

# A REAPPRAISAL OF THE LOWER CARBONIFEROUS LEPIDOPHYTE *ESKDALIA* KIDSTON

by B. A. THOMAS and S. V. MEYEN

ABSTRACT. Two new species of *Eskdalia* are described from the Lower Carboniferous of Siberia. *Eskdalia* has been thought to possess true leaf scars produced as a result of leaf abscission. The new specimens similarly have misleading oval areas thought to indicate leaf abscission. However, closer examination and consideration of sedimentary effects upon preservation, shows that leaves are still attached although their preservation is poor. The genus is rediagnosed and compared with other similar lepidophytes.

*ESKDALIA* was originally thought to be a fern rachis by Kidston (1883), but was later clearly shown to be a ligulate lycopod shoot (Chaloner 1967; Thomas 1968). Such specimens have very distinct longitudinally elongated oval areas which have been interpreted as leaf scars by comparison with other genera and because they lack maceratable cuticle. Stem cuticle can be prepared, but perforations are present at the sites of the ovals. Small depressions can be seen in the upper margins of many of the ovals and macerations showed them to be the remains of ligule pits. Similar cuticle with perforations and ligule pit tubes have been described many times from the Russian paper coal of the lower Carboniferous of the Moscow basin. They were originally described as species of *Lepidodendron* by Eichwald (1860), Auerbach and Trautschold (1860), and Göeppert (1861) or of *Bothrodendron* by Zeiller (1880, 1882). Zalesky (1915), however, named them as species of a new genus *Porodendron* and was followed by most Russian authors until they were referred to *Eskdalia* (Thomas 1968; Meyen 1972, 1976). Meyen (1976), however, also remarked that there is a similarity between *Eskdalia* and certain other Angaran lepidophytes, notably *Tomiodendron varium* (Radcz.) Meyen and those described as *Lepidodendron* (?) cf. *planum* by Rasskazova (1962) (now *Tunguskadendron borkii* Meyen and Thomas *in press*). Also, in comparison with *Angarodendron* and *Ulodendron*, Meyen made the suggestion that the perforations seen in such stem cuticles may possibly be the result of cuticle being absent from persistent leaves, rather than the leaves having been shed by means of definite abscission layers located at the levels of the stem cuticle perforations. There are other genera which similarly show cuticles with perforations but no ligule pits, even though they are leafy and probably heterosporous. So suggestions have been made about leaves having no cuticle, ligules being either short or situated on unclear or unpreserved leaves, or such axes being remnants of cones that have lost their sporophylls and sporangia.

There is an obvious need for much more information on this topic. It was therefore thought to be highly desirable to reinvestigate *Eskdalia* and certain similar forms in an attempt to clarify this situation.

## LOCALITIES AND STRATIGRAPHY OF NEW MATERIAL

Two new collections were available for study, each with several specimens. Both are housed in the collections of the Geological Institute of the Academy of Sciences in Moscow. Collection 1 constitutes specimen nos. 3779/81-92 and 4034/2-5. They are preserved on a blue green siltstone from 'Kyutyungde' locality, the right bank of the Kyutyungde River in Eastern Siberia, 12 km from its mouth and 2 km below the mouth of the Khalomalokh (70° 43' North, 123° East). The sediments have been dated by associated marine fauna as Tournaisian (it is difficult to be more precise, but it is not equivalent to that part of the Tournaisian that is referred in W. Europe to the Devonian. Collection 2 Constitutes specimen nos. 4034/1 and 9. They are preserved

in grey shale from the number K-3 borehole (depth 930 m), between the Kempendyai and Namana Rivers, 65 km east of the village of Kempendyai, Eastern Siberia (roughly 62° North, 119° 48' East). It is dated as the upper part of the Kurunguryakh suite (Visean) of the Vilyui syncline (Kolodeznikov 1982). The miospores from 'Kempendyai' have been described by Pashkevich *et al.* (1978).

