Elatides williamsoni*. The size, shape and insertion of leaves are similar. The cuticle of *E. williamsoni* is much thinner and has definite bands of stomata, while no such bands exist in *Tomaxellia*. In both species the stomata are irregularly orientated. *Elatides bommeri* Harris (1953) has smaller leaves which have stomata only on one side (adaxial), forming two bands. The stomata of this species are usually transversely orientated.

Comparing *Tomaxellia* with fossil species of *Elatocladus* with their cuticles preserved, one almost constant feature is the hypostomatic condition of the latter species. *E. areolatus* Florin (1958) from the Jurassic of Yorkshire is amphistomatic and the very few stomata on the upper side appear to be functionless. There are also other differences such as the papillae present on the epidermal cells, and sometimes wavy walls of cells. The stomatal apparatus is also different.

Harris (1935) described several species of *Elatocladus* from East Greenland, three of them being amphistomatic. The stomatal apparatus of these species is quite different from that of *Tomaxellia*.

The specimens described as *Elatocladus heterophylla* Halle by Menéndez (1956) from the Jurassic of Neuquén, Argentina, have smaller leaves than those of *Tomaxellia* and they are closer to the shoot. There is no information about the stomata. The typical forms of this species were described by Halle (1913) from Graham Land. They are preserved as impressions. I have re-examined all Halle's specimens and the one most similar to our species is figured in his pl. 8, fig. 22a. There is no difference in shape and size of leaves of the two species, but in Halle's specimen the leaves are expanded in one plane as in many species of the living genus *Podocarpus* whilst in *Tomaxellia*, the leaves are directed towards all sides. It is interesting to note that Florin (1940) considers that all *Elatocladus* species described by Halle have Podocarpaceous affinities. *Elatocladus* has definitely dimorphic leaves. Although our material is very fragmentary, in none of the fragments, nor in the numerous detached isolated leaves is there any indication whatsoever that *Tomaxellia* has dimorphic leaves.

The species is dedicated to Dr. José M. de Giusto, geologist of the National Oil Company (YPF).

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PLATE I

Ticoa magnipinnulata sp. n.

FIG. 1. Holotype. (LIL 2540.) $\times 1$.

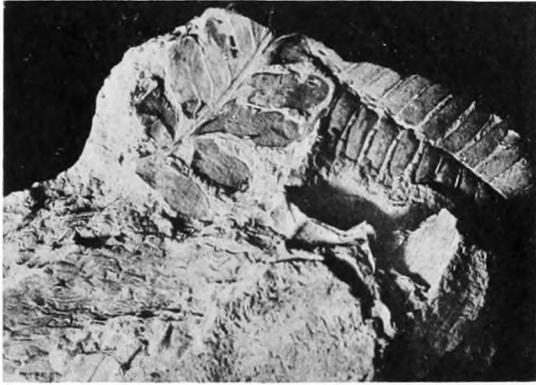
FIG. 3. Upper cuticle of a pinnule showing only trichome bases and no stomata. (Slide LIL 165.) $\times 17.5$.

FIG. 4. Lower cuticle of rachis and bases of three pinnules. Non-stomatiferous bands with trichome bases correspond to veins. Stomata seen as conspicuous black dots. (Slide LIL 166.) $\times 15$.

Ticoa harrisii gen. et sp. n.

FIG. 2. Two pinnae and rachis showing the two compressed flanges. (Slide LIL 164.) $\times 3$.

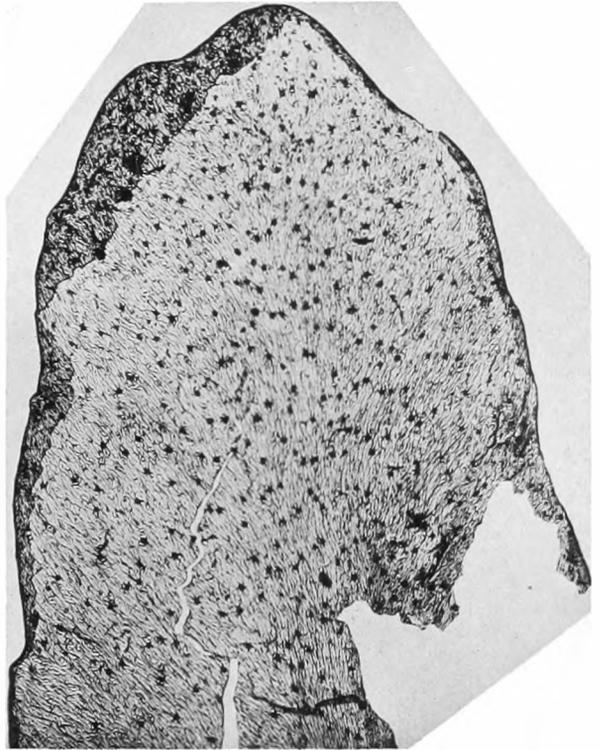
FIG. 5. Lower cuticle of a pinna showing the non-stomatiferous bands (veins) and the general distribution of stomata and trichome bases. (Slide LIL 161.) $\times 15$.



1



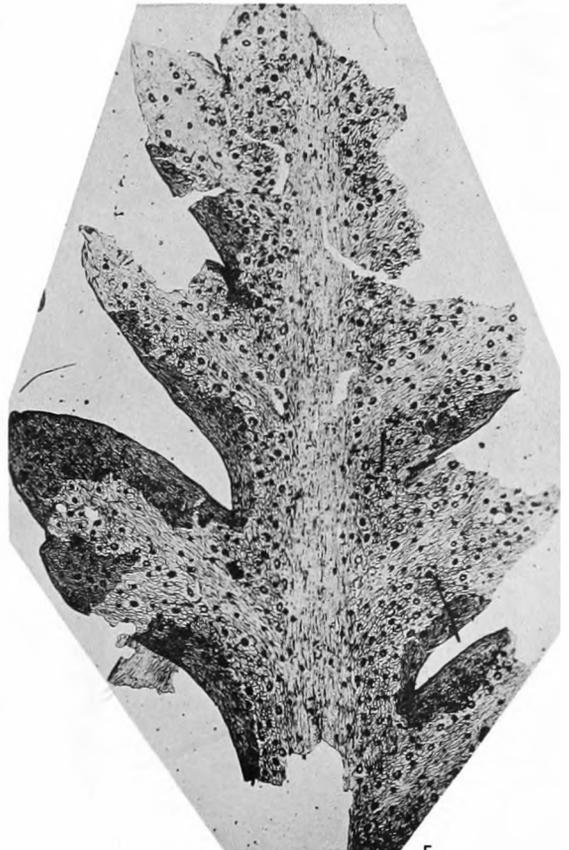
2



3



4



5

PLATE 2

Ticoa magnipinnulata sp. n.

FIG. 6. Lower cuticle showing stomatiferous bands (stomata seen as conspicuous black dots). (Slide LIL 167.) $\times 15$.

