THE PELTASPERMACEAE, A PTERIDOSPERM FAMILY OF PERMIAN AND TRIASSIC AGE

by JOHN A. TOWNROW

ABSTRACT. The three genera comprising the Peltaspermaceae, *Lepidopteris* (leaf), *Antevsia* (pollen organ), *Peltaspermum* (seed organ) are discussed. The following are redescribed: *L. stormbergensis* (Seward) Townrow, *L. martinsii* (Kurtze) comb. nov., *A. zeilleri* (Nathorst) Harris, *A. extans* (Frenguelli) comb. nov., and *P. thomasi* Harris. The evidence for referring isolated organs to their parent plant, and the morphology and affinities of the family are considered. The Peltaspermaceae range from the Thuringian to the Rhaetic (inclusive), the earliest species coming from Europe.

THE Peltaspermaceae were established by Dr. H. Hamshaw Thomas as a small family of Triassic (including Rhaetic) age. They have now been found in the Upper Permian, but only once from rocks later than the Rhaetic. The leaves, *Lepidopteris*, have been known for many years. The pollen organ, *Antevsia*, has hitherto been known from one species; herein a second is described. The seed organ, *Peltaspermum*, is known from two species, but only the type species, *P. rotula*, in detail.

The Rhaetic *P. rotula* is peltate and radially symmetrical, and is thus unique among seed organs. This has led to the belief that the Peltaspermaceae are very isolated morphologically. Examination of the earlier species suggests that the family is not so isolated, and that comparison is possible with Carboniferous fossils.

The ages and distribution of the species of the Peltaspermaceae are shown in Table 1.

LEPIDOPTERIS Schimper

Type species *L. stuttgardiensis* (Jaeger) Schimper 1869

The genus *Lepidopteris* has been redefined and discussed by Frenguelli (1943) and Townrow (1956). Of the five leaves referred to *Lepidopteris*, the youngest, *L. ottonis* (see Antevs 1914; Harris 1932; Lundblad 1950), and the two oldest, *L. stormbergensis* (see Thomas 1933; Townrow 1956) and *L. martinsii* (see below), are known in detail; but the other two, *L. stuttgardiensis* and *L. madagascariensis*, are very incompletely known (Townrow 1956). The finding of thirty-five new specimens of *L. stormbergensis* has added new information on the range of variation of that species, and on the morphology of *Lepidopteris*. This latter with characters of the rachis is taken in the general discussion of *Lepidopteris*; they both are of wider interest, and support the reference of reproductive organs to the leaves.

The gross form of the leaf. In *L. stormbergensis* the pinnae are offset towards the upper (adaxial) side of the rachis, for on this side they are traceable almost to the mid-line of the rachis; but upon the lower (abaxial) side are overlapped by the rachis. Which side is the upper or lower is determined by reference to the leaf base. *L. martinsii* is probably the same as *L. stormbergensis*; the main rachis forms a trench whose bottom lies at a deeper level than the bottom of the trenches formed by the pinna rachises (text-figs. 1A–D, 4A). The matter has not been discussed in the other species.

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The pinnules of *L. stormbergensis*, and probably of the other species, are set obliquely on their rachises, so that if the pinna is considered to be inclined the pinnules lie horizontally (text-fig. 5A, B, E, H; and see Schimper 1869, pl. 34, fig. 1; Harris 1932, pl. 6, fig. 2 and pl. 8, figs. 15, 16). Both asymmetry of pinna insertion and an oblique pinnule insertion seems to be common, if not normal, in living and fossil pinnate leaves.

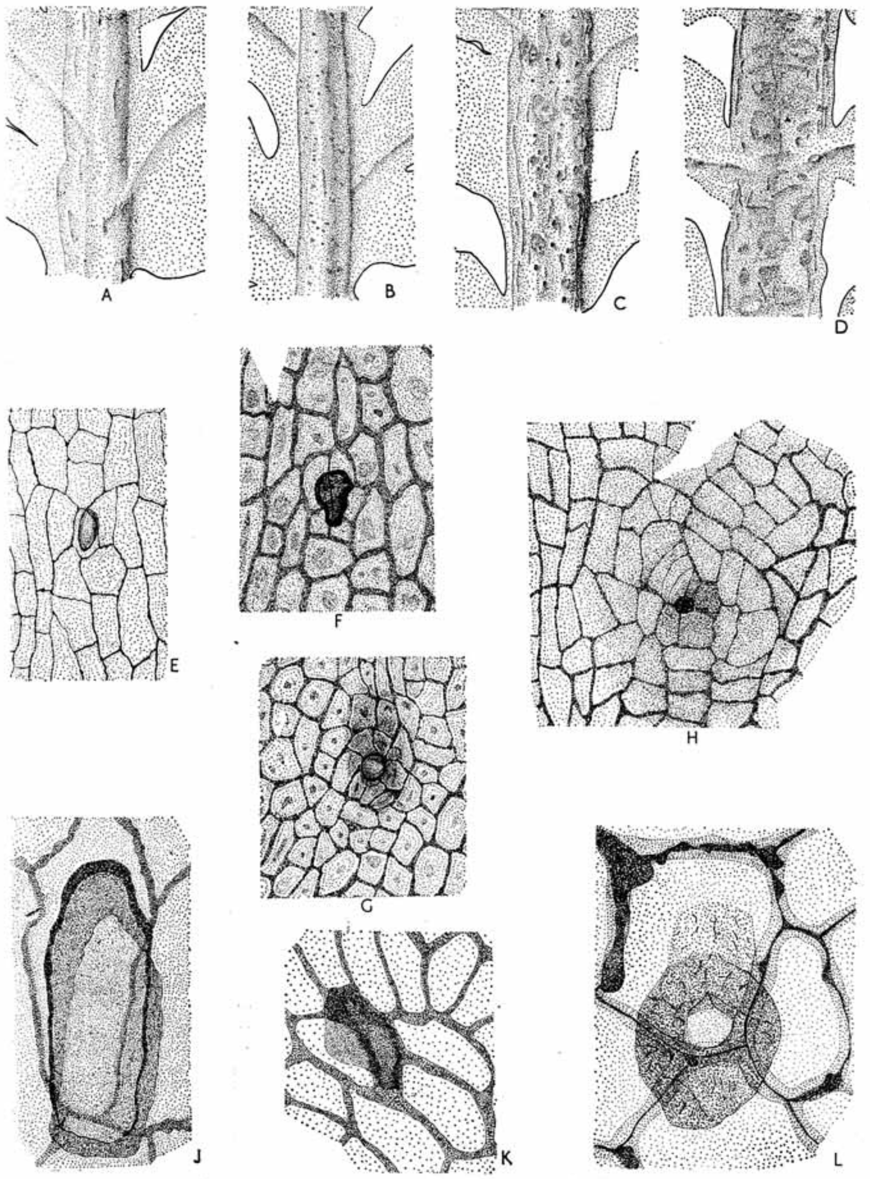
TABLE 1

The Peltaspermaceae

Organ	*Species*	*Geological horizon and age*	*Distribution*
Leaf	*Lepidopteris martinsii*	Kupferschiefer, Obere Zechstein, Marl Slate, Hilton Plant Bed, Lower Marls and Limestone; Upper Permian	Germany, England
Leaf	*Lepidopteris stormbergensis*	Uppermost Beaufort, Molteno, Esk Series, Hawkesbury Sandstone, Estratos de Potrerillos, ? Sakanema; uppermost Lower and Middle Trias	South Africa, Queensland, New South Wales, the Argentine (? Madagascar)
Pollen organ	*Antevsia extans*	Uppermost Beaufort, Molteno, Estratos de Potrerillos; uppermost Lower and Middle Trias	South Africa, the Argentine
Seed organ	*Peltaspermum thomasi*	Molteno; Middle Trias	South Africa
Leaf	*Lepidopteris stuttgardiensis*	Schillfsandstein; Lower Keuper	S.-W. Germany (? Urals)
Leaf	*Lepidopteris madagascariensis*	Sakanema; Middle and ? Upper Trias	Madagascar
Leaf	*Lepidopteris ottonis*	Rhaetic zone fossil	Sweden, Germany, E. Greenland, China, Kazaghistan (? Tonkin)
Pollen organ	*Antevsia zeilleri*	Scoresby Sound Beds, Scanian Coal Measures; Rhaetic	Sweden, E. Greenland
Seed organ	*Peltaspermum rotula*		

In all species of *Lepidopteris* zwischerfiedern occur. These are pinnules set directly on the rachis between adjacent pinnae. In *L. martinsii* some of these pinnules lie on the abaxial rachis surface, appearing to be in series with the pinnules on the pinnae (text-fig. 5J). In four specimens of *L. stormbergensis* the lowest pinnule of a pinna is orientated differently from its neighbours, and is set partly on the abaxial rachis surface (text-fig. 4G). In two of these specimens there are also pinnule tufts, or their remains, inserted

TEXT-FIG. 1. A–J, *Lepidopteris stormbergensis*. A–D, Series of rachises showing increasing degree of lumpiness; A, C, D, adaxial surface exposed, B, abaxial surface exposed; ×7·2. E–H, Rachis cuticles from specimens figs. A–D, showing increasing proliferation at trichome bases; ×200. J, Trichome set on a single cell, top somewhat torn; ×876. K, *L. ottonis*, trichome set on a single cell; ×392. L, *L. martinsii*, trichome set on a single cell, and showing vertical extensions of cell outlines; the pale area in the centre of the trichome is probably a feebly cutinized part of trichome base; ×879 (V/5793).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K
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purely on the abaxial rachis surface, but lying in series with the pinnae (text-fig. 4H). In the other specimens the zwischerfiedern are lateral, joined to one another by a wing of tissue with lamina-like cuticle, but the lowest zwischerfiedern are inserted nearer the abaxial rachis surface than the pinnae. In *L. ottonis* and *L. stuttgardiensis* no difference in level between the pinnae and zwischerfiedern is apparent in published figures.