#### DESCRIPTION

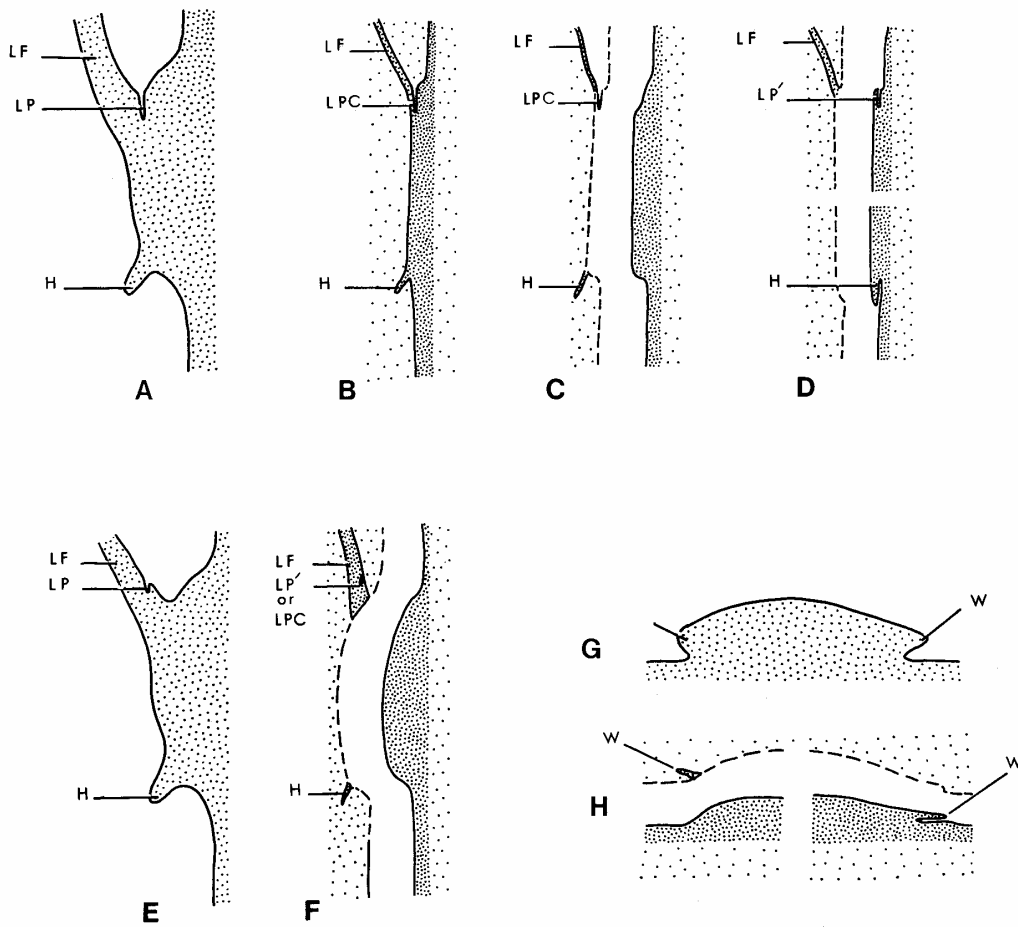
All the specimens clearly show the longitudinal elongated oval areas typical of *Eskdalia* and remains of ligule pits can be seen in their upper angles. One minor difference between the new specimens and those described previously by Zalessky (1915), Chaloner (1967), and Thomas (1968) is the manner of preservation of the pits. The earlier specimens had tubes of cuticle representing the inner linings of the actual pits. The new Russian specimens have their pits preserved as casts similar to those described by Meyen (1972, 1976) and Thomas and Purdy (1982).

Specimens from both collections were examined closely for details. This involved transferring portions of stems using Darrah solution (Darrah 1952), degaging around the edges of the ovals and at the sides of the stems, and macerating stem compressions using Schulze's solution followed by dilute ammonia solution. Both collections show some variation, but there appear to have been enough differences to treat them initially as new species.

The maximum size of the stem fragments is governed by the dimensions of the rock samples, but we have the first evidence of branching within this genus. Two specimens from the borehole each show an equal dichotomy even though these are amongst the smallest fragments of stem referable to this genus. Length of preserved axis is therefore not the controlling factor in showing whether the plants branched.