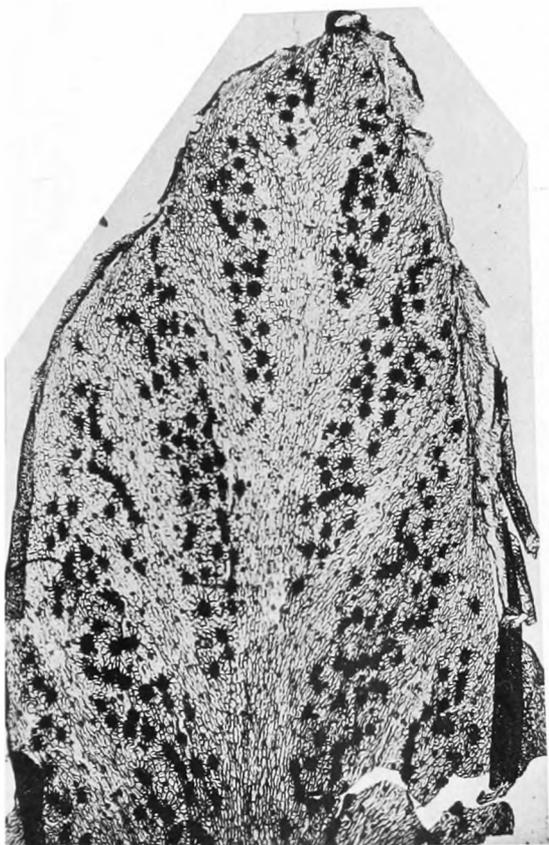
Ticoa harrisii gen. et. sp. n.

FIG. 7. Upper and lower cuticles of two pinnules. Above (upper cuticle) only bases of trichomes are seen. (Slide LIL 160.) $\times 40$.

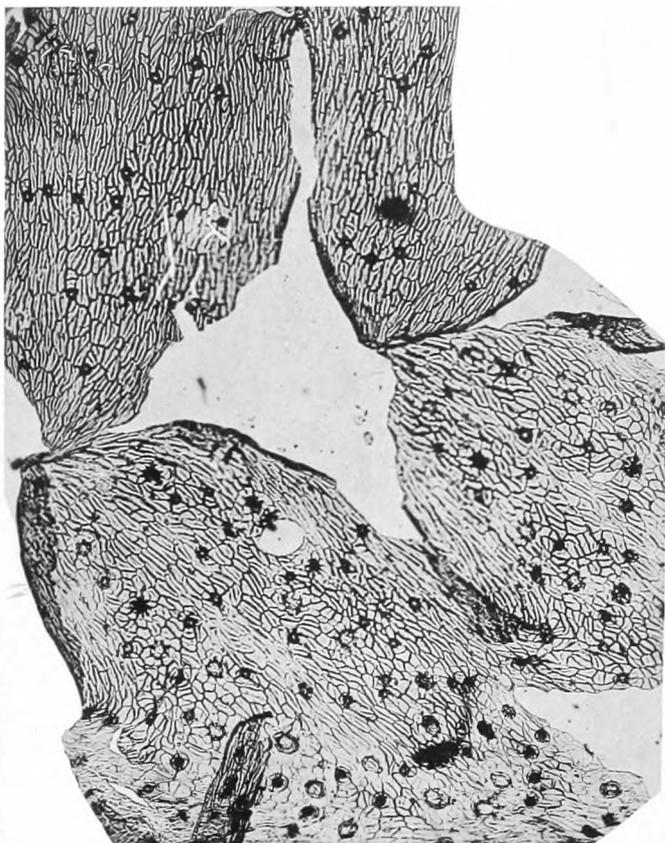
Ruflovinia sierra gen. et sp. n.

FIG. 8. Lower cuticle showing patches of stomata. (Slide LIL 171.) $\times 40$.

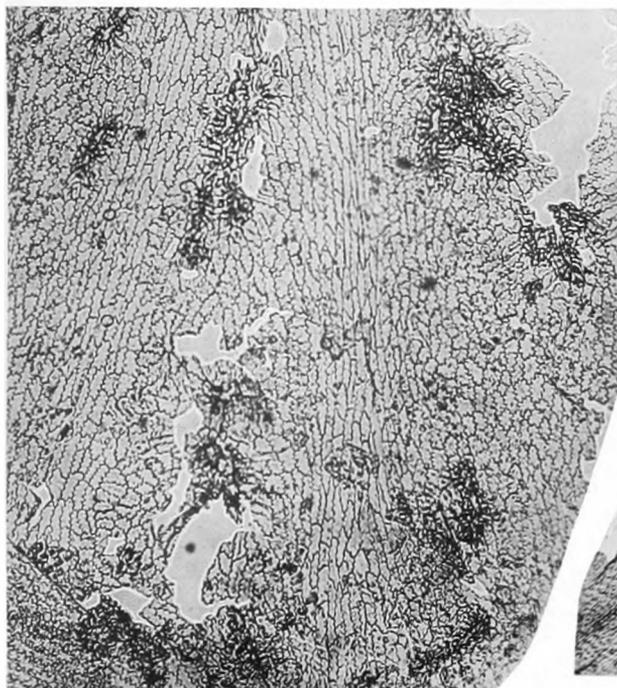
FIG. 9. Lower cuticle showing rachis and decurrent pinnules. Bands of stomata can be seen. (Slide LIL 170.) $\times 15$.



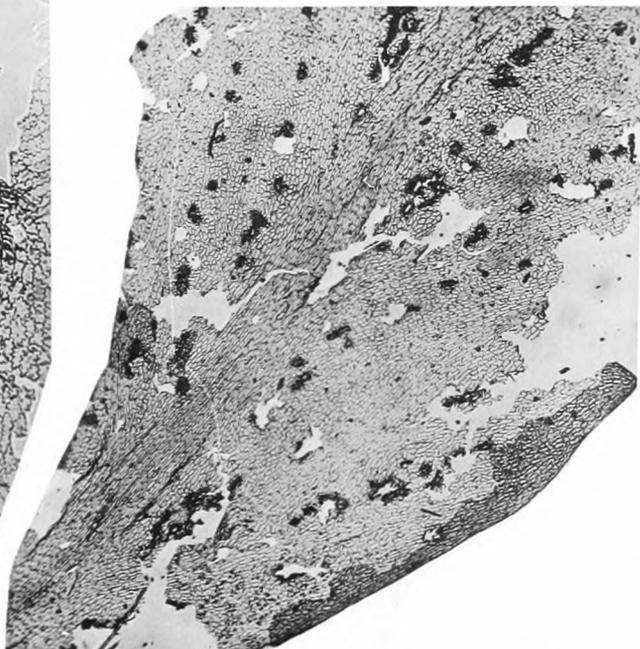
6



7



8



9

PLATE 3

Mesosingeria coriacea gen. et sp. n.

FIG. 10. Upper and lower cuticles ; the lower (left) with stomata. (Slide LIL 173.) ×40.

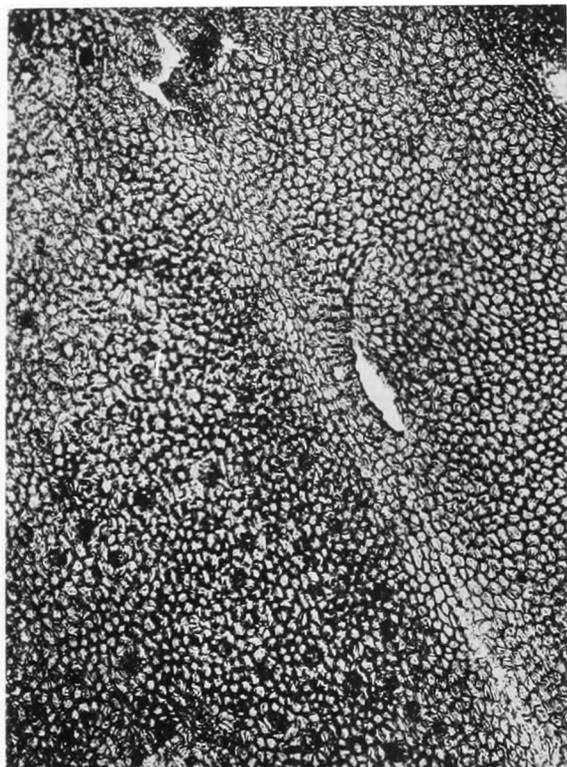
Mesosingeria herbstii sp. n.