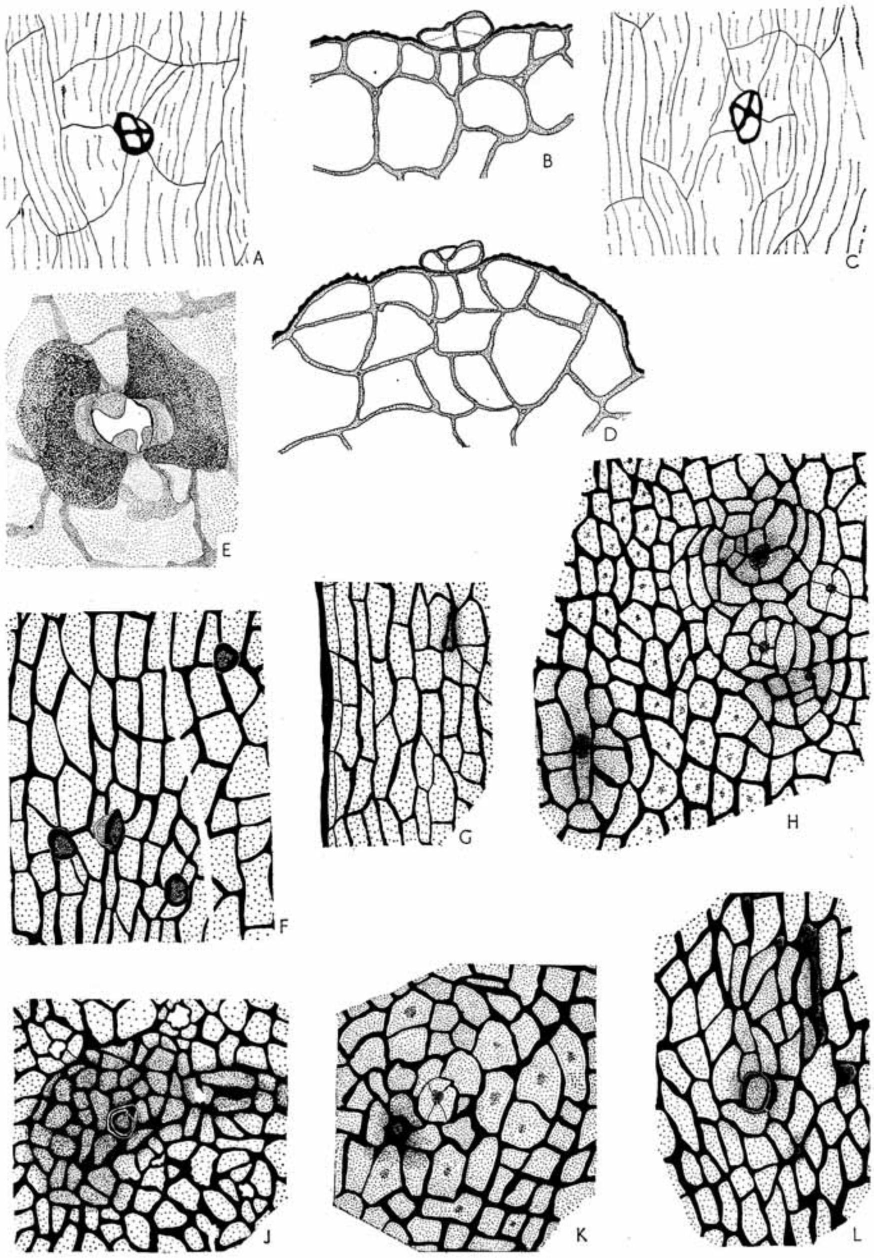
I suggest that this series may be interpreted as a progressive simplification of the leaf. In *L. martinsii* the series of pinnules normally continues, as zwischerfiedern, on to the abaxial rachis surface; in *L. ottonis* and *L. stuttgardiensis* it is wholly lateral and at one level, while *L. stormbergensis* is intermediate.

The leaf-base and vascular trace. Five leaves of *L. stormbergensis* showed the bulbous leaf-base (text-figs. 4E, F; 5C, D, H). It is cutinized on one side only (the abaxial) and here there are strong wrinklings suggesting the compression of a terete organ, and blisters are missing. The cell rows run laterally (text-fig. 4C). On the adaxial surface short cells, without any pattern, are visible, and also two bulges which recall the vascular trace scars on an abscission surface, and from each bulge an indistinct rib can be traced upwards. These ribs join about 1 cm. from the leaf-base; the one rib can then be traced the whole length of the leaf (text-fig. 4F). The ribs are wholly internal, giving dark matter on incomplete maceration, but leaving no mark on the cuticle. I suggest they represent the remains of vascular tissue. There is no information about the vascular trace from the other species.

The structure of the rachis. The swellings on the rachis of *Lepidopteris* were first regarded as scales, but were later shown to be blisters of the cuticle (Antevs 1914). In *L. stormbergensis* there is a series of leaves from some with a smooth rachis to others with a markedly blistered one. From this series one can suggest the nature and origin of the blisters.

On leaves with a smooth rachis, the rachis cuticle shows trichomes, or trichome bases (often numerous), either set on a single cell, or with slight proliferation of the epidermal cells around the trichome base (text-figs. 1A, B, E, F; 2E), the other cells lying in longitudinal rows. On leaves with a slightly blistered rachis the proliferation around the trichome bases is greater (text-figs. 1C, D, G, H; 2F), the area of proliferation corresponding to a small blister. In leaves with a markedly blistered rachis the proliferation is greater still, either to give an area up to twenty cells across in which the cells are set in a concentric pattern (text-fig. 6F), or, rarely, the compressed blisters overlap and the cells appear to be set irregularly. Sometimes, over large blisters, a trichome base is not visible, but usually some trace of it remains. More than one trichome may contribute to a single blister (cf. text-fig. 6F).

TEXT-FIG. 2. A–D, *Rumex hydrolapathum*. A, Trichome on a smooth petiole (cuticle prep.). B, Section of outer tissues of a smooth petiole passing through a trichome. C, Trichome over a swelling, showing slight proliferation of cells (cuticle prep.). D, Section of a swelling beneath a trichome; A–D ×326. E–K, *Lepidopteris stormbergensis*. E, A naturally macerated stoma, showing arcs of dark matter (probably lignine lamellae) flanking stomatal pit; ×730. F, Cuticle of a smooth rachis, showing one trichome and trichome bases. G, Rachis cuticle showing one trichome base, and cell outlines over wing (to left). H, Cuticle of a slightly lumpy rachis, showing trichome bases, proliferated cells, and two stomata. K, Stem cuticle, showing stoma, trichome base over a proliferation. J, *L. martinsii*. Rachis cuticle, trichome base over a proliferation and four stomata (left plain) (V/5963 a). L, *L. ottonis*. Rachis cuticle showing a trichome base and slight proliferation. E–L all ×167.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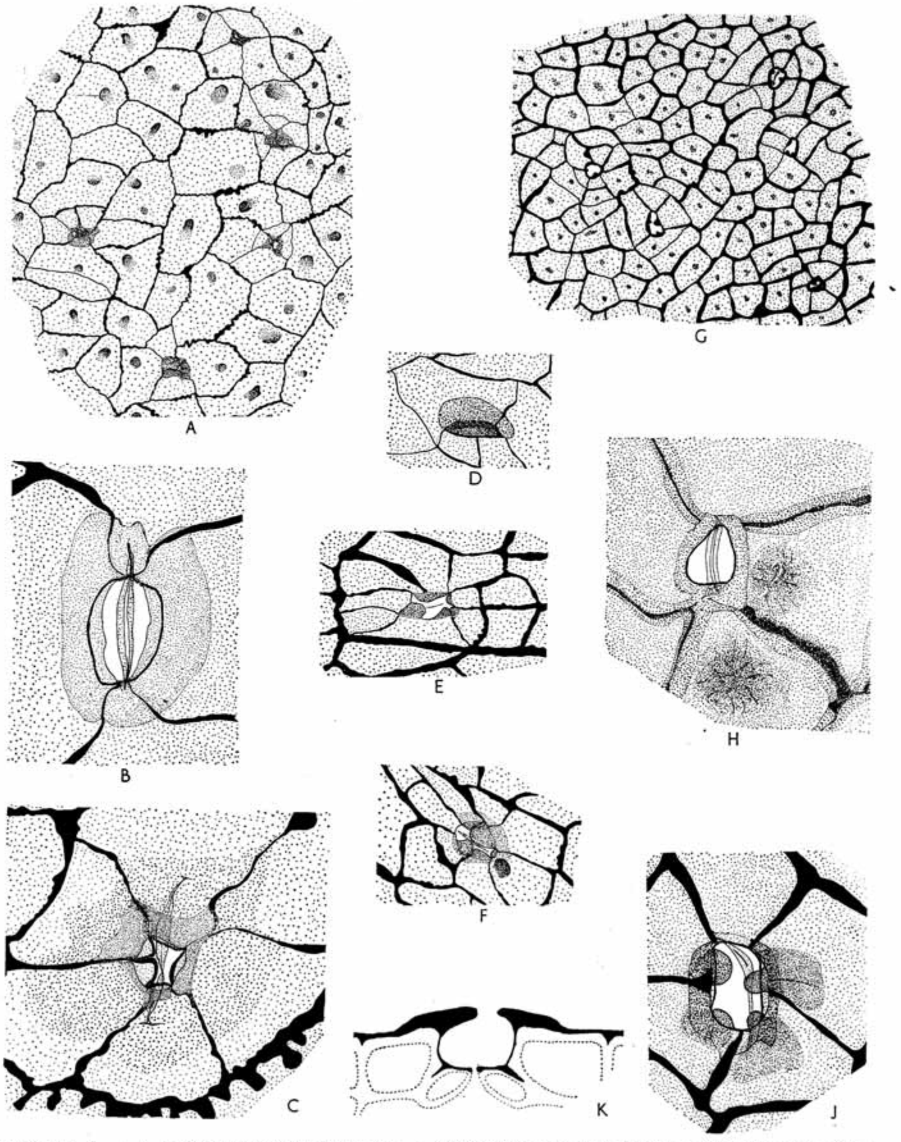
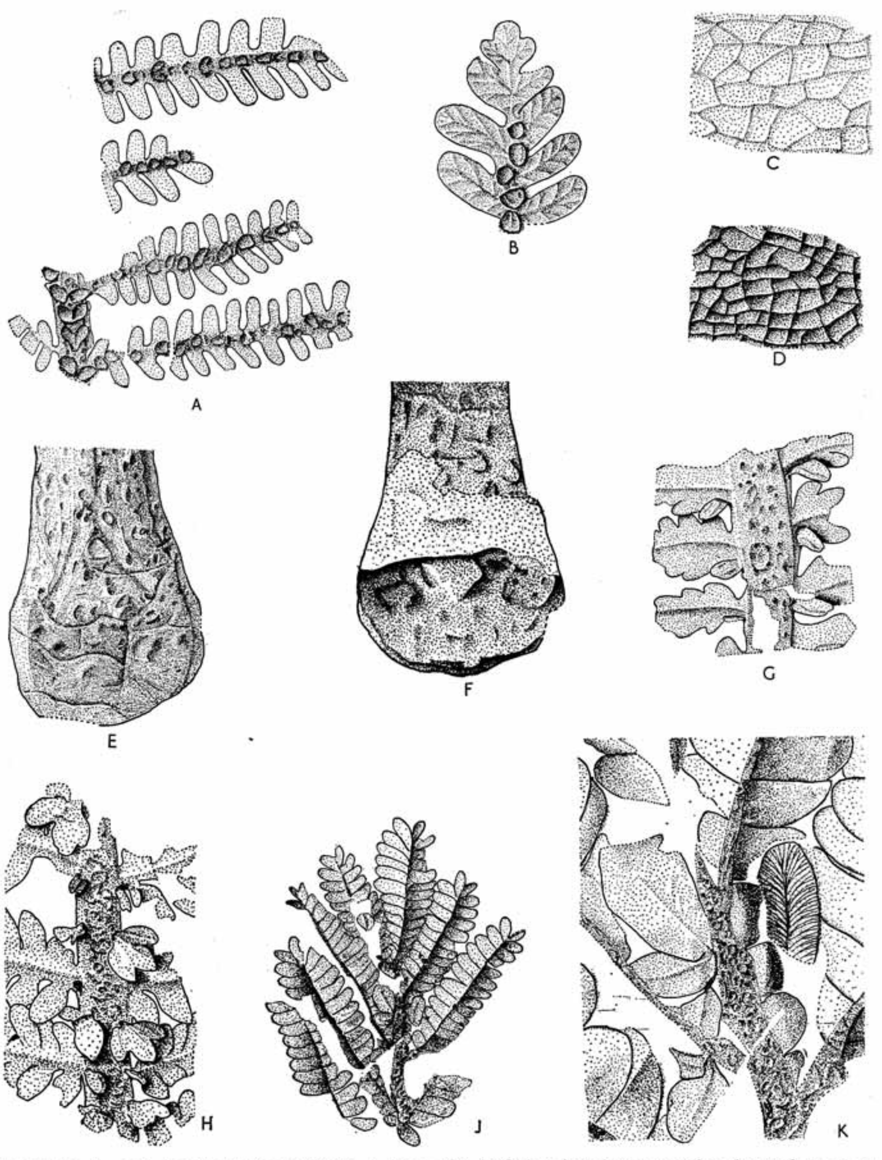


TEXT-FIG. 3. A–C, *Lepidopteris stormbergensis*. A, Cuticle from lamina showing cell outlines, papillae, and stomata; ×167. B, Stoma without cutin papillae; ×876. C. Stoma of normal form; ×876. D–E, *Antevsia extans*. Trichome from the rachis; ×392. E, Stoma from the rachis; ×392. F, *Peltaspermum thomasi*. Stoma from the rachis; ×392 (v/23400). G–K, *L. martinsii*. G, Cuticle from lamina showing cell outlines, papillae, and stomata; ×167 (v/5963 b). H, Stoma lacking cutin lappetts; ×876 (the Hellstedt leaf). J, Stoma with large lappets of solid cutin; ×876 (v/5963 b). K, Section, approximately transverse, reconstructed through stoma shown at J; ×876 approx.