Leaf abscission producing oval leaf scars is one of the main diagnostic characters of *Eskdalia* as interpreted by Chaloner (1967) and Thomas (1968). The degaging and transfer techniques, however, have revealed a very suggestive fact. The longitudinally elongated ovals are outlined by a very thin line of compression which continues into the matrix. The extra compression revealed by degaging and transferring clearly shows that there was a narrow band of compression extending into the matrix around the oval. This compression can be traced upwards into what must have been a persistent leaf and downwards into a distinctive heel. The ovals cannot therefore be true abscission scars. Instead, they must be artificial scars produced by the splitting of the carbon compression during the fracturing of the rock. Such breakage is similar to that described in *Angarophloios* Meyen (1976) and in *Tomiodendron* Radczenko by Meyen (1976) and Thomas and Purdy (1982). It also parallels the artificial loss of leaves shown by Chaloner (1967) and Mensah and Chaloner (1971).

With this new concept of leaf cushion in mind, we can interpret other features shown on the stems. The central ridges shown on the ovals are most probably the very basal expressions of laminae midribs (keels) rather than any features formed by abscission. Some stems have ovals which seem to extend downwards into tails (4034/3-2). This would originally have suggested different-shaped scars, but now they can be interpreted as being the result of heel impressions extending the more normal oval leaf cushion impressions. In this case the heels were closely pressed to the stem and were not separated by rock matrix (text-fig. 1D). This formation of an apparently different character by sedimentary effects is paralleled by similar effects on the ligule pit. The pits can sometimes become filled with sediment producing a pit cast. Meyen (1972, 1976) has clearly shown this to happen in *Tomiodendron* Radczenko, *Ursodendron* Radczenko, and *Angarodendron* Zalessky (see also Thomas and Purdy 1982). If a ligule pit cast is formed in the impression, the corresponding stem compression will obviously have no ligule pit cuticle (text-fig. 1C). Cuticle preparation from the upper angle of such ovals will never reveal the plant to be ligulate. If the ligule pit does not become filled with sediment, it will separate with the main part of the stem compression during the fracturing of the rock (text-fig. 1D). Maceration will then reveal a cutinized ligule pit as described by Chaloner (1967) and Thomas (1968). Such effects of sedimentary infillings on the resultant fossils are all summarized in text-fig. 1. Both collections showed sedimentary infillings of the ligule pits, so no cuticular linings could be prepared as was achieved with *Eskdalia minuta*.



TEXT-FIG. 1. Diagram to illustrate the interrelationships of sedimentation and rock fracture upon the *Eskdalia* type of leaf cushion. A, E, and G represent plant tissues seen in section before fossilization (leaf = LF, ligule pit = LP, heel = H, and lateral Wings = W). The others represent compressed plant material (dark stippling) embedded in rock matrix (light strippling). A, B, and C represent successive stages of plant compression and rock fracture as seen in longitudinal section. In C, the ligule pit cast is formed (LPC) and the leaf and heel are lost. D represents an alternative situation to C after rock fracture. Here there is no ligule pit cast although the pit is retained as a compression (LP') and the heel is pressed against the stem. Either may occur independently so there are four possibilities of preservation. E and F represent similar stages to A and C except that a ligule pit compression or cast is formed further up the leaf lamina and is never seen. The heel may also be visible as in D. G and H are similar stages seen in transverse section. Here the lateral wings may be lost or shown as side extensions to the cushion.

One other sedimentary effect is also of interest to us here. Both types of stem can be seen in transverse section either on the cut side of the core or on the fracture surface of the rock. In both cases there is a compressed central core of coaly plant material inside the matrix of the stem. This is almost certainly the remains of the protostele even though no tracheids can be seen or prepared by maceration.

Stem cuticle was prepared from both collections by maceration with Schulze's solution. Both showed a simple epidermal arrangement with polygonal equal-sided to longitudinally elongated cells. The anticlinal walls are straight and the periclinal walls are flat, smooth, and without the cuticular lumps described from *E. minuta* by Thomas (1968). No cuticle could be prepared from the ovals, although cell outlines were clearly visible and similarly none was obtained from the leaves uncovered from the matrix.

### DISCUSSION

The available information therefore allows us to rediagnose the genus *Eskdalia* and to name the two new species *E. kidstonii* and *E. siberica*. The morphological and cuticular characters of the two new species together with those of *E. minuta* Kidston, are summarized in Table 1. There are differences in leaf cushion and ligule pit sizes, although these two are not directly related. *E. kidstonii* shows much more regularity in cushion size and cushion spacing than the other species, whereas *E. siberica* shows the greatest variation. The latter species also differs in having longitudinal furrows running between the leaf cushion on some of the stems. Stem epidermal details are not sufficiently distinctive to separate the species, although the ranges of cell sizes are not identical. The epidermal lumps described from *E. minuta* are not, however, found in the other two species. *E. kidstonii* alone shows occasional dichotomies, although, as mentioned earlier, this feature is not related to the comparative lengths of the specimens. The other species include large stems but show no evidence of branching. Leaf, heel, and stele sizes are unfortunately not known for all the species.