FIG. 11. Upper and lower cuticles ; lower cuticle (left) having more stomata than upper. (Slide LIL 175.) ×40.

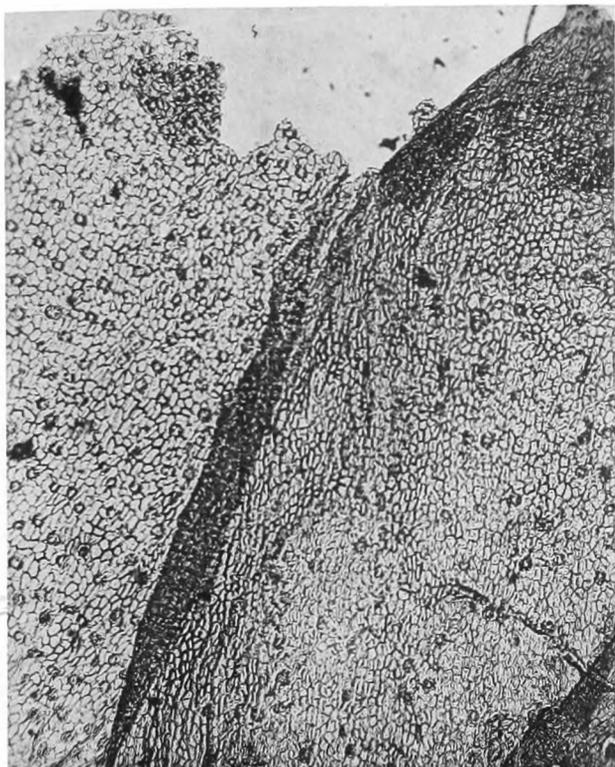
Mesodescolea plicata gen. et sp. n.

FIG. 12. Lower cuticle showing stomata. (Slide LIL 177.) ×200.

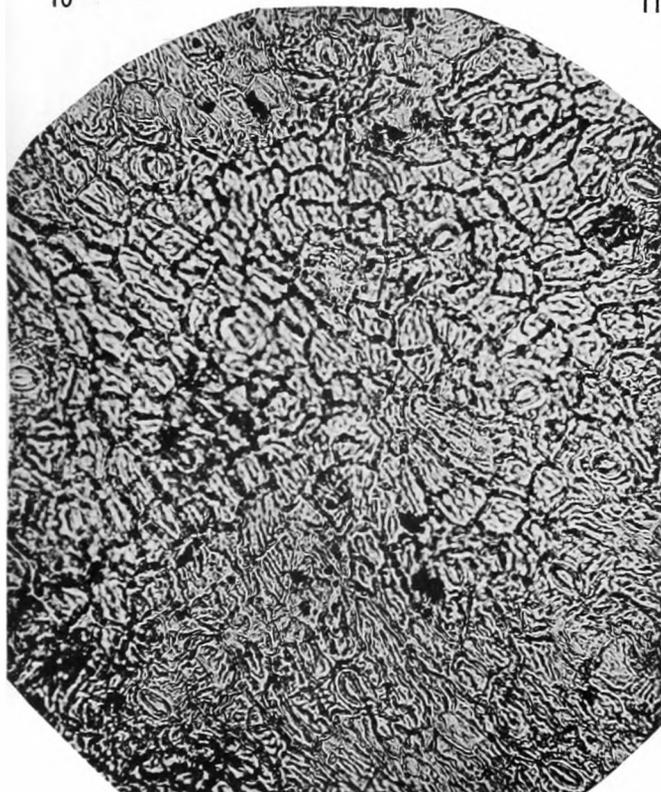
FIGS. 13, 14. Upper cuticle with no stomata. (Slide LIL 178.) ×200.



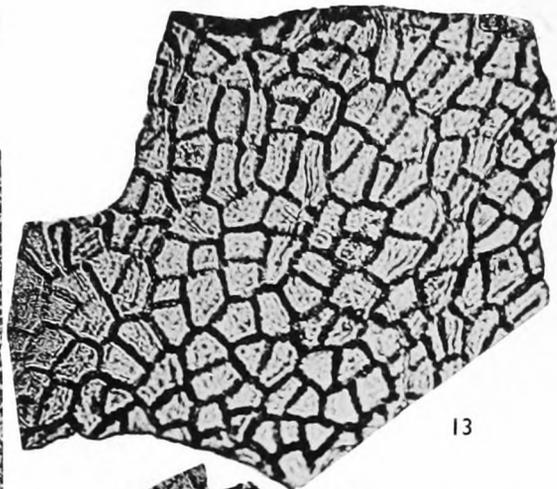
10



11



12



13



14

PLATE 4

Ticoa harrisii gen. et sp. n.

FIGS. 15, 16. Lower cuticle. Stoma focused at two different levels to show mouth of pit (Fig. 15) and guard cells (Fig. 16). (Slide LIL 160.)

FIG. 20. Lower cuticle showing base of a trichome. (Slide LIL 160.)

Ticoa magnipinnulata sp. n.

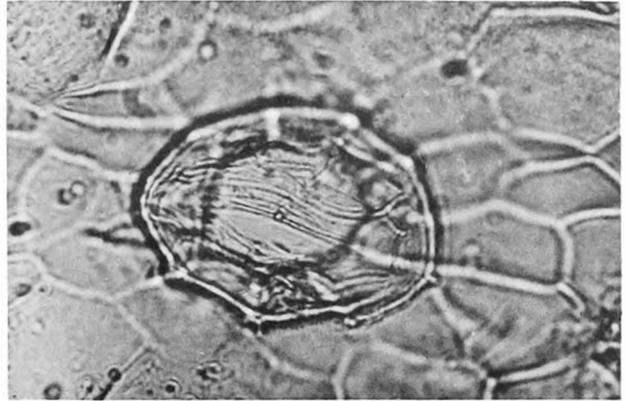
FIGS. 17, 18. Lower cuticle. A stoma focused at two different levels to show mouth of pit (Fig. 17) and guard cells (Fig. 18). (Slide LIL 167.)

FIG. 19. Lower cuticle. Stoma focused at a level between mouth of pit and guard cells, showing several cycles of subsidiary cells. (Slide LIL 167.)

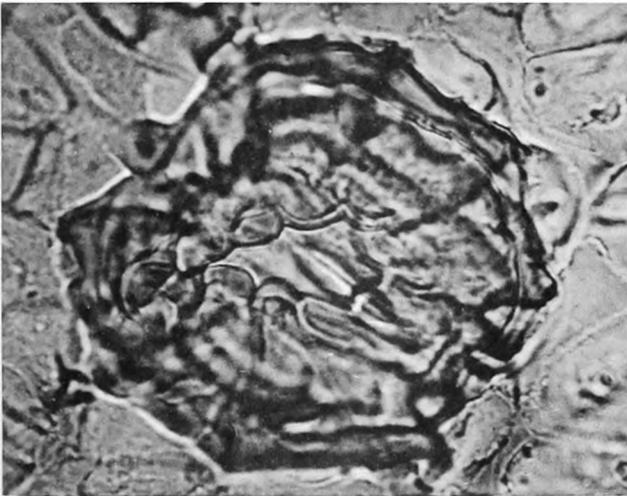
All $\times 500$.