TEXT-FIG. 4. A–B, *Lepidopteris martinsii*. A, Part of a leaf showing decurrent pinnules and more or less paired imprints of swellings on rachises; ×1·6 (V/5963). B, A pinna apex, showing venation and imprints of swellings; ×2 (V/2595). C–H, *L. stormbergensis*. C, D, Cells from abaxial (C) and adaxial (D) surfaces of leaf base; ×106. E, F, Surfaces of the leaf base (E abaxial, F adaxial), showing suggested vascular traces; ×7·2. G, Part of a leaf, showing insertion of lowest pinnule of pinnae partly on abaxial rachis surface; ×7·2. H, Leaf, showing pinnule tufts set on the abaxial rachis surface; ×1·7. J, K, *Paripteris gigantea*. J, Leaf, abaxial side; ×0·4. K, Central part of same leaf showing blisters on rachises, two pinnule tufts on abaxial rachis surface (to left) and venation in one pinnule; ×1·6 (V/1296).

Rumex hydrolapathum [Polygonaceae] provides an analogy. In this plant the petiole bears trichomes, and in some leaves the trichomes are set on small swellings, which show, in a cuticle preparation, proliferated epidermal cells around the trichome base, and in section proliferation of the sub-epidermal layer, which raises the swelling (text-fig. 2A–D). Presumably, therefore, the swellings of *L. stormbergensis* are also formed by sub-epidermal proliferation at the site of a trichome; and the proliferation of the epidermis takes place to accommodate this local increase in girth. In *Lepidopteris*, however, the blisters contain a dense coaly residue, soluble on maceration, suggesting that the blisters were occupied by thick-walled lignified cells rather than cellulose parenchyma.

L. ottonis and *L. martinsii* show the same features as *L. stormbergensis* (text-figs. 1K, L; 2J, L), except that in *L. ottonis* solitary trichomes and small blisters are only seen at the leaf or pinna apices, and blisters lacking any sign of a trichome are commoner (Antevs 1914, pl. 2, figs. 6–8). Further, the reproductive structures show, as far as is known, blisters on their rachises just like those of *L. stormbergensis*, though usually smaller.

The trichomes appear to be unicellular, more or less spherical (text-fig. 1J, K, L), and are very thinly cutinized, the cuticle being minutely functate.

The stomata. One or two naturally macerated leaf fragments with stomata were found. These stomata showed two arcs of dark matter flanking the stomatal pit, and lying on the guard cell surface (text-fig. 2E). These are interpreted as lignine lamellae upon the outward surface of the guard cell, seen generally in living gymnosperms.

The stem of the Lepidopteris *plant.* Text-fig. 5C shows what is possibly the stem of *L. stormbergensis*. Both ends are broken, and at present it measures 2·3 cm. long and 0·5 cm. wide. The surface is of low relief, but shows a number of more or less contiguous raised areas. The cuticle (text-fig. 2K) is as on the rachises. The stem is wider than any rachis seen, and differs further in lacking a wing (Townrow 1956; and text-fig. 2G).

This stem closely resembles the stem referred to *L. ottonis* (see Harris 1932), though it is smaller and with a more delicate cuticle. Since both stems are cutinized they are presumably primary organs. There is no information as to how the leaves were borne.

Lepidopteris stormbergensis (Seward) Townrow

Plate 58, fig. 1; text-figs. 1A–H, J; 2E–H, K; 3A–C; 4C–H; 5A–H; 6A–C; 8H

For synonomy and diagnosis see Townrow 1956

Description and discussion. Nearly all the material of *L. stormbergensis* comes from the

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EXPLANATION OF PLATE 58

Fig. 1. *Lepidopteris stormbergensis* (Seward) Townrow. Leaf with abnormally lumpy rachis, ×1.

Figs. 2, 3. *Peltaspermum thomasi* Harris, v/23400, Brit. Mus. (Nat. Hist.) Part and counterpart of type, ×2.

Figs. 4–9. *Antevsia extans* (Frenguelli) comb. nov. 4, 5, Pollen grains, sulcus facing observer (4) and to left (5), ×500. 6, The type (from du Toit 1927, pl. 29, fig. 3), × 1·7. Specimen showing branching, ×1. 8, 9, Upper and lower surfaces of disk and pollen sacs (different specimens), ×3. (*st*—branchlet, or position of same.)

Fig. 10. *Antevsia zeilleri* (Nathorst) Harris. Pollen grains in three views, ×500.

Burnera Waterfall locality, Upper Umkomaas, Natal; but two leaves are from the Australian Trias (v/32106 and v/32472, Brit. Mus. (Nat. Hist.)). The Waterfall locality is regarded as falling within the Middle Triassic Molteno (see Haughton 1954; Townrow 1957). At the Waterfall the leaves of *L. stormbergensis* are found scattered more or less evenly through the thickness of plant-bearing rock; and this is different from the other common leaves, which are markedly patchy.

L. stormbergensis proves to be a variable leaf, and the variation is set out in Table 2 and in text-figs. 3A–C; 5A–H; 6A–C.

TABLE 2

Range of variation in *L. stormbergensis*

Variation	*Characters showing variation*				
	Leaf length	*Leaf width*	*Pinna length*	*Pinnule length*	*Pinnule width*
Largest	20 cm.	13 cm.	7 cm.	14 mm.	7 mm.
Normal	12 cm.	8 cm.	4 cm.	6 mm.	4 mm.
Smallest	7 cm.	2·5 cm.	1·3 cm.	3 mm.	2 mm.
	Cell size (away from veins)	*Size of sinuosities of cell outlines*	*Height and width of papillae*	*Cuticle thickness*	
				Upper	*Lower*
Largest	60 μ	5 μ	4 μ, 10 μ	3·5 μ	3·0 μ
Normal	45 μ	2–3 μ	1 μ, 5 μ	2·0 μ	1·0 μ
Smallest	24 μ	0·5 μ	0 0	1·5 μ	0·5 μ
	Number of subsidiary cells	*Stomatal frequency mm.^{2}*	*Stomatal index*		
Most	8	108	9·3		
Normal	5 or 6	34	7·0		
Least	3	20	4·7		

The stomata are all of essentially the same pattern, but they differ in detail. The commonest sort (about 75 per cent.) shows subsidiary cells bearing a cutinized papilla, now hollow (text-fig. 3C). A second sort, making up nearly all the remainder, shows a lappett of solid cutin (cf. text-fig. 3J). One or two leaves showed some stomata of an abnormal sort (text-fig. 3B). These stomata (about 1 per cent.) are important, for they match a sort of stoma seen on the pollen sacs of the pollen organ referred to *L. stormbergensis*.

Though variable, I do not believe that species other than *L. stormbergensis* are present. The groups given in Table 3 intergrade, and no other character gives ground for splitting up the material. The characters vary about one mean, and if more than one species was involved this would scarcely be so. Such characters are the number of pinnae per leaf (about 32), the interval between veins (about 0·25 mm.), the stomatal density and index, and the stomatal form.

A list of records believed to be synonyms of *L. stormbergensis* is given by Townrow (1956); in only one of them was the cuticle examined (Thomas 1933). The variation in

TEXT-FIG. 5. A–H, *Lepidopteris stormbergensis*. Leaves to show variation in gross form, stem shown in C at *a*; ×0·75 (G is V/32472). J, *L. martinsii*. Large tripinnate leaf, showing pinnules on abaxial surface, and zwischerfiedern between pinnae; ×0·75 (redrawn from Gothan and Nagalhardt 1921, pl. 3, fig. 1).

gross form of the present material easily includes the variation seen in these records, and the cuticle of Dr. Thomas's specimen is typical.

I have examined two Australian specimens of *L. stormbergensis* (v/32106 and v/32472, Brit. Mus. (Nat. Hist.)) and Mr. J. M. Pulley has very kindly sent me some excellent photographs of other leaves from Queensland (described but not figured by Walkom 1924 and 1929), which, though only one has a cuticle, with nearly straight cell outlines, I identify as *L. stormbergensis*. These photographs show the same variation as the Natal leaves. I think that there is no doubt that the same leaf is involved in both Australia and South Africa.

TABLE 3

Variation in a number of characters in *Lepidopteris stormbergensis*

	Specimen	*Leaf length/ width*	*Lumpiness of rachis*	*Cuticle thickness (μ)*		*Stomatal density (per H.P. field)*		*Stomatal index*		
				Upper	*Lower*	*Upper*	*Lower*	*Upper*	*Lower*	*Averages*
GROUP I	1	3·6	A							*Stomatal density*
	8	..	A	3·5	3·0	3·0	1·4	10·4	5·6	upper 2·6
	18	3·6	B	2·0	1·0	2·8	1·2	9·6	5·0	lower 1·5
	11	..	A	3·0	1·5	2·2	1·0	7·3	4·3	
	16	..	B	2·0	1·0	1·6	1·2	5·3	4·1	both 2·0
	A	2·7	C	3·5	3·0	3·0	1·4	10·5	5·6	
	10	1·5	B	2·0	0·5	2·8	1·0	8·4	5·2	*Stomatal index*
	9	..	A	2·0	1·0	2·2	1·4	7·1	4·9	upper 8·7
	12+	1·7	D	3·0	1·0	2·6	1·4	6·6	3·9	lower 5·1
	23+	..	D	2·0	0·5	4·2	3·0	10·0	7·6	
	15+	2·3	B	2·0	2·0	1·4	1·2	5·5	4·6	both 6·9
GROUP II	7	1·7	D	3·0	2·5	2·4	2·6	7·6	9·3	*Stomatal density*
	6°	..	E	2·0	1·5	1·8	2·8	7·3	9·9	
	34	..	C	2·0	1·5	1·4	1·6	5·0	5·2	upper 1·48
	33	1·5	D	2·0	1·5	1·0	1·2	5·0	6·6	lower 2·4
	22	..	C	2·0	1·5	1·4	2·0	5·6	7·2	both 1·96
	27+	..	E	1·5	1·0	2·0	3·0	6·6	9·6	
	4	1·3	E	3·5	0·5	1·8	2·6	6·5	8·4	*Stomatal index*
	5°	..	D	3·5	0·5	2·2	3·0	7·5	9·4	upper 6·25
	B	..	B	2·5	0·5	0·2	2·2	0·8	9·3	lower 8·45
	30°	..	E	3·0	2·0	2·4	3·4	7·6	11·0	
	31+	..	D	2·5	1·5	2·8	1·8	9·0	6·6	both 7·35

Notes: (i) Rachis quantities A–E refer to 5-figd. rachises (text-fig. 1A–D; pl. 58, fig. 1) taken as standards. (ii) Leaves marked + exceptional in one value. (iii) Leaves marked °, the length/width probably less than 1·5, but specimen too small for certainty. (iv) Counts averages of $10\frac{1}{8}$ in. fields.