### COMPARISON

*Eskdalia* in its new concept is a sparsely branched ligulate lycopod shoot. It has persistent leaves borne on leaf cushions which also possess distinct heels at their lower ends. There are many other similar genera and doubtfully placed specimens which now need to be reconsidered in the light of this new interpretation of *Eskdalia*. Some are clearly better understood than others and some may never

TABLE 1. Comparison of *Eskdalia kidstonii* sp. nov. and *E. siberica* sp. nov. with the type species of the genus, *E. minuta*

	<i>E. minuta</i>	<i>E. kidstonii</i>	<i>E. siberica</i>
Size of leaf cushions (mm)	4.5-5.5 × 3.4	2 × 1.2	1-2 × 0.6-1.3
Ligule pits (μm)	flask shaped 400 × 150	cylindrical 200 × 100	globular 300 × 150
Heels (mm)	?	0.7	?
Leaves (mm)	?	4	4
Stem epidermal cells (μm)	130 × 25-35 with lumps	60-125 × 25 no lumps	90-150 × 25 no lumps
Observed stem sizes (mm)	110 × 4-25	75 × 4	130 × 13
Branching	none	occasional dichotomies	none
Stele/axis ratio	?	1:3	1:4

TABLE 2. Comparison of *Eskdalia* and other genera of ligulate lycophytes

	Angarodendron Zalesky emend Meyen (1976)	<i>Eskdalia</i> Kidston (1903)	<i>Lepidodendron perforatum</i> Lacey (1962)	<i>Lepidosisgillaria</i> Kräusel and Weyland (1949)	<i>Porodendron</i> Zalesky (1915)	<i>Pseudolepidodendron</i> V. Ananiev (1974)	<i>Tomiodendron</i> Radezko emend. Meyen (1972)	<i>Ursodendron</i> Radezko (1960)	<i>Uliodendron</i> L & H emend. Thomas (1967)	<i>Lycopodiopsis Renault</i> emend. Lemoigne and Brown (1980)	<i>Valmeyerodendron</i> Jennings (1972)
Leaf cushion/base shape	transversely elongated, lenticular, rhombical to nearly square	elongated oval	elongated oval	elongated oval	elongated oval or cordate	elongated oval	elongated oval, rhomboid, or sagittate	transversely elongated	rhomboidal	rhomboidal to transversely elongated	quadrangular to hexagonal
Leaf abscission	+	+	+	+	+	+	+	+	+	+	+
Axillary fold	+	+	+	+	+	+	+	+	+	+	+
Heel	+	+	+	+	+	+	+	+	+	+	+
Corner folds	+	+	+	+	+	+	+	+	+	+	+
Vascular scar	?	+	+	+	+	+	+	+	+	+	+
Infrafoliar bladder	+	+	+	+	+	+	+	+	+	+	+
Phyllotaxis	lepidodendroid	lepidodendroid	lepidodendroid	sigillarioid and parichnos	lepidodendroid	lepidodendroid	sigillarioid or lepidodendroid	lepidodendroid	lepidodendroid	lepidodendroid	lepidodendroid
Leaf shape	?	linear	slender	short, narrow, Lax	linear	?	?	?	long and linear	long and linear	nearly triangular
Branching	?	rarely dichotomous	frequently dichotomous	?	?	occasionally dichotomous	+/-	repeatedly forked	frequently dichotomous	?	frequently dichotomous (often equally)

be satisfactorily included in any well-defined genus. The apparent lack of leaf cuticle is an important feature which deserves careful consideration. Rock fragmentation can give an illusion of leaf abscission, and maceration will not reveal the presence of leaves. Therefore, we must be very cautious when interpreting similar specimens and in making generic comparisons.

We believe there are three taxa which are better included as *Eskdalia*. They are *Porodendron*, which has already been described as a synonym of *Eskdalia* by Thomas (1968), *Tomiodendron varium* (Radcz.) Meyen, and *Pseudolepidodendropsis igrischense* (A. R. Ananiev) V. A. Ananiev. Those other taxa which are thought to be better kept distinct from *Eskdalia* are compared in Table 2.