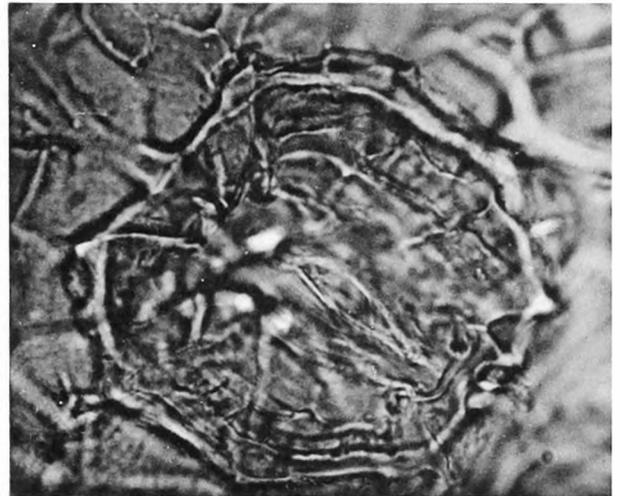
15



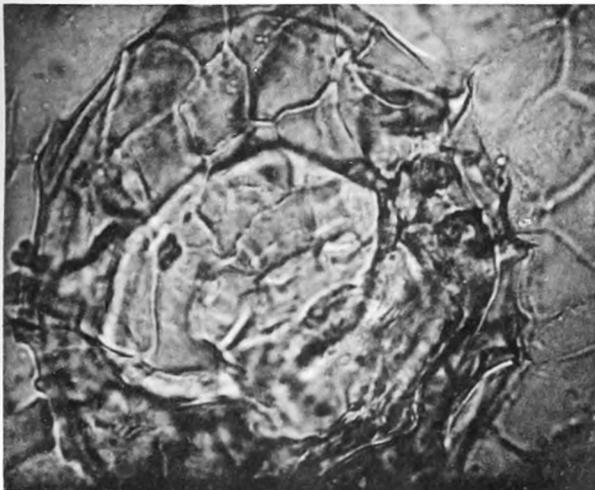
16



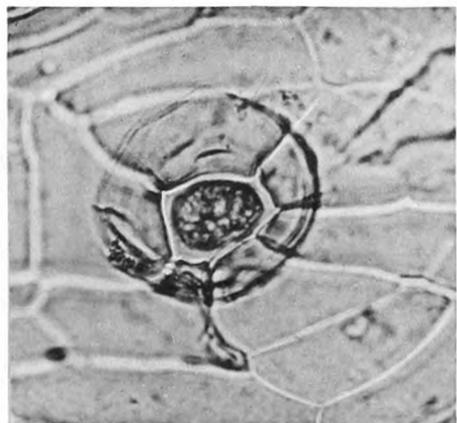
17



18



19



20

PLATE 5

Ruflofloria sierra gen. et sp. n.

FIG. 21. Lower cuticle. Stoma showing papilla-like projections over mouth of pit. (Slide LIL 170.) × 500.

Mesosingeria coriacea gen. et sp. n.

FIGS. 22, 23. Lower cuticle. Stoma focused at two different levels showing the mouth of pit and the guard cells slightly out of focus (Fig. 22) and the rim of cutin at the uppermost level (Fig. 23). (Slide LIL 173.) × 600.

Mesodescolea plicata gen. et sp. n.

FIG. 24. Lower cuticle. Stoma with oval rim of cutin. (Slide LIL 177.) × 600.

FIG. 25. Lower cuticle. Trichome base showing strong radiating striae. (Slide LIL 177.) × 600.

Mesosingeria herbstii sp. n.

FIG. 26. Lower cuticle. Stoma showing mouth of pit and, slightly out of focus, the rim of cutin projecting outwards. (Slide LIL 175.) × 500.

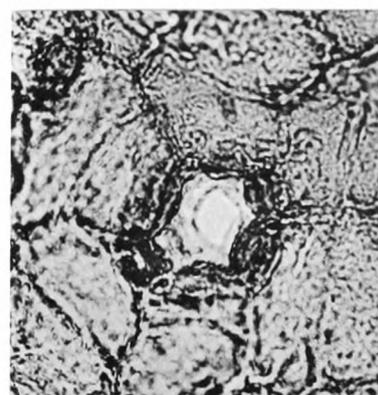
FIG. 27. Lower cuticle. Two hairs. (Slide LIL 175.) × 500.



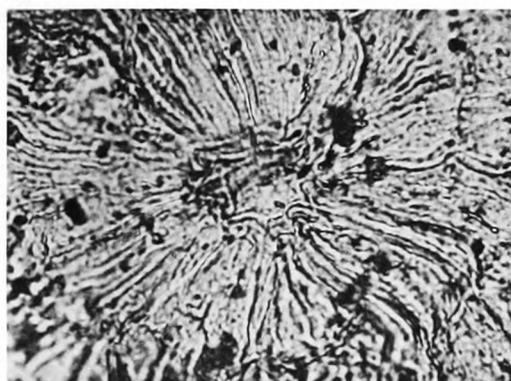
21



24



26



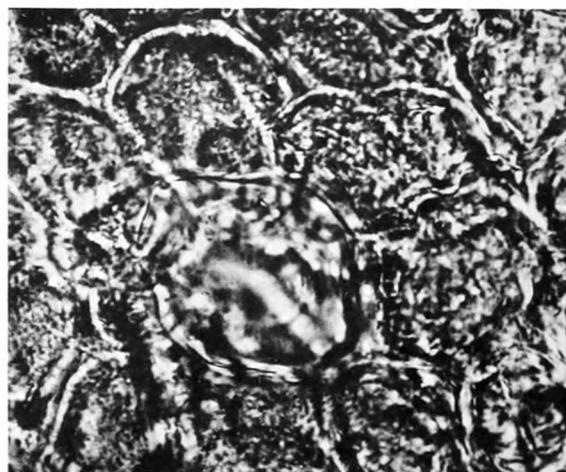
25



22



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23

PLATE 6

Ktalenia circularis gen. et sp. n.

FIG. 28. General aspect of the holotype. (Slide LIL 181.) $\times 15$.

FIG. 29. Seed showing nucellus and integument membranes. At bottom chalaza and at top micropilar canal. (Slide LIL 182.) $\times 15$.

FIG. 30. Seed showing nucellus membrane. At the bottom, chalaza (black). At the top, micropilar canal (somewhat obliterated) and integument membrane. (Slide V.44687.) $\times 15$.

FIG. 31. Magnification of Fig. 29 showing the top of the nucellus with cutinized micropilar canal and integument membrane. $\times 60$.

FIG. 32. Circular bodied inside cuticle of nucellus, probably oily endosperm. (Slide LIL 183.) $\times 60$.

FIG. 33. Cuticle of the fruit wall showing an opening. (Slide LIL 182.) $\times 40$.

Tomaxellia degiustoi gen. et sp. n.

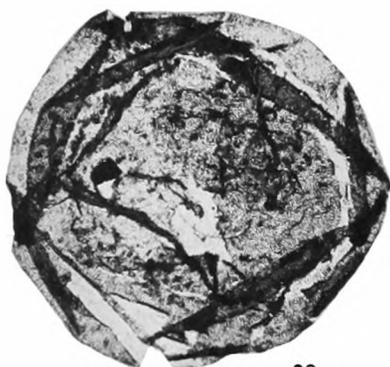
FIG. 34. Median part of leaf showing the longitudinal division in four sectors. The dark longitudinal band on the lower left corresponds to a strong cutinized ridge separating the two sectors of the lower cuticle. (Slide LIL 229.) $\times 40$.