The possible habit of L. stormbergensis. The leaves of *L. stormbergensis* can be placed in two groups. In the first the leaves are narrow, with smooth or nearly smooth rachises, and with more stomata on the upper (adaxial) leaf surface than on the under (abaxial) surface. In the second group the leaves are wide, the rachises blistered, and the distribution of stomata normal (Table 3).

In many, but by no means all, waterside herbs of the British flora the leaves arising from the upper and lower nodes are of different form. The difference parallels the variation between the two groups found in *L. stormbergensis* (see Table 4 for some examples). Also, to refer again to *Rumex hydrolapathum*, the swellings on the petiole

TABLE 4

Stomatal densities (per H.P. field) and indices of some waterside herbs

		Upper surface		*Lower surface*		*Upper surface*		*Lower surface*	
Species	*Leaf position (mode)*	*Stomatal density*	*Stomatal index*	*Stomatal density*	*Stomatal index*	*Stomata counted*	*Cells counted*	*Stomata counted*	*Cells counted*
Alisma	Upper	2·8	9·1	2·0	7·5	21	211	21	257
plantago	Lower	3·5	4·6	1·8	8·0	35	266	22	254
Menianthes	Upper	1·8	4·75	3·66	8·7	22	441	44	461
trifoliata	Lower	4·0	6·8	4·7	7·0	39	533	47	630
Mentha	Upper	0	0	12·2	17·2	0	317	72	346
aquatica[1]	Lower	2·8	11·0	4·7	13·0	28	230	47	317
Myosotis	Upper	6·5	12·0	13·6	27·0	65	477	136	365
palustris[2]	Lower	6·8	15·0	6·1	14·0	68	392	61	377
Nasturtium	Upper	8·1	20·0	11·6	27·0	81	398	116	308
officinale	Lower	9·3	25·0	5·7	16·5	93	271	57	292
Polygonum	Upper	0·9	2·7	5·0	17·3	9	325	50	245
amphibium	Lower	13·8	22·0	7·0	18·0	138	489	69	317
P. hydropiper[1]	Upper	0·9	2·5	18·0	22·0	9	355	85	331
	Lower	4·0	13·2	5·0	13·2	35	231	41	269
Ranunculus	Upper	6·0	18·0	3·7	16·5	71	323	44	226
flamula	Lower	7·8	20·0	1·25	5·5	78	306	15	264
Rumex	Upper	2·3	9·2	3·0	12·0	28	270	36	230
hydrolapathum	Lower	4·8	14·5	4·4	10·5	48	282	44	376
Sium	Upper	2·9	7·1	15·7	26·0	29	382	157	543
angustifolium	Lower	4·7	11·7	4·2	9·6	47	352	42	397
Typha	Upper	21·5	20·0	24·0	22·0	129	501	145	528
latifolia[3]	Lower	22·0	24·0	16·0	27·0	65	477	136	365
Veronica	Upper	8·0	16·0	14·5	25·0	80	422	145	437
beckabunga	Lower	7·6	22·0	5·5	17·0	89	317	66	321

[1] Hair bases not counted. [2] On side shoots. [3] In stomatiferous areas only.

are characteristic of leaves from the upper nodes; the leaves from the lower nodes are smooth.

In Dicotyledonous trees stomata are generally few or absent on the leaf upper surface. In terrestrial Dicotyledenous herbs stomata may be frequent on the upper leaf surface, but they are regularly still more abundant on the under leaf surface, whatever the position of the leaf on the plant (see Salisbury 1927; Walter 1951). There are exceptions to this statement, but among plants which have more protected upper leaf surfaces as the Graminae, *Trifolium* (see Erban 1916), or cushion-forming alpines (see Salisbury 1927).

In these respects *L. stormbergensis* is more like a waterside herb than a tree or terrestrial herb. It might be argued that its rather thick cuticle is against this, but in fully adult leaves of *Rumex hydrolapathum* or *Alisma plantago* the cuticle, as prepared by oxidative maceration, may be up to 2·5 μ thick.

Lepidopteris martinsii (Kurtze) comb. nov.

Text-figs. 1L; 2J; 3G–K; 4A, B; 5J; 6D

1839 *Alethopterin martinsii* Germar MS; Kurtze, p. 34, pl. 3, fig. 2. German material, type specimen.

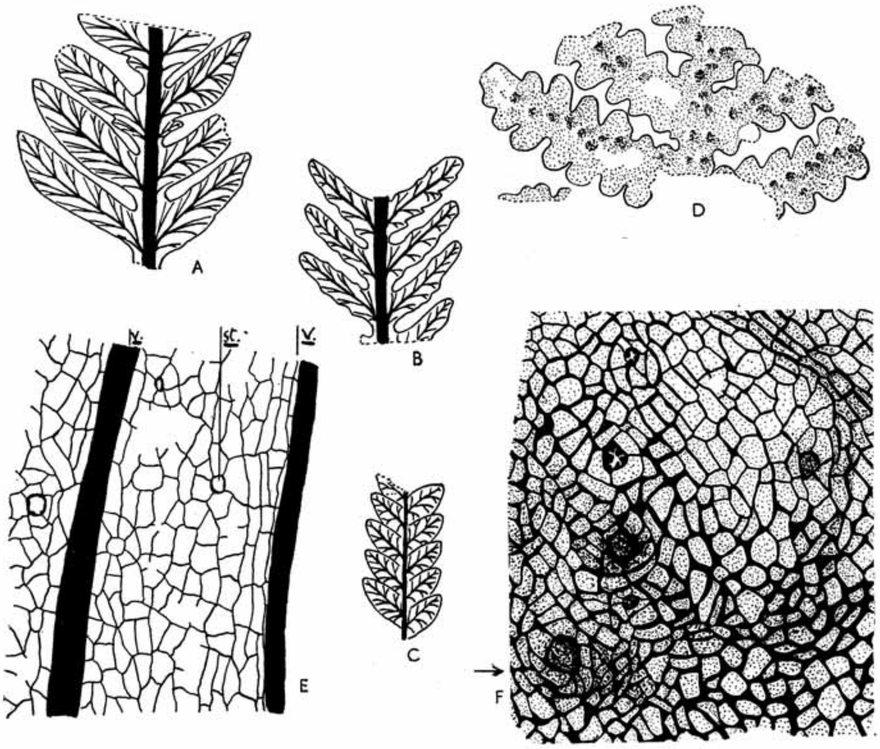
1907 *Callipteris martinsii* (Germar); Gothan, pp. 1–4, figs. 1, 2. German material figured.

1921 *Callipteris martinsii* (Germar); Gothan and Nagalhardt, pp. 451–3, pl. 6, figs. 5, 6; pl. 7, figs. 1–3. Good German material with cuticle.

1958 *Callipteris martinsii* (Germar); Stonely, pp. 313–15, pl. 37, figs. 2, 5; text-figs. 5, 6. English material, cuticle figures.

(For full synonomy see Gothan 1907 and Stoneley 1958.)

Diagnosis (emended). Leaf bipinnate, sometimes tripinnate, pinnules parallel-sided with very obtuse apex. Zwischerfiedern simple or pinnate, in smallest leaves absent, forming



TEXT-FIG. 6. A–C, *Lepidopteris stormbergensis*. Pinnules to show venation; ×1·33 (B is v/32472). D, *L. martinsii*. The Hellstedt leaf, showing form and swellings; ×1. E, *Paripteris gigantea*. Portion of naturally macerated cuticle, showing cell outlines, veins (*v*) and supposed stomata (*st*); ×53 (v/1293). F, *L. ottonis*. Cuticle over a large swelling, showing three trichome bases each over a proliferated area of cells, somewhat concentric cell arrangement at swelling margins, and two stomata; ×66.

a series from pinna base towards abaxial leaf surface. Blisters prominent. Cell outlines usually straight, sometimes showing minute processes running horizontally, but regularly with peg or strap-shaped processes at the cell corners running vertically. Stomatal pit usually overhung by small lappetts of solid cutin borne partly on the anticlinal surface of the subsidiary cells. Encircling cells often absent.

Description. The material described comes mostly from the Marl Slate of Kimberley (Notts.), with some from the Hilton Plant Bed (Westmorland). These horizons are approximately equivalent to the Kupferschiefer (Stoneley 1958). One additional leaf from the Zechstein of Hellstedt (referred to as the Hellstedt leaf) was most kindly lent me by the Director, Paleobotaniska Avdelningen, Naturhistoriska Riksmuseet, Stockholm. The English material is all in the collections of the British Museum (Nat. Hist.). It is rather fragmentary, few specimens have a cuticle, and only the Hellstedt leaf is cutinized over the main rachis.

The leaf is shown in text-figs. 4A; 5J. The larger specimens figured in the literature are tripinnate, and the smaller bipinnate. In some German specimens the series of zwischerfiedern can be seen continuing on to the abaxial rachis surface, but in my specimens the lowest pinnule of a pinna is simply somewhat decurrent (see, for example, Gothan and Nagalhardt 1921 and text-figs. 4A; 5J). The rachises of all the specimens show rather prominent swellings, or imprints which are interpreted as their remains; frequently rather regularly in pairs (text-figs. 4A; 6E). On the cuticle trichomes and trichome bases surrounded by proliferated cells can be seen (text-figs. 1L; 2J). The venation is shown in text-fig. 4B; the distance between the veins at the margin is about 0·75 mm.

The features of the cuticle are shown in text-figs. 2J; 3G. On both lamina and rachis one cuticle is thicker than the other. I suppose that the thinner cuticle is from the lower surface of the leaf. The cell outlines in two of the English specimens (v/5963b and v/5964) show in places minute processes, less than 1 μ high (text-fig. 3G). In all the specimens, especially over the rachis, the cutin on the periclinal cell walls penetrates rather deeply, sometimes lying crushed on one side, sometimes still upright so that the various levels can be determined by focusing. All also show projections of cutin inwards at least at the cell corners, up to 3 μ long (text-figs. 1L; 3H). In v/5963 the cells also show each a single (often obscure) papilla set more or less centrally; all the other leaves have a smooth cuticle.