*Porodendron* was originally described by Zalesky (1909) for specimens from Mugaoda. He included other specimens of Auerbach and Trautschold that were preserved rather differently as cuticles. Zalesky later (1915) described these cuticles together with some compression-impression specimens as species of *Lepidodendron*, although Bode (1929) retained them in *Porodendron*. Zalesky's original *Porodendron* specimens are very poorly preserved and we see no characters to distinguish them from *Eskdalia*. The specimens described by Zalesky in 1915 have been referred to *Eskdalia* by Thomas (1968) because of the very great similarity between their cuticles. Both stems have simple epidermal cells which are either isodiametrical or elongated and neither have stomata. The stem cuticles all possess regular perforations which have been described as leaf scars and many have their ligule pits preserved in the upper angles of the perforations. If the illustrations of Zalesky are carefully examined, certain other features are apparent. His plate 2, figs. 5 and 5a, illustrates a leafy specimen, while plate 6 shows a further specimen with indications of heels. Unfortunately, we have no idea of the whereabouts of his specimens, for they have either been destroyed, lost, or mislaid. The lack of leaf and heel cuticles in the paper coal cuticles was originally explained as leaf abscission, but it could equally well be the result of their having a very thin cuticle which was not preserved. Evidence for this alternative view has been provided by Wilson (1931) who described some of the Russian paper coal cuticles that had fragments of thinner cuticle attached to the basal angles of some ovals. The stomata present in these thinner cuticles suggest that they were fragments of the basal parts of leaves.

Zalesky's material clearly shows variation but, without examining the original material or additional stem specimens, it is impossible to decide if such variation is gradual or not. We cannot therefore be certain if it suggests intraspecific variation or whether there is more than one species present within the collection. Leaving apart this question of specific independence of these varieties we believe that they can all be included within *Eskdalia*.

Meyen (1972, 1976) has reinvestigated the type of material of *Prelepidodendron varium* Radczenko and come to rather a different conclusion the generic identification. The specimens were shown to have persistent leaves and axillary-positioned ligule pits, so for these reasons the species was transferred to *Tomiodendron* (Radczenko, 1955) 1956 emend. S. Meyen 1972. It was noted, however, that the specimens differed from other *Tomiodendron* species by having dichotomizing axes and much small leaf cushions. No wings have been shown on its leaf cushions and infrafoliar bladders are not convincingly shown. Also, the cushions have asymmetrically attenuated lower parts unlike the other species which have more oval cushion outlines. We are now suggesting that the species is better included within *Eskdalia*. Its persistent leaves and axillary ligule pits indicate eskdalian affinity. The

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#### EXPLANATION OF PLATE 62