Athrotaxis ungeri (Halle)

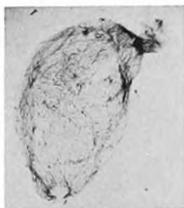
FIG. 35. General aspect of a leaf showing dentate margins, some papillae on the base and a portion of the upper cuticle at the top. (Slide LIL 228.) $\times 40$.

Mesosingeria herbstii gen. et sp. n.

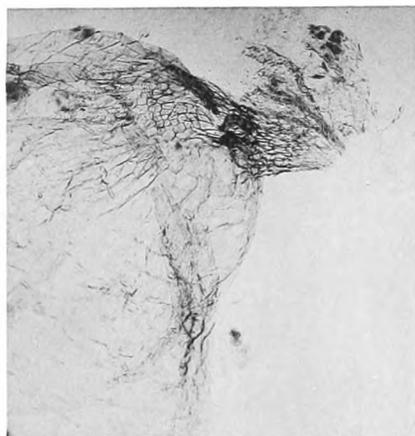
FIG. 36. Lower cuticle showing stoma. The opening of the slender cutin rim projecting upwards is seen. On a lower level, the mouth of the pit is also seen. (Slide LIL 175.) $\times 600$.



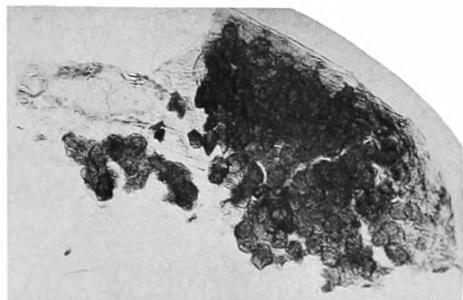
28



29



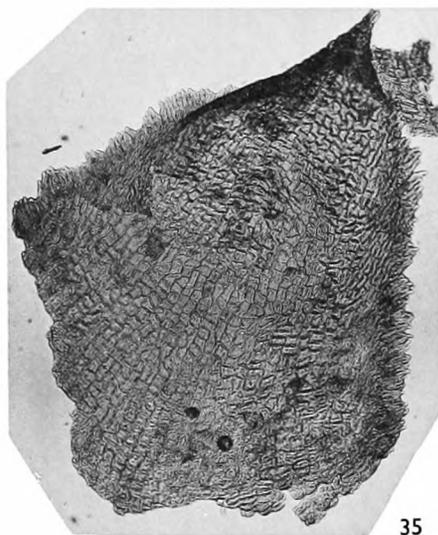
31



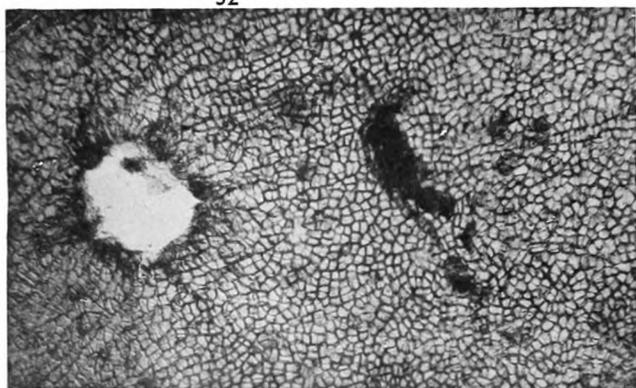
32



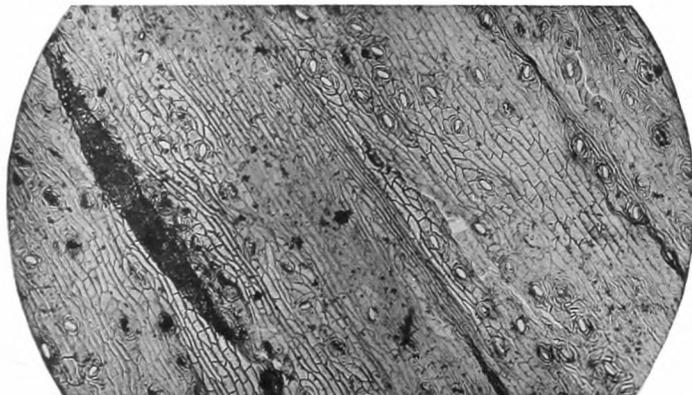
30



35



33



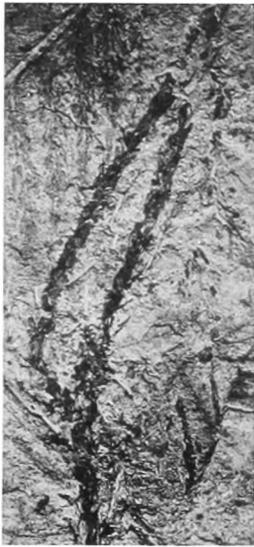
34



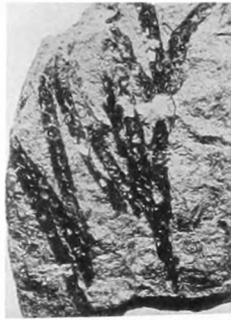
36

PLATE 7

- FIG. 37. *Brachyphyllum brettii* sp. n. A branched twig. V.44686. ×1.
FIG. 38. *Brachyphyllum brettii* sp. n. Holotype. (LIL 2565.) ×1.
FIG. 39. *Tomaxellia degiustoi* gen. et sp. n. Fragmentary twig. V.44661. ×1.
FIG. 40. *Tomaxellia degiustoi* gen. et sp. n. Holotype. (LIL 2542.) ×1.
FIG. 41. *Brachyphyllum mirandai* sp. n. Holotype. (LIL 2560.) ×1.
FIG. 42. *Athrotaxis ungeri* (Halle). General aspect of small fragmentary twigs. (LIL 2563.)
×1.
FIG. 43. *Brachyphyllum mucronatum* sp. n. Holotype. (LIL 2569.) ×1.
FIG. 44. *Brachyphyllum irregulare* sp. n. General aspect of fragmentary twigs. (LIL 2579.)
×1.
FIG. 45. Male cone. Longitudinal compression. (LIL 2562.) ×3.
FIG. 46. Pollen grain. (Slide LIL 221.) ×1000.



37



38



39



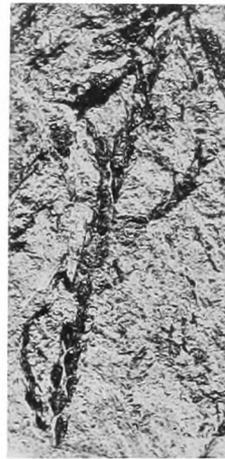
41



42



40



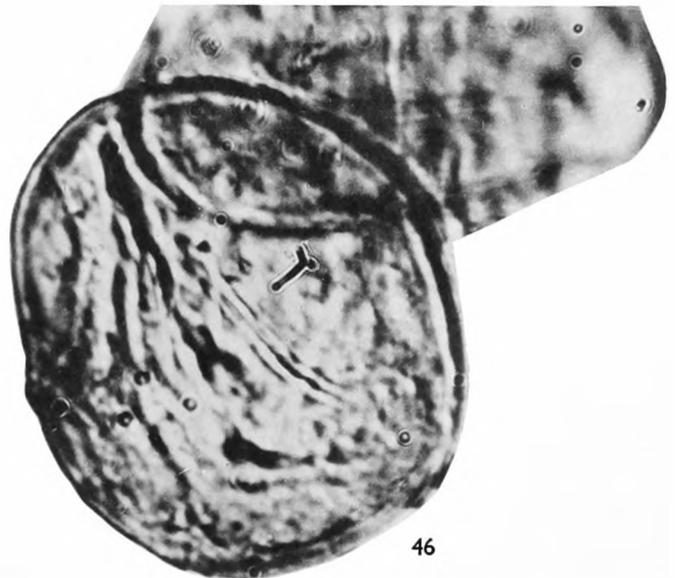
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46

PLATE 8

FIGS. 47-49. *Brachyphyllum brettii* sp. n. Small leaves. (Slide LIL 188.) $\times 8$.

