

A REVISION OF THE CARBONIFEROUS LYCOPOD GENUS *ESKDALIA* KIDSTON

by B. A. THOMAS

ABSTRACT. *Eskdalia minuta* Kidston has previously been described as a fern stem, but closer examination of its macroscopic features and a study of its cuticle shows it to be a ligulate lycopod stem. The genus of Russian paper coal cuticles, *Porodendron* Zalessky, is shown to be a synonym of *Eskdalia*.

THE type specimen was originally described by Kidston (1883) as *Caulopteris minuta*. This specimen, together with three others, later provided Kidston with the basis for his new genus *Eskdalia* and all four specimens were named *E. minuta*. Kidston still believed them to be probably fern stems, but subsequent examination of the specimens and of their cuticles has shown the species to consist of ligulate lycopod shoots (Chaloner 1967).

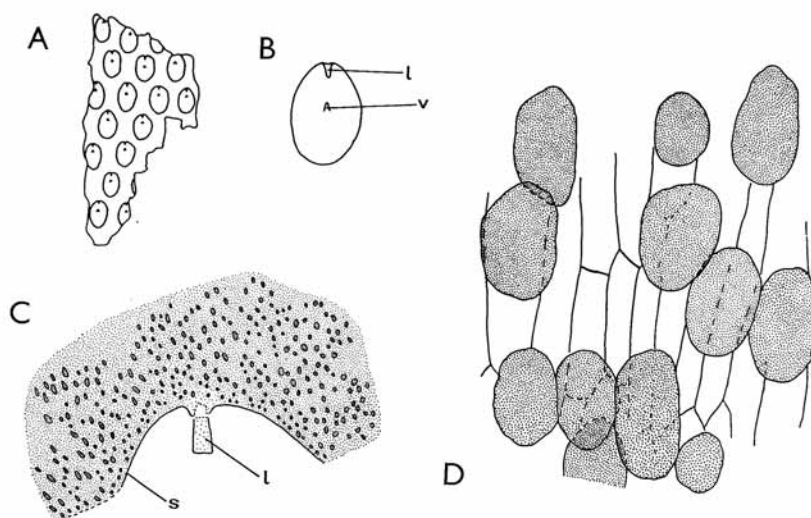
Kidston's specimens are the type, No. 5594, Geological Survey, Edinburgh, from Kershope Burn, Liddesdale, Dumfriesshire and Nos. 2739, 2740, and 6731, Kidston collection, Geological Survey and Museum, London, from Clencartholm, Eskdale, Dumfriesshire. The species has also been recorded from the river Coquet, half a mile north-north-east of Holystones, Northumberland (Kidston 1903, p. 820). The known distribution is therefore limited to the Cementstone group of the Lower Carboniferous.

Cuticle was prepared from the type specimen and No. 2740 by macerating portions of coalified compression in concentrated nitric acid and potassium chlorate. Large pieces were obtained from No. 2740 but only small fragments from the type specimen as its carbon split and sometimes completely broke up during maceration. No. 6731 is preserved as an impression so no cuticle could be prepared from it and No. 2739 although a compression gave no cuticle.

Nos. 5594, 2740, and 6731 are large stems but No. 2739 is much narrower than the others and its description is best kept separate. The three large specimens are straight unbranched shoots with oval elongated scars. The stem surface between the scars is flat but ornamented in all three specimens with large numbers of minute lumps, up to 100 μ wide. These lumps are sparsely scattered in No. 5594 but rather more crowded in the other two specimens. No stomatal pits are visible. The leaf scars are in a low-angle spiral of about 10–15° to the horizontal. They are separated from those scars above and below by about a length of a scar and from those on either side by one to two widths of a scar. The scar surface is slightly raised in Nos. 2740 (Pl. 82, figs. 3–5) and 6731 (Pl. 82, fig. 6) but slightly sunken in No. 5594 (Pl. 82, figs. 1, 2). The scars have a sharp margin and the stem cuticle ceases abruptly at this margin, there being none over the surface of the scar; this shows that it is truly a scar. The scar outlines are almost perfectly oval, but may be interrupted at the apex by a slight notch. A minute groove, about 0.4 mm. long and 0.15 mm. wide is sometimes visible running down from the scar apex. These grooves are plainly seen in most of the leaf scars of No. 2740, but not in Nos. 6731 and 5594 where the notch alone is seen in a few scars and there only obscurely. Maceration