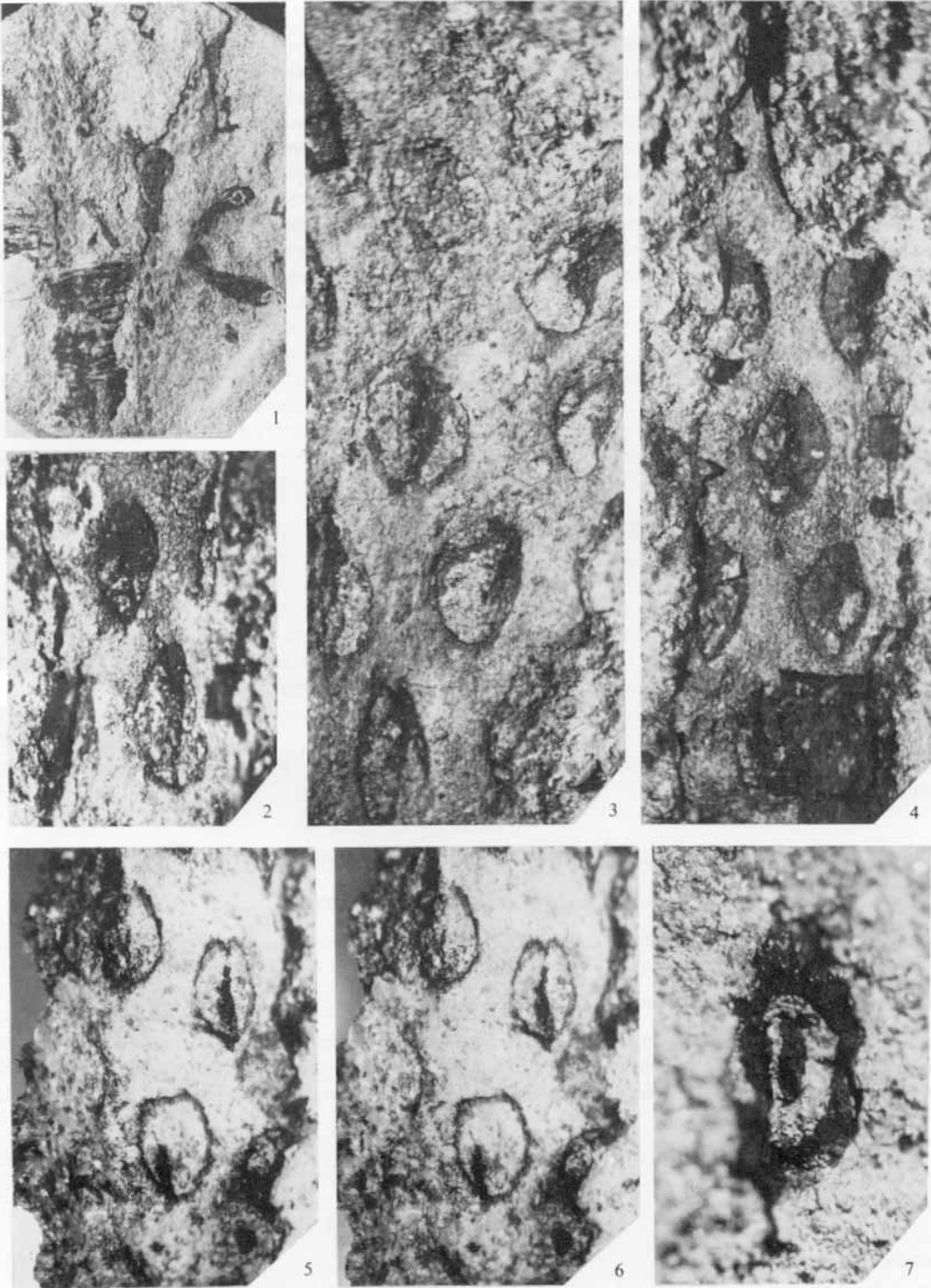
*Eskdalia kidstonii* sp. nov.

Figs. 1-3. Holotype, no. 4034/1a-1. 1, core sample 4034/1a with holotype,  $\times 1$ . 2, 3, enlargements of same,  $\times 10$ .

Fig. 4. No. 4034/1a-3,  $\times 10$ .

Figs. 5, 6. No. 4031/1-b(g). Transfer preparation on cellulose acetate film. Stereopair,  $\times 10$ .

Fig. 7. No. 4034/1a-4. Broken end of axis. Enlargement of the lower of the two fractured axes seen on the right-hand side of fig. 1,  $\times 10$ .



THOMAS and MEYEN, *Eskdalia*

pits are flask-shaped as in *Eskdalia*, whereas those of other *Tomiodendron* species are much more massive and do not have narrowed necks. *Eskdalia* has distinct heels which could be preserved in two different ways, which would give two rather different results when the rock was split (text-fig. 1C, D). When flattened against the stem such heels would appear as attenuated lower ends of the leaf-base oval areas. Therefore the new combination of *E. varia* (Radcz.) Thomas and Meyen is proposed here.

The third probable member of *Eskdalia* is the lepidophyte originally described by A. R. Ananiev (in Ananiev and Graizer 1957) as *Sublepidodendron igrischense* and subsequently referred by V. A. Ananiev (1974) to his monotypic genus *Pseudolepidodendron*. The only evident difference between *Eskdalia* and *Pseudolepidodendron* is the presence in the latter of vertical leaf cushion fusion, with the corresponding lack of heels, and rather deep grooves between the orthostichies. Variation in *P. igrischense*, as shown by Ananiev, is similar to that of Zalessky's material mentioned earlier. Usually the cushions are fused into orthostichies, but sometimes they are very clearly not. Another lepidophyte showing the same type of stem relief is *Lepidodendron concinna* Radczenko, 1960. However, this species shows denticulate leaves (Meyen 1976) and there is no evidence of a ligule. Although the leaf structure of *P. igrischense* is unknown, it seems possible that *L. concinna* might be a younger synonym of *P. igrischense*. Such a synonym must be supported by a more detailed study of both species. Meanwhile, in spite of the lack of data on leaf structure, it seems reasonable to include *P. igrischense* within *Eskdalia*. The new combination *E. igrischensis* (A. R. Ananiev) is therefore proposed.