FIG. 50. *Brachyphyllum brettii* sp. n. A large leaf. (Slide LIL 186.) $\times 8$.

FIGS. 51, 52. *Brachyphyllum mucronatum* sp. n. Leaves of normal size. (Slide LIL 200.) $\times 8$.

FIGS. 53, 54. *Brachyphyllum mirandai* sp. n. Small and normal leaves. (Slide LIL 215.) $\times 8$.

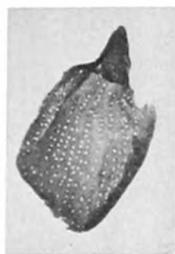
FIG. 55. *Brachyphyllum mirandai* sp. n. A large leaf. (Slide LIL 216.) $\times 8$.

FIGS. 56, 57. *Brachyphyllum irregulare* sp. n. Leaves of normal size. (Slide LIL 225.) $\times 8$.

FIG. 58. *Tomaxellia degiustoi* gen. et sp. n. Complete leaf showing the longitudinal division into four parts. (Slide LIL 229.) $\times 9$.

FIG. 59. *Tomaxellia degiustoi* gen. et sp. n. Complete leaf showing irregular distribution of stomata in the decurrent part of lower cuticle. (Slide LIL 232.) $\times 8$.

FIG. 60. *Tomaxellia degiustoi* gen. et sp. n. Leaf showing stomatiferous bands in the middle and top of lamina. (Slide LIL 229.) $\times 9$.



47



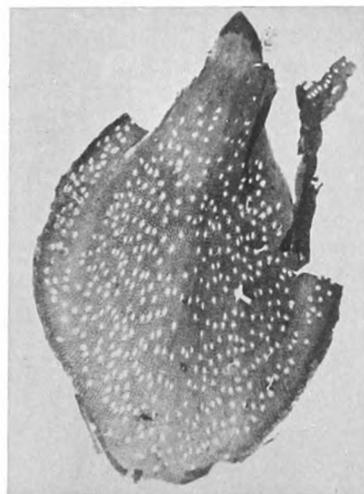
48



49



50



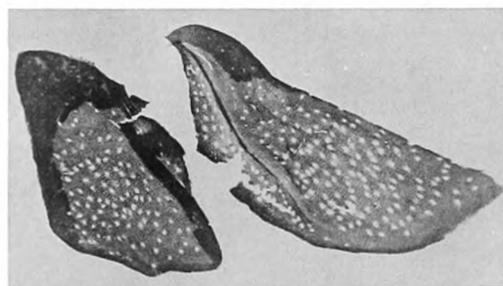
55



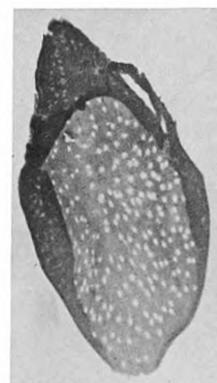
51



52



53



54



58



56



60



59



57

PLATE 9

Brachyphyllum mirandai sp. n.

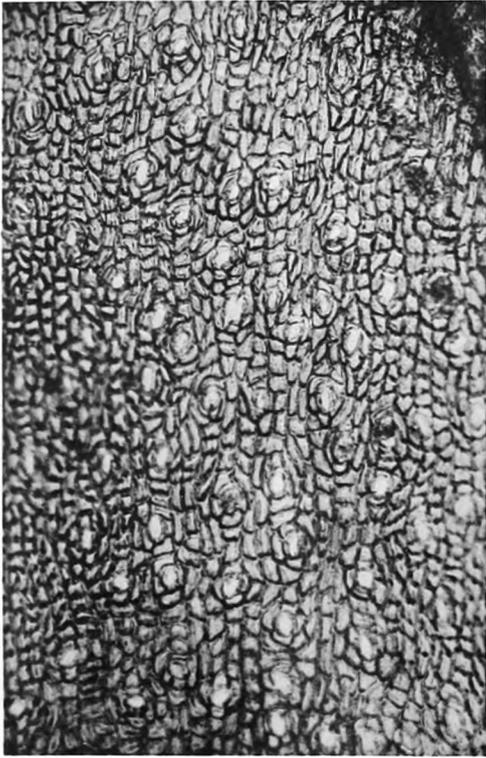
FIG. 61. General aspect of lower cuticle showing distribution of stomata. (Slide LIL 215.)
× 50.

FIG. 62. Leaf margin showing elongated marginal cells. (Slide LIL 215.) × 500.

Brachyphyllum brettii sp. n.

FIG. 63. Apical part of leaf showing the marginal elongated cells along the whole length of upper cuticle. (Slide LIL 195.) × 50.

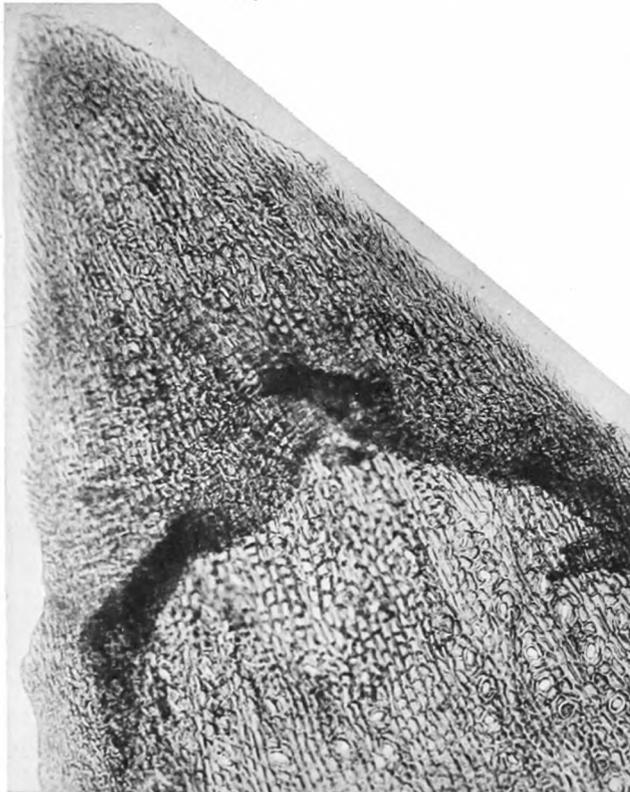
FIG. 64. General aspect of lower cuticle showing distribution of stomata tending to form longitudinal rows. (Slide LIL 188.) × 50.