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of coaly material from the top of the scar proves that a ligule pit is present. It is situated under the groove and is the same shape and size; I imagine that the groove is not an original feature but is caused by a collapse during compression. The cuticle of the ligule pit is attached to the margin of the stem cuticle surrounding the scar (Pl. 82, fig. 7, and text-fig. 1). The vascular prints are shown most clearly in No. 5594 and their structure



TEXT-FIG. 1. *Eskdalia minuta* Kidston, No. 2740, Kidston collection. A, complete specimen showing the arrangement of the leaf scars. $\times 1$. B, single leaf scar showing the position of the underlying ligule pit (l) and the vascular print (v), $\times 4$. C, stem cuticle from the apical region of a leaf scar showing the outline of the leaf scar (s) and the ligule pit cuticle (l). Some, but not all, of the resistant excrescences have been included to give an indication of their size. Slides PF.4417 and PF.4418, $\times 20$. D, stem cuticle showing epidermal cells and overlying resistant excrescences. Slide PF.4417, $\times 300$.

is described and discussed later. In No. 2740 the vascular prints are very faint, being only visible as raised ridges, and in No. 6731 they are indistinguishable.

The fourth stem figured by Kidston (No. 2739) is much narrower than the other specimens, being only 4 mm. broad. The scars are oval and slightly raised but only a few have visible vascular prints and no ligule pits can be seen. The stem surface is smooth possessing no lumps and unfortunately no cuticle could be prepared to show epidermal details. However, the shedding of leaves on such a small shoot is an important feature and can be taken as evidence of its lycopod affinity.

The cuticles of both Nos. 5594 and 2740 are rather thick. The only cells visible are elongated and have straight, rather finely marked outlines; the anticlinal walls only projecting slightly. In part of the cuticle of both specimens there is a border to the cell outline especially at the cell corners, making the cell interior rounded. The cell surfaces are flat but many solid lumps of resistant matter are present on the outer surface of the cuticle. These are most probably the same as the bulges which ornament the stem

surface. These lumps are oval-rounded, usually slightly elongated, and vary in size to about 100 μ . They are irregularly arranged and in many places partly obscure the underlying epidermal cells. The lumps often overlap and where the cuticle is torn many project beyond the broken edge, suggesting that they are somewhat separate excrescences. In No. 6731, where the stem has been lost and the imprint alone remains, many of these lumps are still embedded in the rock.

DISCUSSION

The reason Kidston gave for believing *Eskdalia* to be a *Caulopteris*-like stem was that he thought the vascular prints to be horseshoe shaped. The lower part of the holotype clearly shows oval areas within each leaf scar which are often interrupted at the apex to resemble horseshoes and are evidently the features referred to by Kidston. These 'horseshoes' are raised, but it must be made clear that the lower half of the specimen is really an impression as most of the specimen except a little carbonized material has been lost. Chaloner (1967, p. 525) suggested that they represented matrix infilling of lacunae which more or less surrounded the leaf traces as they passed through the outer cortex. However, the 'horseshoes' and the shallower central areas they surround are entirely carbonaceous. Thus it seems more probable that the 'horseshoes' of Kidston represent the remains of a strong relatively non-compressible tissue. Graham (1935, p. 605, figs. 50, 51) has described such a condition in a lycopod leaf where the xylem and phloem are almost surrounded by an arc of sclerenchyma. This might well have been the condition in *Eskdalia*; Kidston's 'horseshoe' being on this interpretation sclerenchyma and not an arcuate scar as Kidston supposed. The differential compression of the tissues has probably been brought about by the infilling of the stem with mineral matter. In contrast, No. 2740 does not show horseshoe-shaped marks because very little mineral matter ever got inside this specimen and the surfaces came to lie in close proximity like a collapsed tube.

The cuticle of *E. minuta* is very similar to that described from the Russian paper coal of the Lower Carboniferous of the Moscow basin. Both are flat sheets with regularly spaced perforations marking the positions of leaf scars. A small tube of cuticle hangs from the edge of the cuticle at the apex of each perforation. These tubes of cuticle were originally described as rolled up portions of leaf cuticle (e.g. Zeiller 1882, Zalesky 1915) or rolled up cuticle which had formed over the leaf abscission area (Bode 1929). However, Walton (1925) and Wilson (1931) have shown them to be really the internal linings of ligule pits. The Russian cuticles have been given various names. They were originally described as a species of *Lepidodendron* by Eichwald (1860), Auerbach and Trautschold (1860), and Göppert (1861), then as *Bothrodendron punctatum* by Zeiller (1880, 1882), but Zalesky (1915) instituted a new genus *Porodendron* for them and is followed in his nomenclature by modern Russian workers (e.g. Orlov 1963). Nathorst (1894) had suggested *Porodendron* as a possible alternative name to *Bothrodendron* but did not finally use it, nor did he give it a diagnosis. He should not, therefore, be regarded as its author as quoted by Bode (1929). The species of *Porodendron* have been defined on leaf scar shape which varies from round to oval or heart-shaped and on the structure of the epidermal cells which are normally hexagonal, isodiametric, or slightly elongated. No species has been described with any resistant excrescences on their outer surface.