The stomatal density is about 40 mm.^{2} (upper surface) and 80 mm.^{2} (lower surface); and the stomatal index about 7 (upper surface) and 14 (lower surface) (count of 20 high-power fields). About three-quarters of the stomata examined showed lappetts of solid cutin overhanging the stomatal pit, and in about a tenth of these lappetts were so large as almost to close the stomatal pit, but normally were much smaller (text-fig. 3G, J). The stomata without lappetts showed a rim of thick cutin (text-fig. 3H). The lappetts were set partly on the anticlinal surface of the subsidiary cells, so that they pointed obliquely upwards, and did not lie in the same plane as the cuticle surface (text-fig. 3J, K).

Various thin places and irregular holes, presumably pathological, and smaller holes and irregularities that were probably caused by sand damage (the holes were about the same size as the grains of the matrix) were present.

Discussion. Many specimens of *L. martinsii* have been figured, and these form an intergrading series; most fall between the extremes, and the series is not easily divisible into more than one entity. The cuticle has been much less studied (see Gothan and Nagalhardt 1921; Florin 1931; Stoneley 1958), but here too there seems to be a gradation of forms that cannot conveniently be divided. Not enough cutinized specimens have been examined, however, to say whether there is any correlation between leaves of a certain form and certain cuticle characters. Stoneley (1958) points out that in the German specimens whose cuticle has hitherto been figured the cuticle is papillate, whereas in the English specimens the cuticle appeared to be smooth. However, staining in safranin shows that in at least one English leaf there are papillae, and in at least one German leaf there are not.

The similarity between *L. martinsii* and species of *Lepidopteris* has been noted before (e.g. by Gothan 1907), and *L. martinsii* is now removed from *Callipteris*, and placed in *Lepidopteris*, because it agrees in the construction of the leaf, particularly in its series of zwischerfiedern; in the detailed construction of the blisters on the rachis; and in overall stomatal construction, which is of a rather unusual sort. This extends the range of the genus *Lepidopteris*, and therefore of the Peltaspermaceae, from the Thuringian to the Rhaetic.

L. martinsii may be distinguished from *L. ottonis* and *L. stormbergensis* by its parallel-sided and obtuse pinnules, by the details of its stomata (text-figs. 5J; 3J) and by the presence of cutin projections inwards at the cell corners. A tripinnate specimen may be told from the bipinnate *L. stuttgardiensis*, but a smaller specimen may look like *L. stuttgardiensis*. They may then be distinguished because *L. stuttgardiensis* has, it appears, shorter pinnules.

ANTEVSIA Harris 1937

Type species *Antevsia zeilleri* (Nathorst) Harris

Diagnosis (emended). Microsporophyll bipinnate, primary branching alternate, in one plane, second branching irregular. Main and branch rachises with blister-like swellings. Ultimate branches bearing four to twelve pollen sacs. Pollen sacs sessile, unilocular, 2–5 mm. long and 1–2 mm. wide, dehiscing by a longitudinal slit on ventral face. Pollen-sac wall massive, showing midrib and a few stomata on dorsal surface. Interior cuticle lining pollen sac absent, all other parts cutinized, and showing stomata overhung by hollow or solid cutin papillae. Pollen grains oval with slight projection at each end, monosulcate, sulcus same length as grain, lips of sulcus touching or almost touching along its whole length. Cuticle without other markings. Length 23–40 μ, width 13–28 μ, depth 12–25 μ, ratio length/width about 1·7.

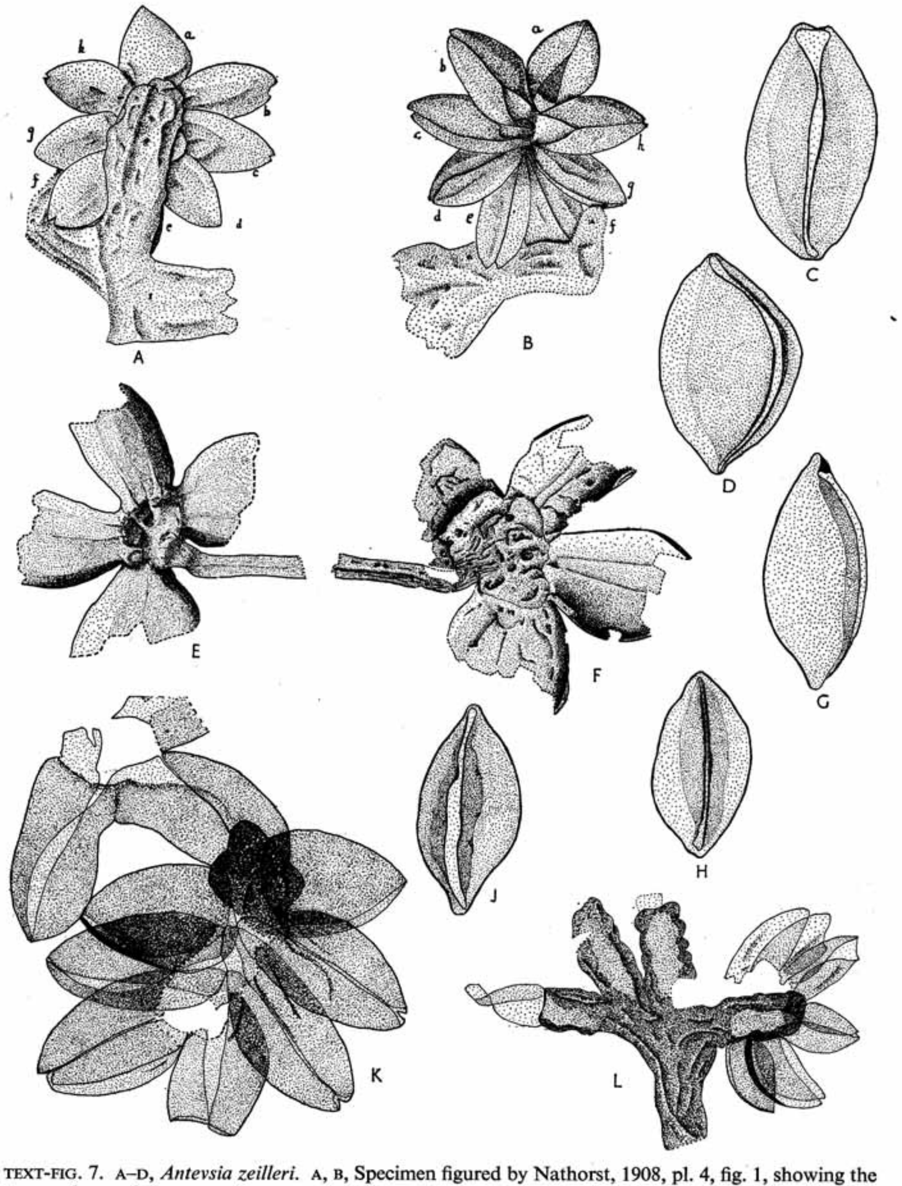
Antevsia zeilleri (Nathorst) Harris

Plate 58, fig. 10; text-figs. 7A–D, K, L; 8E, F, J, K; 9E

1910 *Antholithus zeilleri* Nathorst, pp. 20–24; pl. 2, figs. 59, 60; pl. 4. Type specimen pl. 4, fig. 1; Swedish material.

1914 *Antholithus zeilleri* (Nathorst); Antevs, pp. 10–15, pl. 3 (except figs. 17, 18). Nathorst's material redescribed.

1922 *Antholithus zeilleri* (Nathorst); Johansson, p. 28, pl. 1, figs. 11–13. Additional Swedish material.



TEXT-FIG. 7. A–D, *Antevsia zeilleri.* A, B, Specimen figured by Nathorst, 1908, pl. 4, fig. 1, showing the two surfaces of the organ (A upper, B under); ×7·2. C, D, two pollen grains, area of darker cuticle interpreted as the internal cuticle of furrow; ×875. K, Macerated specimen showing pairs of pollen sacs and fragment of branchlet (dark); ×14. L, A specimen showing four fertile branchlets, one showing lateral bulges clearly, another retaining its pollen sacs; ×7·2. E–J, *A. extans.* E, F, Fertile branchlet ending in disk and four dehisced pollen sacs, E upper side, F lower side (in transfer). F, Lit from bottom right; ×7·2. G–J, Three pollen grains, area of darker cuticle as in C, D; ×875.

1932 *Lepidopteris ottonis* (*Antholithus zeilleri*) (Nathorst); Harris, pp. 62–65, pl. 7, figs. 1, 2, 10, 11; text-figs. 27E, F. Abundant Greenland material.
1937 *Antevsia zeilleri* (Nathorst) Harris, p. 35, diagnosis.

Description. The second species of *Antevsia* raised questions that made a re-examination of the type species desirable, and the Director of the Paleobotaniska Avdelningen, Naturhistoriska Riksmuseet, Stockholm, kindly lent me Nathorst's material.

The whole organ is bipinnate, about 9 cm. long, the rachis bearing alternate branches in one plane about 1·5 cm. apart; these then divide, in a plane more or less at right angles to the rest of the organ, into two to five ultimate branchlets. The rachis and branches show blisters, but the branchlets do not.

The sterile region of the branchlets is 1·5–2·0 mm. wide, and was probably thick in life, for the cuticle shows irregular wrinklings, presumably arising during compression (text-fig. 7L). The cuticle of the two surfaces differs slightly in thickness, and in cell pattern (text-fig. 8E). The fertile region is the same width, or very slightly wider than the sterile part, and the cuticle is only slightly different (text-fig. 8K); stomata number about 20 mm.^{2}, and in four out of six specimens the cells were papillate. The margin of the fertile region is usually produced into a number of bulges, which lie more or less opposite to one another, and are 0·25–1·0 mm. wide, and the same high (text-fig. 7A, B, L). These lobes now appear to be of the same thickness as the branchlet, and the cuticle on *both* their sides is as in text-fig. 8F.

The pollen sacs lie in two rows up the under side of the branchlet end, as preserved from 0·25–0·5 mm. in from the margin. They tend to lie in opposite pairs, one pollen sac to each lobe, but this is not entirely regular, and there is sometimes an unpaired terminal pollen sac. They commonly overlap laterally, and the inner faces of the pollen sacs approximate, so that there is very little, or no, discernible tissue of the branchlet between them (text-fig. 7A, B, K, L). Near the pollen sac's outer edge the cuticle of the lateral bulge shows a varying number of cell rows whose orientation is the same as on the pollen sac itself. There is usually a strong fold, interpreted as caused during fossilization, at the apparent junction of the lateral bulge and pollen sac. These features are much the same whether the pollen sacs are dehisced or not. I suggest that they show that the pollen sacs were borne wholly on the under surface of the branchlet, and that the sides of the thick branchlet overlapped the line of insertion of the pollen sacs.