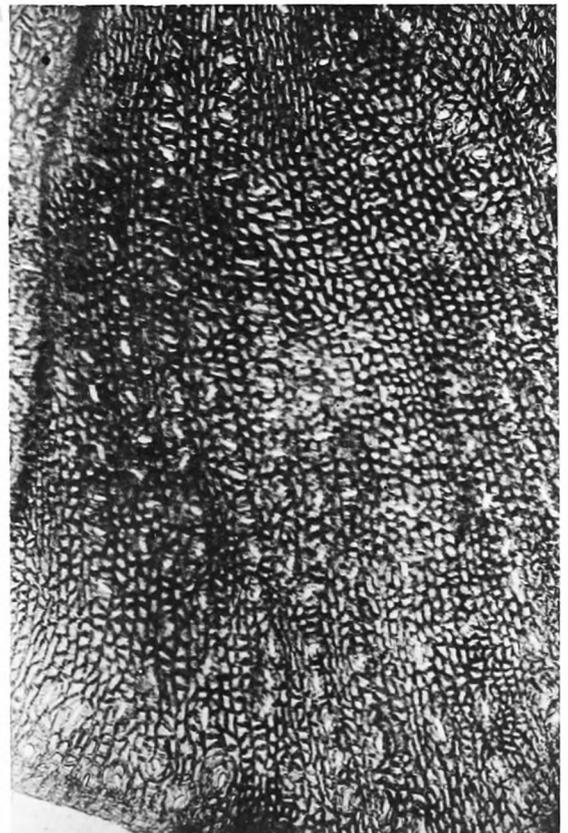
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62



63



64

PLATE 10

Brachyphyllum irregulare sp. n.

FIG. 65. General aspect of lower cuticle showing distribution of stomata. (Slide LIL 225.)
× 50.

Brachyphyllum mucronatum sp. n.

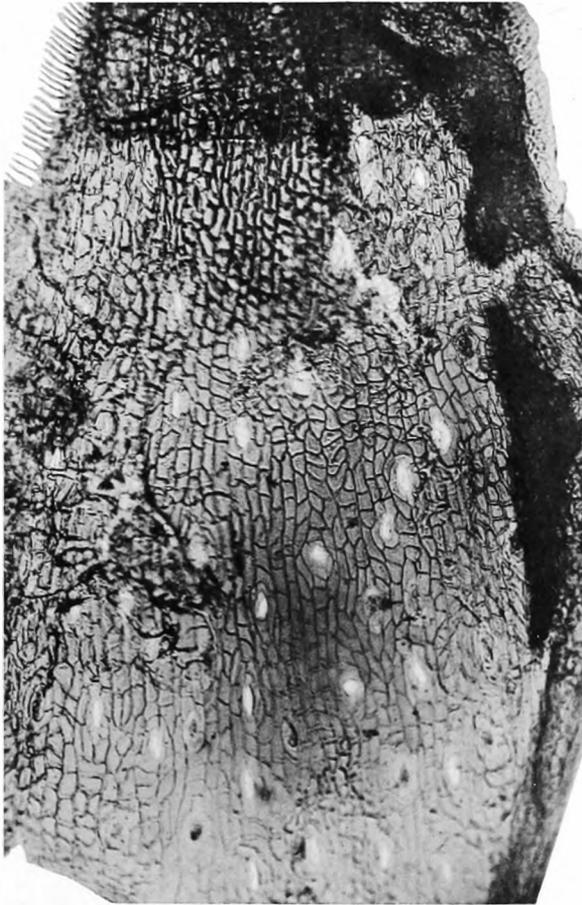
FIG. 66. General aspect of lower cuticle showing distribution of stomata. (Slide LIL 201.)
× 50.

Athrotaxis ungeri (Halle)

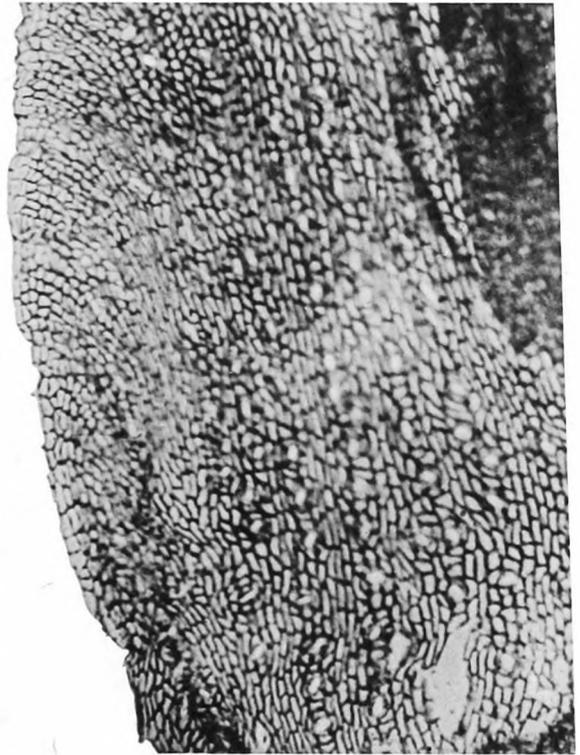
FIG. 67. Basal part of lower cuticle showing papillae and elongated marginal cells. (Slide
LIL 228.) × 100.

FIG. 68. General aspect of lower cuticle. (Slide LIL 228.). × 40.

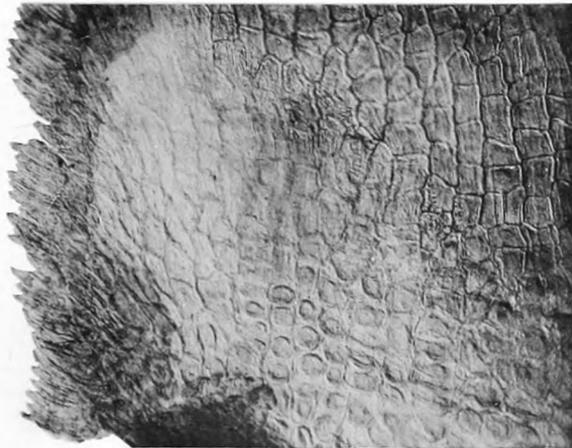
FIG. 69. Upper cuticle showing some stomata. (Slide LIL 228.) × 50.



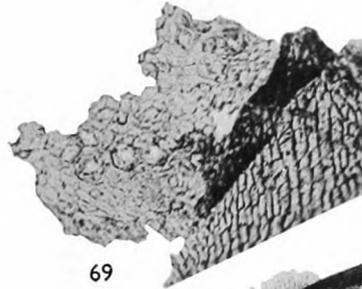
65



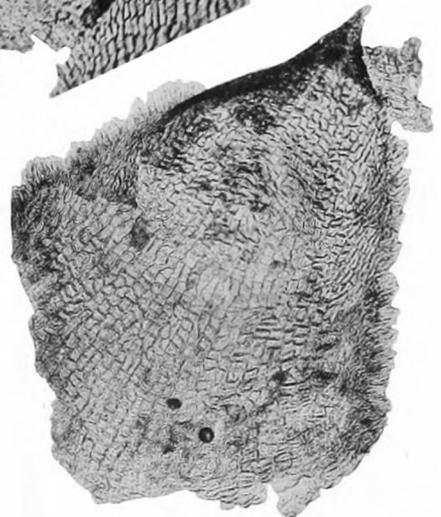
66



67



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68

PLATE 11

Tomaxellia degiustoi gen. et sp. n.