Distinction between the Russian paper coal cuticles and that from *E. minuta* is therefore limited to leaf scar shape, epidermal cell shape and size and presence or absence of resistant excrescences. Such differences are of value only at the specific and not the generic level and thus *Porodendron* Zalessky is a synonym of *Eskdalia* Kidston.

Nathorst (1914) described a small lycopod cone compression as *Porostrobus zeilleri* believing it to be the fructification of *Porodendron*. Bhardwaj (1958) has subsequently shown the holotype to be heterosporous as might have been expected for a ligulate shoot such as *Porodendron* (= *Eskdalia*). However, as Chaloner (1962, p. 83) has already pointed out, the cone was not found in organic connexion with the stem and mere association is not sufficient evidence for believing them to be parts of the same plant.

SYSTEMATIC DESCRIPTION

Genus *Eskdalia* Kidston

- 1903 *Eskdalia* Kidston, p. 750.
 1909 *Porodendron* Zalessky, p. 5.
 1914 *Porodendron* Zalessky; Nathorst, p. 68.
 1929 *Porodendron* Nathorst (non Zalessky); Bode, p. 134.

Type species. Caulopteris minuta Kidston, p. 541, pl. 31, figs. 1, 1a.

Emended diagnosis. Lycopod stem with round-oval or heart-shaped leaf scars in low angle spirals. Leaf scars almost level with stem surface. Ligule pit at apex of leaf scar and projecting beneath it, forming a narrow cutinized tube. One simple vascular print present slightly above middle of leaf scar. No parichnos present.

Eskdalia minuta Kidston

Plate 82, figs. 1-9; text-fig. 1

- 1883 *Caulopteris minuta* Kidston, p. 541, pl. 31, figs. 1, 1a.
 1903 *Eskdalia minuta* Kidston, pp. 750, 820, pl. 1, figs. 4-8.
 1967 *Eskdalia minuta* Kidston; Chaloner, pp. 525-6, fig. 361.

Holotype. Specimen No. 5594, Geological Survey of Scotland, Edinburgh.

Emended diagnosis. Leaf scars oval, length about one and a half times breadth. Scars separated from those above and below by about a scar length, from those on either side by one to two scar widths. Epidermal cells elongated, about 130 μ long, 25-35 μ broad. Anticlinal walls 1 μ thick, straight, smooth. Periclinal walls flat. Surface bearing

EXPLANATION OF PLATE 82

Figs. 1-9. *Eskdalia minuta* Kidston. 1, 2. Holotype, No. 5594, Geological Survey, Edinburgh. 1, Near side of specimen visible in upper half and the impression of its far side in the lower half, $\times 1$. 2, Portion showing the structure of the leaf scars and vascular prints, $\times 3\frac{1}{2}$. 3-5, No. 2740, Kidston collection. 3, Complete specimen, $\times 1$. 4, 5, Parts of bark surface showing leaf scar and stem details, $\times 4$. 4, Illuminated from above to show leaf scars and vascular prints. 5, Illuminated from below to show ligule pits and surface markings between the leaf scars. 6, No. 6731, Kidston collection, $\times 1$. 7-9, Cuticle from No. 2740. 7, Cuticle from immediately above a leaf scar showing the outline of the scar and point of attachment of a broken ligule pit, $\times 20$. 8, 9, Cuticle showing cellular detail and the resistant excrescences on the outer surface, $\times 100$. Slide PF.4417.

resistant lumps up to about $100 \times 50 \mu$. No stomata. Ligule pit about 400μ long, 150μ broad with rectangular cells $15-20 \mu$ long, 20μ broad in longitudinal files. Anticlinal walls 1μ thick, straight, smooth. Periclinal walls flat, smooth.

Stratigraphic occurrence. Cementstone Group, Calciferous Sandstone Measures, Lower Carboniferous Limestone Series of Northern England and Southern Scotland.