The bluntly pointed pollen sacs measure about 2 mm. long and 1 mm. wide. The dehiscence slit runs all the way up the inner face to just below the tip on the outer face (text-fig. 9E) and at this point the cuticle commonly shows a little group of equidimensional cells on which the cell rows on the rest of the pollen sac converge. The pollen-sac cuticle is strongly dorsi-ventral. Near the dehiscence line it is thick, showing markedly elongated cells (text-fig. 9E), and opposite to the dehiscence line there is another area of thick cuticle showing roughly rectangular cells ($54 \times 25\ \mu$), but at the base one or two strips of markedly elongated cells, about four cells wide and thirty high (text-fig. 8J), and a few stomata (cf. text-fig. 8G). Between these areas the cuticle is thin, showing elongated cells ($61 \times 19\ \mu$). The outer face of the unmacerated pollen sac is sometimes raised in the area opposite the dehiscence line, and in one or two cases (text-fig. 7A) there is a suggestion of a small mid-rib. The cell rows sometimes converge slightly towards the pollen-sac base, suggesting that the base was slightly contracted.

Four pollen sacs were still filled with pollen, and several others contained some grains. All these grains were alike and no others were seen (Pl. 58, fig. 10; text-fig. 7C, D). When the grains lie sulcus uppermost a curving line can be seen arising at each end of the sulcus (text-fig. 7C) which presumably marks the interior margin of the furrow; while when the grains lie on one side, a further curved line can be seen running under the sulcus (text-fig. 7D), and this I suppose represents the bottom of the furrow. The dimensions of a sample of twenty grains are as follows (extremes in parentheses): length 36·2 μ (46·25 μ, 29 μ); width 22·6 μ (29·8 μ, 20 μ); depth 21·35 μ (26·4 μ, 19·8 μ); interior width of furrow 8·73 μ (13·2 μ, 6·6 μ); depth of furrow 6·3 μ (9·9 μ, 3·3 μ), this value was measured directly from grains lying on their side; the proportions of the grains are: average ratio of length/width 1·6 (1·55 longest grain, 2·3 shortest grain, 1·0 broadest grain, 1·45 narrowest grain); and average ratio of length/depth 1·7 (corresponding figures of extreme specimens, 1·8, 2·32, 1·12, 1·46).

Antevsia extans (Frenguelli) comb. nov.

Plate 58, figs. 4–9; text-figs. 3D, E; 7E–J; 8G; 9A–D; 10A

1927 *Sagenopteris sp.* (non Presl gen.) du Toit, pp. 399–400, pl. 29, fig. 2. Single pollen-sac group; Aliwal North, South Africa.

1944 *Fanerotheca extans* Frenguelli (part), pp. 393–402, pl. 1; pl. 2, fig. 1; pl. 4, fig. 1. (Excluded are pl. 2, figs. 2–4; pl. 3; pl. 4, fig. 2.) Three specimens; near Cacheuta, the Argentine.

?1915 Equisetaceous tubers (?) Walkom, p. 31, pl. 3, figs. 3, 4. Ill-preserved fragments; Denmark Hill, Ipswich, Queensland.

Diagnosis (emended). (Main rachis unknown) presumed branches twice pinnate, ultimate branchlets 0·5–1·0 mm. wide expanding to 2·25 mm. at their ends and bearing four radially arranged pollen sacs. Pollen sacs attached partly marginally and partly on (presumed) under surface, when dehisced about 5 mm. long and 2 mm. wide. Cuticle 1 μ thick or less, on upper surface of branchlet end showing equidimensional cells, stomata, and trichome bases, between pollen sacs showing elongated cells only.

Description and discussion. The material consists of five specimens from the Waterfall locality (see p. 340), and one, v/20796 (Brit. Mus. (Nat. Hist.)), from an unknown locality in the Argentine. The most complete specimens (Pl. 58, fig. 7) show alternate branching. The larger branches show small blister-like swellings, but the branchlets cellular striae only. The cuticle shows trichomes, trichome bases sometimes proliferated, and stomata like those of *L. stormbergensis* (see text-figs. 3D, E; 9B). On the larger branches the

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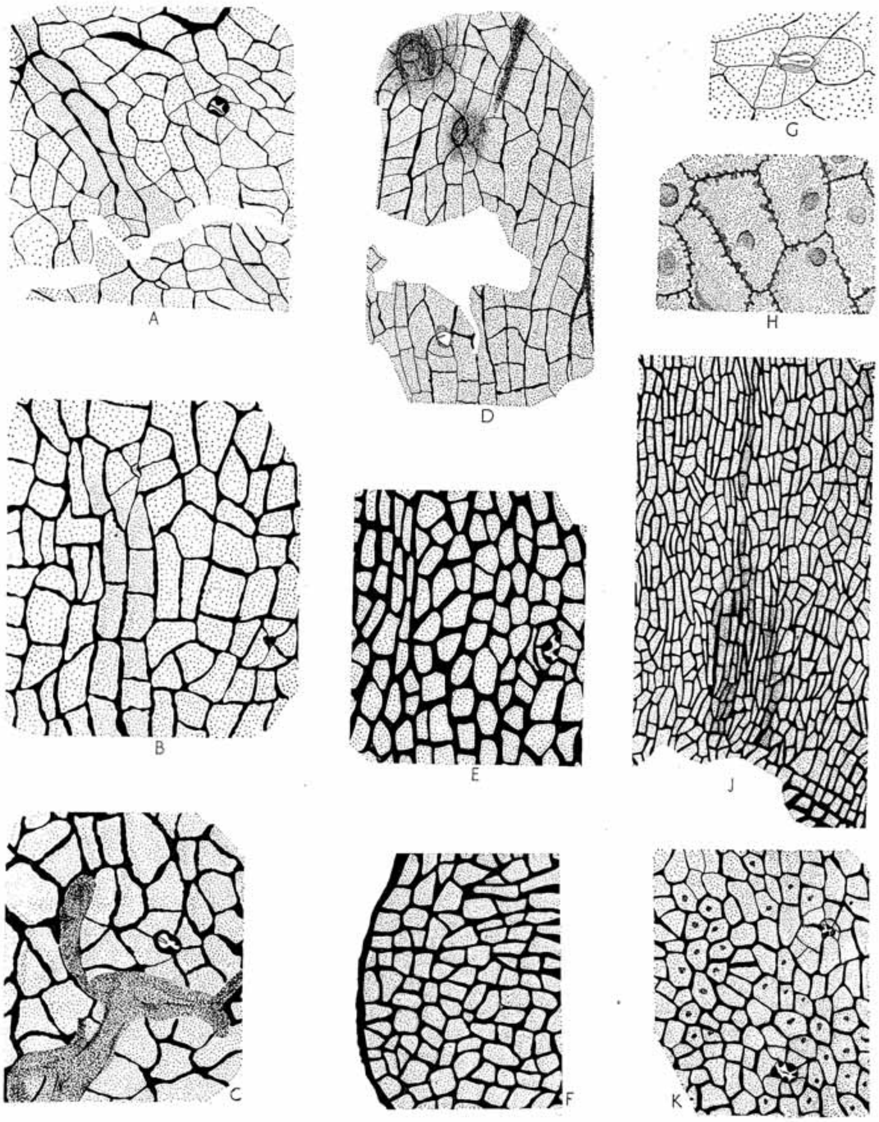
TEXT-FIG. 8. A–D, *Peltaspermum thomasi*. A, Cuticle of outer surface of marginal lobe, showing elongated cells possibly marking the course of a vein. (*Note*: the specimen was torn, and slightly rotated, in preparation); ×167. B, C, Cuticle of upper and lower surfaces of seed head (B lower, C upper), showing cell outlines and stomata. In B darker area of rectangular cells marks course of a vein: in C stippled area marks a fold in which cells are not visible; ×167. D, Cuticle of main rachis showing stoma and two trichome bases, one with proliferated cells; ×167 (A–D all v/23400). E, F, J, K, *Antevsia zeilleri*. E, Cuticle from ultimate branchlet, a part without pollen sacs. F, Cuticle from under surface of a lateral bulge, note cells at top right are similar in shape to the cells at bottom right in J; E, F ×167. J, Cuticle at pollen-sac base, showing elongated cells over mid-rib (centre), and cells probably of branchlet (bottom right); ×88. K, Cuticle from upper surface of ultimate branchlet from a place with pollen sacs on lower surface; ×167. G, *Antevsia extans*, a stoma from a pollen sac; ×327. H, *Lepidopteris stormbergensis*, cell outlines showing form of the sinuosities and papillae; ×327.


A
D
G
H
B
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J
C
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K

cuticle is of a different thickness on the two sides, and in the largest specimen the pollen sacs were all the same way up—with the dehiscence line hidden by the rock. This side corresponds to the branch surface with thicker cuticle, so I suppose the pollen sacs were borne with the dehiscence line facing downwards.

The ultimate branchlet is expanded at its apex, and this part is termed the disk. Viewed from the upper side the branchlet lies at a lower level than the disk surface and cellular striae cannot be traced from one on to the other: but viewed from the under surface, the disk surface and branchlet lie at the same level, and the cellular striae continue from one on to the other. The branchlet therefore was attached partly to the under surface of the disk as well as to its margin (Pl. 58, fig. 9; text-fig. 7E, F).

Viewed from the under side the edges of the open pollen sacs meet laterally and at the same level (Pl. 58, fig. 8; text-fig. 7F) and radiate out from the disk. Viewed from the upper side the pollen sacs and disk are in complete continuity, and though the centre of the disk is collapsed (presumably it was thick) it is not possible to see where the pollen sac ends and the disk begins (Pl. 58, fig. 8; text-fig. 7E). Supposing that the empty pollen sacs were supported by the matrix during compression (Walton 1936) the union of the pollen sacs and disk lies at the edge of the collapsed region. These appearances mean that the pollen sacs were borne partly marginally and with part of their area of attachment on the under surface of the disk. It seems clear that they were not borne wholly on the under surface of the disk.

The cuticle of both surfaces of the disk are shown in text-fig. 9B, C. Both surfaces show irregular wrinklings, and solitary trichomes were present on the upper surface. One pollen sac shows the cells of its interior surface clearly. Other pollen sacs are similar, though less clear. Along a thicker rib running for about half the length of the pollen sac (here termed the mid-rib) the cells are elongated, and the other cell rows diverge from it (text-fig. 9A). The cuticle of the pollen sacs (text-fig. 9B) is very delicate, and the cells obscure, partly owing to wrinkling of the cuticle, but the cells over the mid-rib are plainer and more elongated than the others. A few stomata are scattered over the outer face of the pollen sacs, mostly near the mid-rib (text-figs. 9B; 3E). Most of these stomata show neither radially disposed subsidiary cells, nor cutinized papillae. There is no sign of an interior cuticle. The whole pollen-sac wall is of dense substance, and only translucent in one or two places next to the dehiscence slit; in one place the pollen-sac wall is now 0·2 mm. thick.

No unopened pollen sacs were available as a source of uncontaminated pollen, but there were pollen grains adhering to the macerated pollen sacs. Of these forty-six were from 23 to 40 μ long and of one sort, eight were well over 40 μ long, but of the same sort, while three were clearly different. I accept only those grains from 23 to 40 μ long as belonging to *A. extans*, though it is possible that the larger grains belong also. The form of the grains is shown in Pl. 58 and text-fig. 7G–J. They show the same features as *A. zeilleri* and are interpreted in the same way. The dimensions of a sample of twenty grains are as follows: length 31 μ (35 μ and 23 μ); width 17·5 μ (23 μ and 13 μ); depth 16 μ (24 μ and 12 μ); interior width of furrow 8 μ (5 μ and 12 μ); depth of furrow 3 μ (5 μ and 1·6 μ), this last value I regard as rather unreliable as it was taken from ten grains only. The proportions of the grains are: length/width 1·7 (1·8, 1·7, 2·2, 1·4) and length/depth 1·6 (1·8, 1·5, 2·3, 1·4).