The other taxa included in Table 2 are other ligulate lycophytes, but they all differ in sufficient ways to remain distinct from *Eskdalia*. *Valmeyrodendron* was described by Jennings (1972) for dichotomously branching lycopod systems with eligulate leaf cushions. However, we believe the genus to be ligulate because some of the Jennings' figures (notably figs. 4, 5, 9, 10, and 22) show structures in the upper angles of the leaf cushions comparable to the ligule pits described by Thomas (1968) and Meyen (1972, 1976). However, it is clear that no single character is consistently important for this purpose. All seem to have some characters of the other genera which makes their separation more difficult. Indeed, we are inclined to believe that *Angarodendron*, *Lycopodiopsis*, and *Valmeyrodendron* are synonyms, even though we are leaving them separate here. Future work might well reveal new synonyms or characters that will precipitate a whole new approach to naming such genera.

## SYSTEMATIC PALAEOLOGY

### Genus *Eskdalia* Kidston 1903

*Synonymy.* *Eskdalia* Kidston 1903. *Porodendron* Zalessky 1909. *Porodendron* Zalessky; Nathorst (1914, p. 68). *Porodendron* Nathorst (*non* Zalessky); Bode (1929, p. 134). *Eskdalia* Kidston; Thomas (1968, p. 442).

*Type species.* *E. (Caulopteris) minuta* Kidston; (Kidston 1883, p. 541, pl. 31, figs. 1, 1a).

*Emended diagnosis.* Leafy lycopod shoot. Leaves in low angle spirals. Basal attachment areas of leaves (leaf cushions) with heels and sometimes shoulders. Ligule pit at apex of leaf cushion, often appearing as a ridge. One simple vascular trace slightly above middle of false leaf scar. No parichnos present.

### EXPLANATION OF PLATE 63

*Eskdalia siberica* sp. nov.