COMPARISON

There are many other arborescent lycopod genera rather similar to *Eskdalia*. Of these *Cyclostigma* Haughton, *Pinakodendron* Weiss, *Scutellocladus* Lele and Walton, and *Angarodendron* Zalessky are described as eligulate and thus differ in a very important respect. *Bothrodendron* Lindley and Hutton differs in having parichnos prints on the leaf scar. Moreover, most of the species of this genus have the ligule pits situated a little above the leaf scar and separated from it by a narrow band of stem epidermis. The described epidermises of *Bothrodendron* also differ in having many stomata (Thomas 1967).

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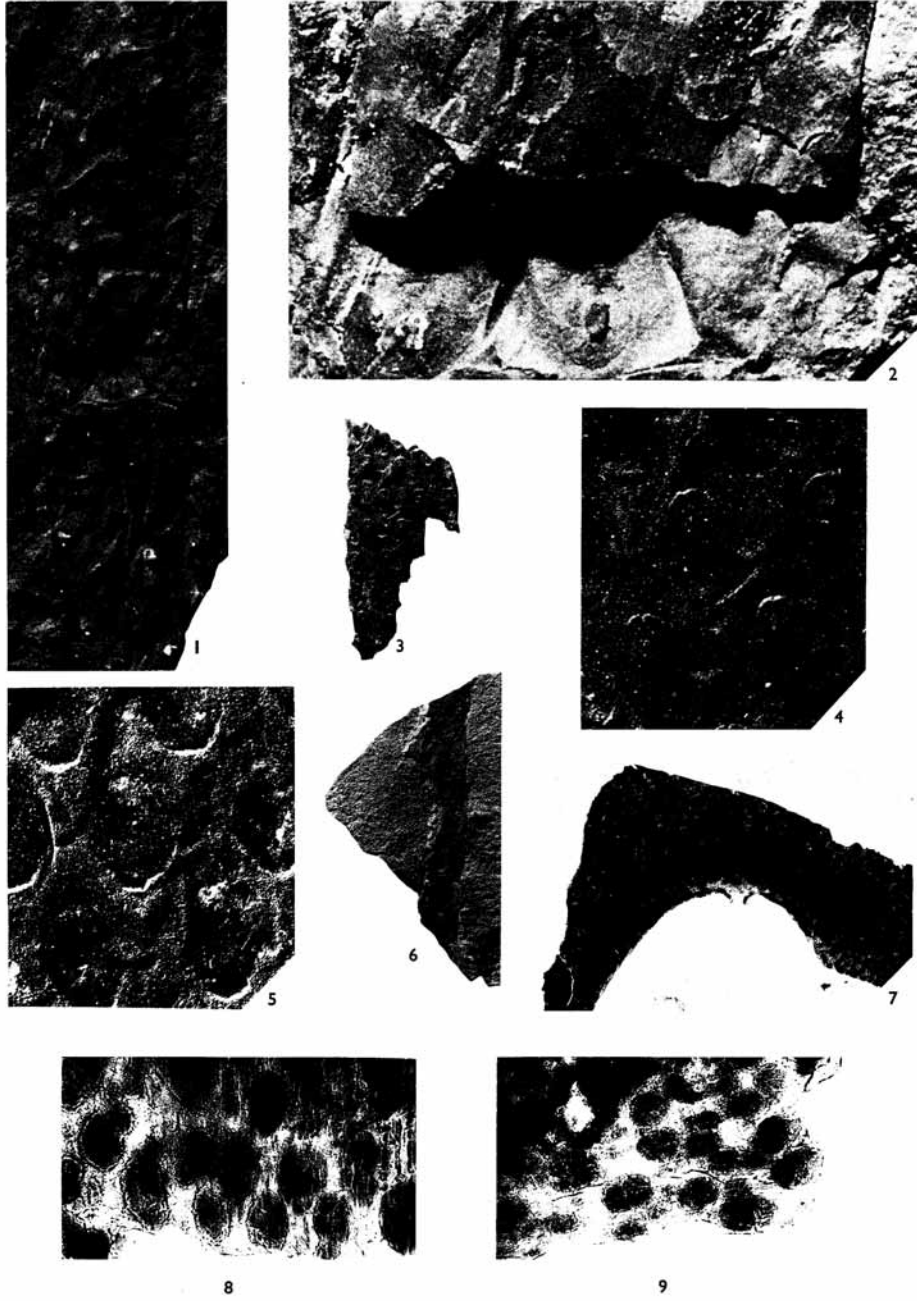
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B. A. THOMAS
Department of Botany
The University
Newcastle upon Tyne 1

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