Du Toit's pollen-sac group (see Pl. 58, fig. 6) is identified with the present material, for it shows the same form of pollen sac, disk, and branchlet, and the dimensions agree. No microscopic detail was available to du Toit. Frenguelli's material also agrees with the present in dimensions, in showing blisters on the larger branches, and, rather obscurely, a disk to which the pollen sacs are attached (text-fig. 10A) and possibly a median rib. No microscopic detail is given. The specimens quoted above as distinct differ; I believe they belong to another plant, but here discuss them no further.

Discussion of Antevsia. The main rachis of *A. extans* is unknown, so that the two species can only be compared as regards their lateral branches, branchlets, pollen sacs, and pollen. The pollen sacs of both species are strikingly alike. The walls are massive, and the presence of stomata (a most unusual feature) suggests that photosynthetic tissue may have been present. Both species show a mid-rib. The nature of this structure is unknown, but it shows those characters which in compressions indicate vascular tissue; a strand of thicker substance, and epidermal cells modified in shape over it. The pollen of the two species is indistinguishable. I can find no difference in form and an effort to separate the two statistically (sample of 46 grains of *A. extans* and 50 of *A. zeilleri*) failed since the Standard Error of each sample was greater than the difference between the Means.

These resemblances are held to justify the inclusion of both *A. zeilleri* and *A. extans* in one genus.

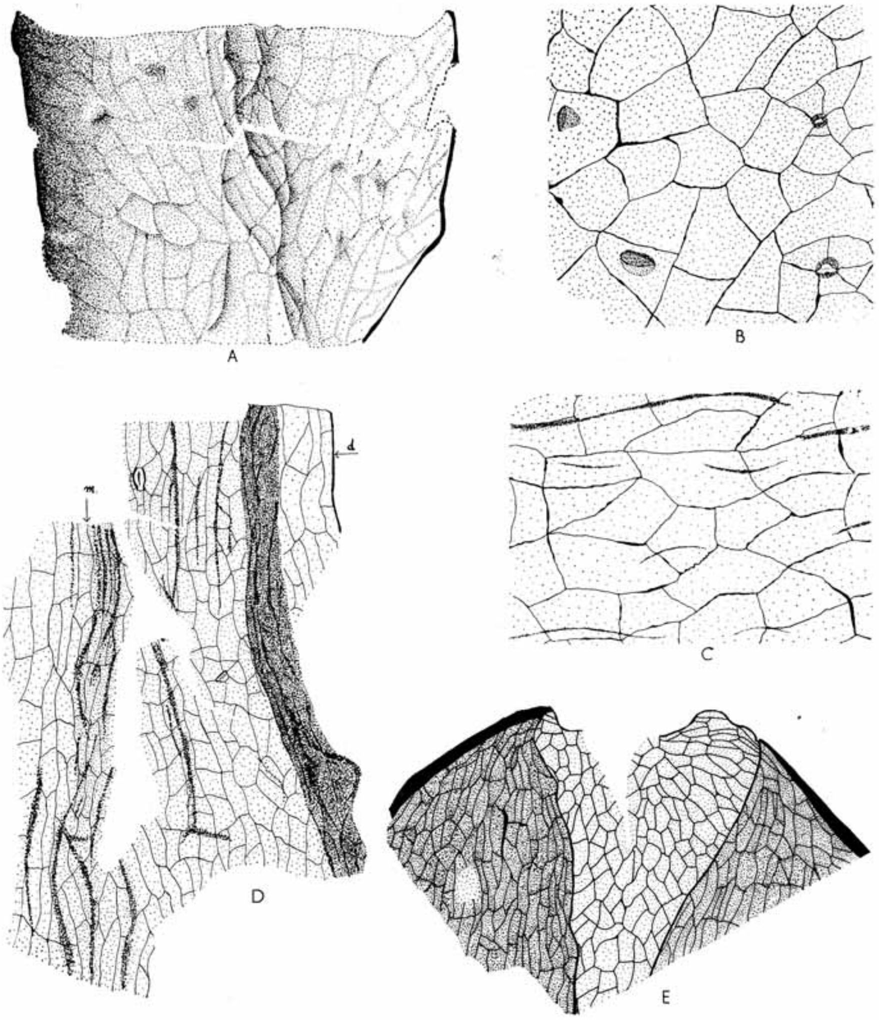
The differences lie in the number and the manner in which the pollen sacs are borne (p. 349 and see text-fig. 7). These differences I regard as variations on a common plan, and they can be explained away in at least three ways. Either we may regard *A. extans* as arising from *A. zeilleri* by specialization of the fertile part and reduction of the pollen sacs to four—perhaps two pairs; or *A. zeilleri* can be regarded as derived from *A. extans* either by amplification in the number of pollen sacs, or by the condensation of several fertile apices of *A. extans* to form one fertile apex of *A. zeilleri*. All three alternatives have to face considerable difficulties, and I do not think it is possible at present to make a choice between them.

Antevsia does not closely resemble other known Mesozoic pollen organs. Two show some approach, *Sphenobaiera furcata* (see Krausel 1943, 1955) and *Antholithus wettsteini* (see Krausel 1955), but both differ in the shape and number of pollen sacs at each fertile apex, and apparently in the construction of the pollen-sac wall and stomatal construction. The isolated pollen grain *Monosulcites minimus* Cookson (see Couper 1953, 1958) is, in figures, indistinguishable from the pollen grains of *Antevsia*. *M. minimus* is an artificial assemblage ranging the Mesozoic which cannot in Couper's opinion be subdivided as yet.

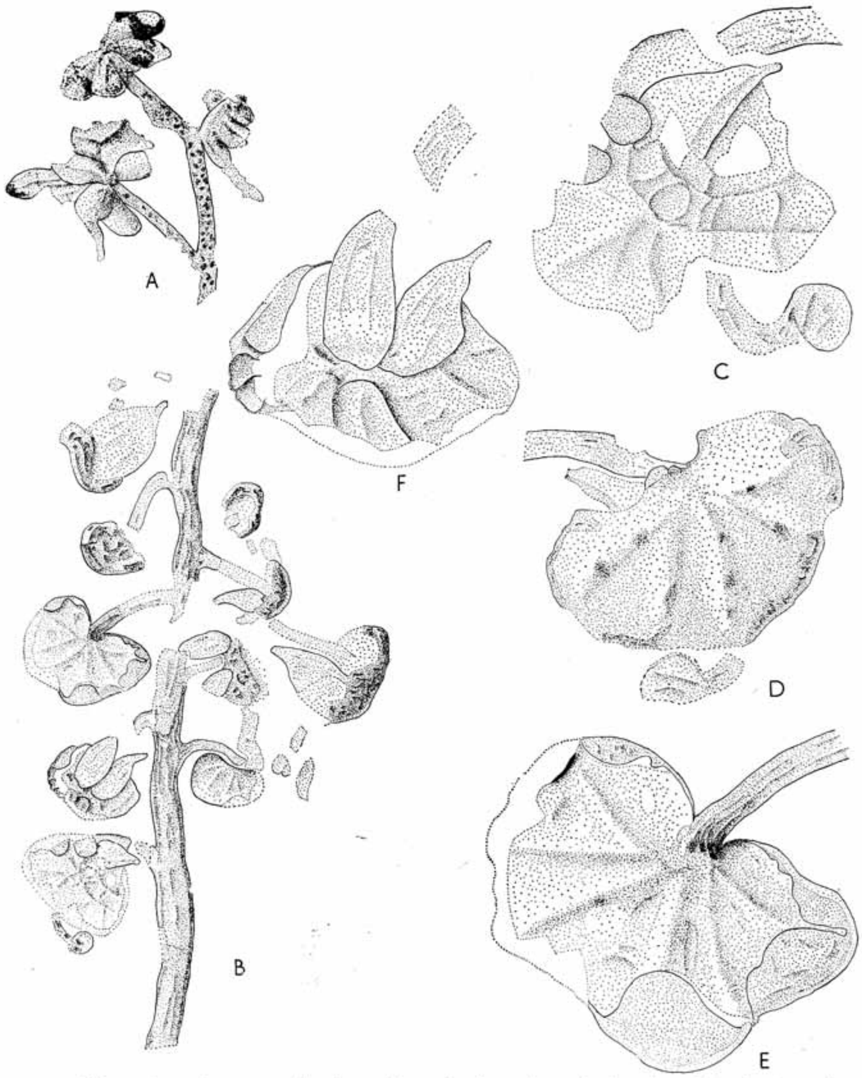
PELTASPERMUM Harris 1937

Type species *P. rotula* Harris

Diagnosis (emended). Whole organ with alternate branches in one plane. Seed-bearing heads borne at branch ends, of thick substance, showing five to fifteen (probably vasculated) marginal lobes over arching surface of head bearing the seeds. Rachis and branches showing blister-like swellings, upper surface of seed head similar. Seeds borne on lower surface of head, either two, lateral to insertion of branch (*P. thomasi*), or ten to twelve in a ring around insertion of branch (*P. rotula*). Cuticle showing stomata of *Lepidopteris* sort. Seeds (*P. rotula* only) with prominent micropyle and free nucellus.



TEXT-FIG. 9. A–D, *Antevsia extans*. A, Interior of pollen sac in transfer, showing cells and mid-rib; ×156. B, Cuticle of upper surface of disk showing cells, two stomata, and two trichomes; ×167. C, Cuticle of lower surface of disk; ×167. D, Cuticle of pollen sac, a fold to right, two stomata; *d*=dehiscence line, *m*=midrib; ×156. E, *A. zeilleri*. Cuticle at apex of pollen sac showing cells along the dehiscence line and equidimensional cells near apex; ×100.



TEXT-FIG. 10. A, *Antevsia extans*. Specimen from the Argentine, showing branching (redrawn from Frenguelli 1944, pl. 1, fig. 1); ×1. B–F, *Peltaspermum thomasi*. B, The part of type specimen, showing pinnate arrangement of branches; ×6. C, D, First seed head on left showing seed-scar (C on left), seed, veins, and two marginal lobes (part and counterpart; the detached object is of unknown nature); ×9. E, Third seed head on left of part, showing four marginal lobes and veins (the other lobes are broken off); ×9. F, Second seed head on left of part, showing two seeds and three marginal lobes; ×9. All from v/23400.

Peltaspermum thomasi Harris

Plate 58, figs. 2, 3; text-figs. 3F; 8A-D; 10B-F; 11

1933 *Lepidopteris natalensis* Thomas (in part only), pp. 251, 254, pl. 24, fig. 75; text-fig. 55. Type specimen described (under same name as leaf).
1937 *Peltaspermum thomasi* Harris, pp. 34–35. Diagnosis.

Diagnosis (emended). Main rachis showing small blisters and lateral wing; seed-bearing heads attached marginally, showing five or six marginal lobes, and pinnately branched veins on lower surface; interval between veins about 0·5 mm. Seeds two per head, attached laterally to branch insertion, about 3 mm. long and 1·5 mm. wide.

Description. The material consists of the type and two other specimens (v/23400, v/35798, and v/35799, Brit. Mus. (Nat. Hist.)), all from the Burnera Waterfall locality. The type was described by Thomas (1933), but my interpretation differs from his.