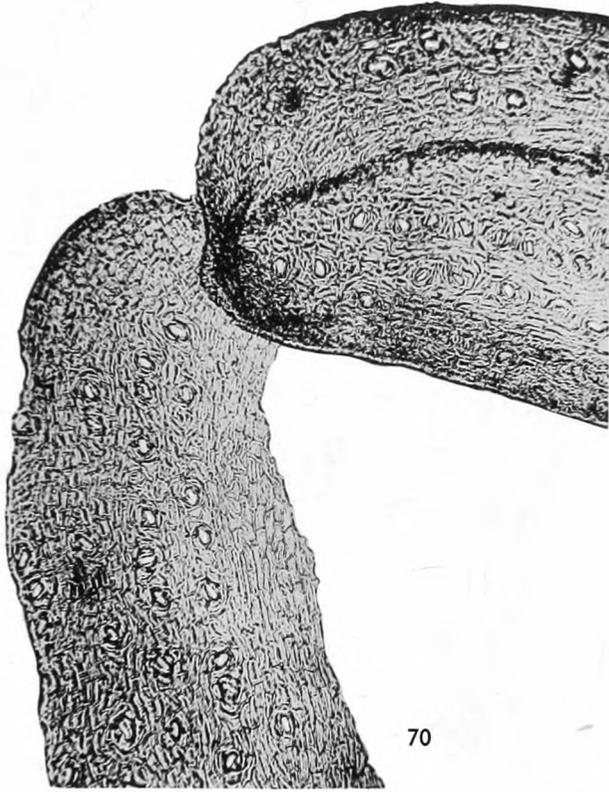
FIG. 70. Apical part of leaf (upper and lower cuticles). (Slide LIL 231.)

FIG. 71. Median part of leaf showing the longitudinal division into four parts, the two upper parts correspond to the upper cuticle. (Slide LIL 229.)

FIG. 72. Margin of leaf separating lower cuticle (left) from upper one (right). (Slide LIL 229.)

FIG. 73. Decurrent part of leaf (lower cuticle) showing irregular distribution of stomata. (Slide LIL 232.)

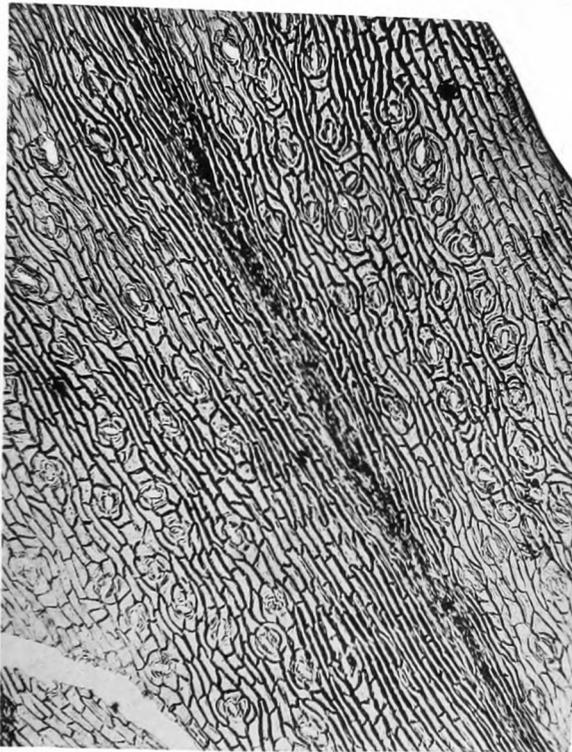
All $\times 50$.



70



71



72

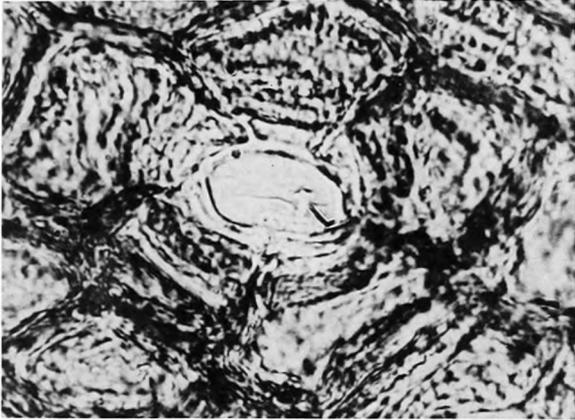


73

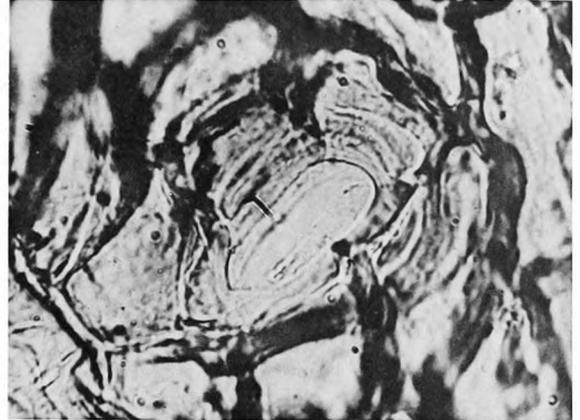
PLATE 12

STOMATA

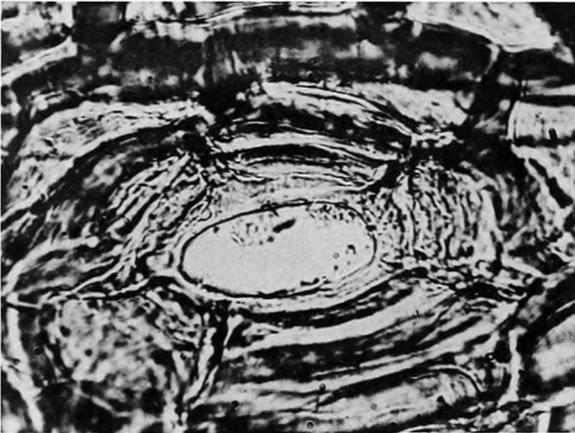
- FIG. 74. *Brachyphyllum brettii* sp. n. (Slide LIL 194.) $\times 500$.
FIG. 75. *Brachyphyllum mucronatum* sp. n. (Slide LIL 201.) $\times 500$.
FIG. 76. *Brachyphyllum mirandai* sp. n. (Slide LIL 215.) $\times 350$.
FIG. 77. *Brachyphyllum irregulare* sp. n. (Slide LIL 225.) $\times 350$.
FIG. 78. *Athrotaxis ungeri* (Halle). (Slide LIL 228.) $\times 500$.
FIG. 79. *Tomaxellia degiustoi* gen. et sp. n. (Slide LIL 229.) $\times 500$.



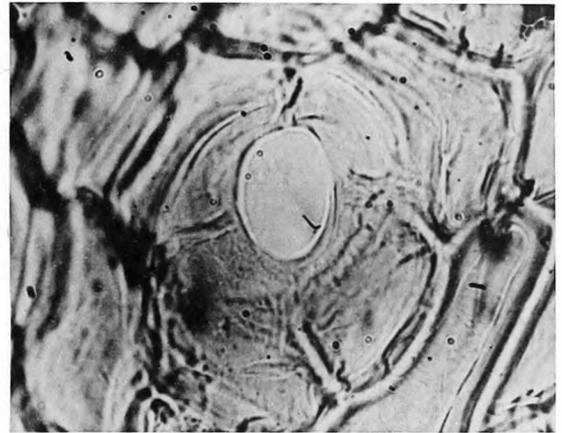
74



75



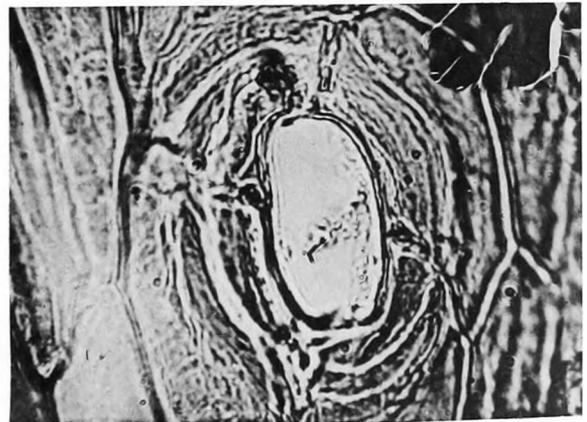
76



77



78



79