In v/23400 the specimen is compressed on one bedding plane, but the others traverse several, and probably preserve the original shape of the organ more nearly. Upon this view the seeds pointed down towards the base of the organ. The cuticle of one side of the rachis is thicker than the other, and this suggests that the organ may have been upright or inclined rather than pendulous.

The rachis and branches have a cuticle like that of *L. stormbergensis*, showing trichomes, stomata, and a wing (text-figs. 3F; 8D). Though not all are clearly shown the evidence is fully consistent with the view that the branching was pinnate, for the wing on the branches is decurrent on to the wing on the rachis without sign of twisting in the cell rows (Pl. 58, fig. 2; text-fig. 10B). Like the pinnae of the leaf the branches are attached towards one (presumably the upper) surface of the rachis (text-fig. 11A).

The round or cordate seed-bearing heads are attached at one edge and not in the middle. The lower epidermis of the branch passes gradually into the lower epidermis of the head, and the upper into the upper epidermis of the head, but most of the attachment lies on the lower surface of the head, so that head and branch do not lie at the same level (text-fig. 10D, E). The whole head is of thick substance, and its upper surface is raised in irregular wrinkles, especially towards the margin, but at the extreme margin there is a flat rim about 0·5 mm. wide (text-fig. 10D, E). Presumably, therefore, the whole head was thick, or dome-shaped, and the flat rim is a compression border (Walton 1936). At the margin of the heads, lying just inside the compression border (text-fig. 10C, E, F), there are semicircular lobes, about 1 mm. high at a maximum. In one head (text-fig. 10E) there were six occupying the whole circumference. The cuticle of the lobes is similar to the cuticle of the head, and there are no internal cuticles, or signs of a micropyle, so that they cannot be seeds. The arrangement of epidermal cells (text-fig. 8A) suggests the lobes may have been vasculated, and there appear to be as many lobes as veins in the head.

The lower cuticle of the heads is only broken by the seeds, and by scars believed to mark the insertion of seeds. Three heads show clearly (text-fig. 10C–F) a system of raised lines, over which the cells are elongated, and which on incomplete maceration show a strand of dark substance (text-fig. 8B). These lines are therefore veins. The cuticle of the upper surface of the head is shown in text-fig. 8C.

In two heads there are two seeds lying laterally to the branch insertion, and more or less over the first dichotomy of the vein (text-fig. 10F). In another head only one seed was present, but there is a scar in the corresponding position (text-fig. 10C). In the other heads there is one seed shown. I suggest that two seeds per head is probably the normal.

The seeds (which may not be mature) are about 3 mm. long and 1·5 mm. wide, with a micropyle which is slightly curved away from the branch. I have not macerated any seeds, since there are so few.

Discussion of Peltaspermum. The two species of *Peltaspermum* are superficially rather different. *P. rotula* has peltate radially symmetrical seed heads, 10–12 seeds, and 10–15 marginal lobes: *P. thomasi* has bilaterally symmetrical seed heads, attached marginally, 2 seeds and 5 or 6 marginal lobes. Nevertheless, the two species appear to be organized on the same plan, so they are left in one genus. Thus the seed heads of *P. rotula* were unattached, but there is evidence that they were borne in two rows on a central rachis (Harris 1932, p. 66). The seed heads of *P. rotula* were certainly thick (Harris 1932, pp. 65–66), and I suggest that the rim shown in Harris's reconstruction is a compression border. This is supported by the appearance of some Swedish material of *P. rotula* (Lundblad 1950) which is preserved 'in the round'. Lundblad found that in her Swedish material there were as many ridges between the seeds as marginal lobes (cf. also Harris 1932, pl. 8, figs. 1, 2, 9), while the cuticle of the lower surface of the heads is stated to consist of elongated (rectangular or polygonal) cells. Lundblad's discovery suggests that, as in *P. thomasi*, the lobes may have contained vascular tissue which continued within the head, between the seeds.

GENERAL DISCUSSION

(*a*) *Reference of isolated organs to the parent plant. Lepidopteris ottonis*, *Antevsia zeilleri*, and *Peltaspermum rotula* are all referred to the same plant because they all show blisters on their rachis cuticles and the same sort of stomata, two features not found together in other plants of the holoarctic Rhaetic floras. In addition, leaf, pollen, and seed organ are found together in several localities in Greenland and Sweden, and in some of these *L. ottonis* is the local dominant (Harris 1932; Lundblad 1950).

The same arguments are applied to *Lepidopteris stormbergensis*, *Antevsia extans*, and *Peltaspermum thomasi*, and as far as I know no other plant in their flora shows the combination of blisters and stomata of the *Lepidopteris* sort. Evidence from association is weaker than in the case of the *L. ottonis* plant. If the identifications suggested hold, *L. stormbergensis* and *A. extans* are found together in three localities, the Waterfall, near Cacheuta, and Aliwal North; but other plants are also common to these three localities. *P. thomasi* is known only from the Waterfall. However, the evidence for relationship between the *L. ottonis* and *L. stormbergensis* plants automatically supports also the reference of each isolated organ to its parent plant.

(*b*) *The Morphology of* Antevsia *and* Peltaspermum. Previous authors (e.g. Harris 1932; Thomas 1932; Hirmer 1939; Frenguelli 1944) have considered *Antevsia* to be a microsporophyll. I agree, taking 'sporophyll' to mean an organ that is like a leaf, but not pursuing the question of the ultimate meaning of the term. *Antevsia* shows pinnate branching like a compound leaf, and not spiral or whorled branching like a stem. The organ also is flattened in one plane, at least as regards the first branching.

Likewise, I think that *Peltaspermum* is a sporophyll (but see Thomas 1933). *P. thomasi* is flattened in one plane, and shows pinnate branching like the leaf; and probably *P. rotula* is similar. The seed-bearing heads of *P. thomasi* are bilaterally symmetrical, and show a pinnate plan of venation. *P. rotula*, however, is unique (see Harris 1932; Hirmer 1939; Lundblad 1950), but is referred to the youngest member of the family, and I suggest that the form of its seed heads can be regarded as secondary and derived, just as peltate Dicotyledonous leaves are regarded as derived.

TEXT-FIG. 11. *Peltaspermum thomasi.* Part (A) and counterpart (B); v/35798; ×3.

Peltaspermum thomasi can be compared with the multi-ovulate cupule *Gnetopsis elliptica* Renault 1885 (and see Walton 1949), for they are about the same size, and the basic construction of the seed-bearing portions appears to be similar. There are important differences; for example, *G. elliptica* has seeds which somewhat resemble *Lagenstoma* (see Oliver and Salisbury 1911). This similarity between *Gnetopsis* and *P. thomasi* strengthens Harris's (1932) suggestion that *Peltaspermum* is best regarded as a multi-ovulate cupule (for a discussion of the cupule see, for example, Halle 1937; Walton 1949); and makes it improbable that the seed heads of *Peltaspermum* are more or less unmodified pinnules such as bear seeds in some pteridosperms (see Halle 1929, 1931).

(*c*) *The relationships of the Peltaspermaceae*. As they are interpreted, the Peltaspermaceae resemble the Pteridospermae (= Cycadofilicales) and no other group of gymnosperms. They show no particular approach to the other groups of (presumed) pteridosperms in the Mesozoic, the Corystospermaceae (Thomas 1933) and *Harrisia marsilioides* (see Lundblad 1950) with its leaf *Ptilozamites*. Gothan and Weyland (1954) have classified the Peltaspermaceae with the Caytoniales (probably having affinities with pteridosperms, see Harris 1951), but the only similarity is that both groups have reproductive organs built on a pinnate plan.

Among Palaeozoic pteridosperms, the Peltaspermaceae show one distinct point of resemblance to the Lyginopterideae, namely that two vascular traces enter the leaf base which then unite. This is quite different from the structure of the medulloseaen petiole.

The leaf *Lepidopteris* shows some interesting similarities with the leaf *Paripteris* Gothan (1941, 1953). In both the rachises are blistered (text-fig. 4J, K, and Gothan 1941), though the structure of the blisters in *Paripteris* is not known; in both there are zwischerfiedern, which continue on to the abaxial leaf surface, where they may form tufts (text-fig. 4J, K, see Bertrand 1930); and both have stomata typically surrounded by radially disposed subsidiary cells (text-fig. 6E). None of these features appears to be very common among fossil leaves, and, so far as I can discover, no other leaves show the combination. There are differences; *Paripteris* is at least tripinnate, paripinnate, and of neuropteroid pinnule form and venation.

The reproductive organs of *Lepidopteris* cannot be closely compared with any known Palaeozoic pollen or seed organ. *Antevsia* has been tentatively compared with *Urnatopteris* (see Harris 1932) and *Crossotheca* (see Harris 1932; Thomas 1936; Frenguelli 1944), but *Crossotheca* has bilocular pollen sacs (at least in the better-known species) partly adnate to the 'fertile pinnule', and round pollen grains without a sulcus but with a triradiate mark (see Kidston 1906, 1923; Florin 1937; Remy 1955). *A. extans* can be visualized in terms of a *Potoniea* in which the pollen sacs have been reduced to four and the 'fertile pinnule' to the disk (see Halle 1933; Florin 1937; Remy 1955), and this comparison gains force slightly since *P. adiantiformis* has been found in organic connexion with *Paripteris gigantea* (Gothan 1913). But the differences in form between *Potoniea* and *Antevsia* are great, and the pollen is different. The isolated Rotliegend fossil *Pteridospermostrobus gimmianus* Remy (1954) appears to have a structure a little like *Antevsia*, but its pollen is quite different from *Antevsia*.

Gnetopsis elliptica is the only fossil that appears to be at all like *Peltaspermum*; it has only been found isolated, and its affinities are uncertain, though it is not medulloseaen.

Among the Pteridospermae, therefore, the Peltaspermaceae show one distinct point of resemblance to the Lyginopterideae, and a rather tenuous resemblance to the Potonineae. Nowhere do they show any resemblance to the Medulloseae. They must still be considered a group on their own, but perhaps lying not far from the Lyginopterideae. I can find no support for Thomas's (1932) suggestion that they might show some approach to the Angiosperms.

The earliest record of *Lepidopteris* is from the Thuringian of Europe; the southern hemisphere records are all Triassic. It thus seems more probable that the family originated in the northern hemisphere and spread over the rest of the world from there, than that it is southern in origin.

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JOHN A. TOWNROW,
Botany Department,
University of Reading

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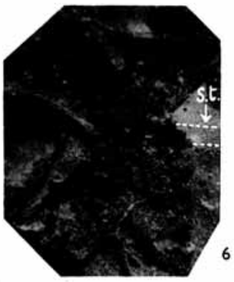

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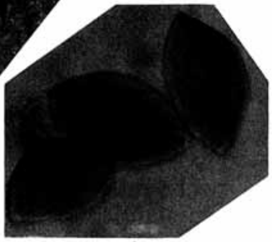
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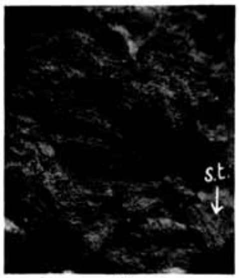

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TOWNROW, Peltaspermaceae