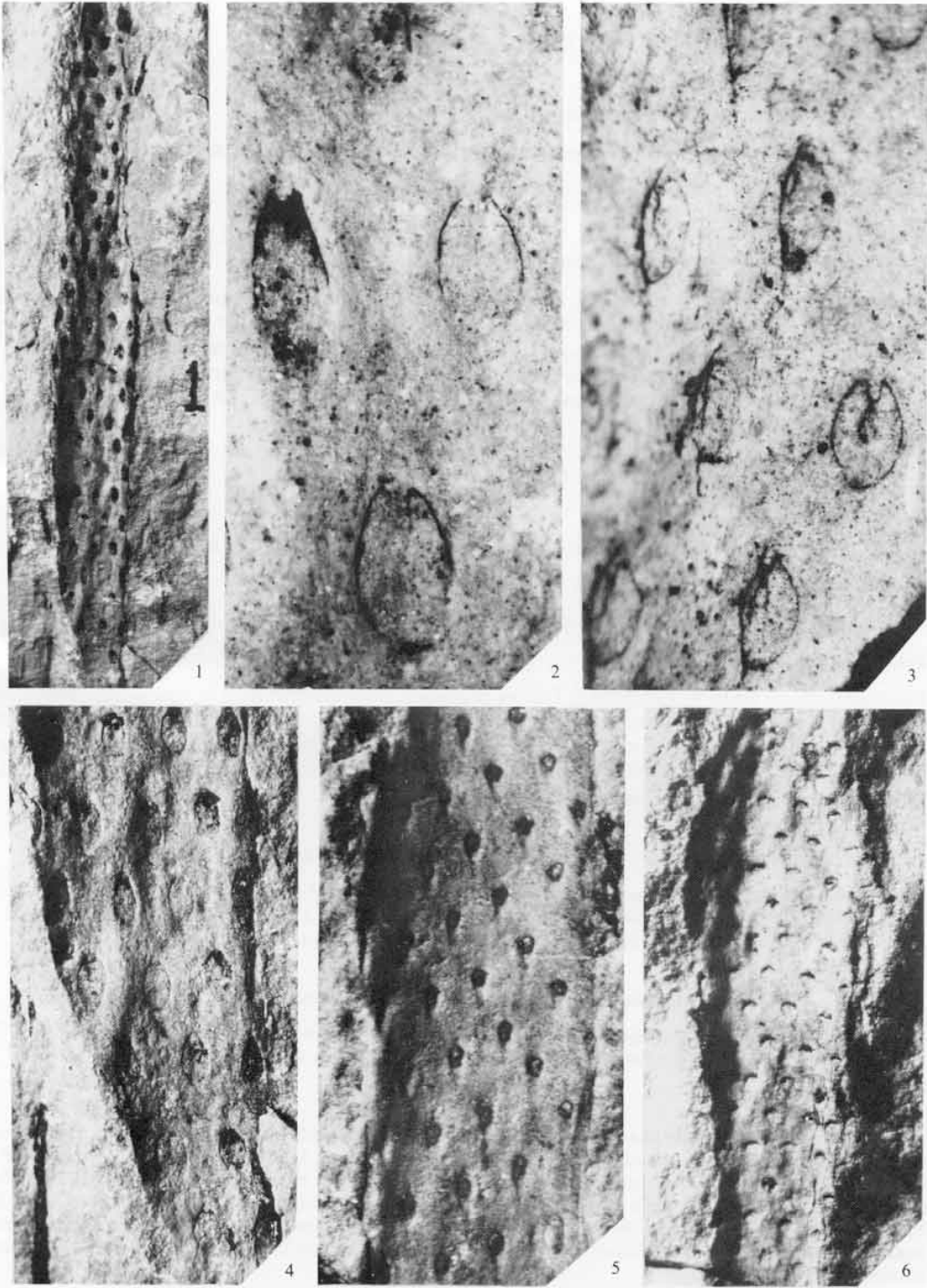
Figs. 1-3. Holotype, no. 4034/4-1. 1,  $\times 1$ . 2,  $\times 10$ . 3, photographed under alcohol,  $\times 8$ .

Fig. 4. No. 4034/32,  $\times 3$ .

Fig. 5. No. 3779/88-1, photographed under alcohol,  $\times 3$ .

Fig. 6. No. 3779/82,  $\times 3$ .





THOMAS and MEYEN, *Ekdalia*

*Eskdalia kidstonii* sp. nov.

Plate 62, figs. 1-7

1972 *Eskdalia* sp. Meyen, p. 154, pl. 1, figs. 3-6; text-fig. 4.*Type specimen.* Geological Institute of the Academy of Sciences, Moscow, no. 4034/4.*Locality.* 'Kyutyungde', Eastern Siberia (70° 43' North, 123° East).*Horizon.* Tournaisian.*Derivation of name.* For the late Dr. Robert Kidston.

*Diagnosis.* Stems up to 4 mm broad, with occasional dichotomies. Leaves in spirals, sometimes in nearly horizontal rows. Leaves linear and tapering up to 4 mm long, heels 0.7 mm long. Leaf cushions oval, 2 mm long, 1.2 mm broad, separated vertically by 2.0-2.5 leaf cushion lengths and horizontally by 1.0-1.5 leaf cushion breadths. Stem surface epidermal cells rectangular to polygonal, 60-125  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  broad. Anticlinal walls straight, periclinal walls flat and smooth. Ligule pits linear, about 200  $\mu\text{m}$  long.

*Eskdalia siberica* sp. nov.

Plate 63, figs. 1-6

*Type specimen.* Geological Institute of the Academy of Sciences, Moscow, nos. 4034/1-2, 1a-2 (counterpart).*Locality.* 'Kempendyai', Eastern Siberia (62° North, 119° 48' East).*Horizon.* Visean (Upper part of the Kurunguryakh suite).*Derivation of name.* From Siberia.

*Diagnosis.* Stems up to 13 mm broad. Leaves in spirals, sometimes in nearly horizontal rows. Leaves linear and tapering up to 4 mm long. Leaf cushions oval, 2 mm long and 1.3 mm broad, separated vertically by 1.0-1.5 cushion lengths and horizontally by 0.5-1.0 cushion breadths. Stem surface cells rectangular and polygonal, 90-150  $\mu\text{m}$  long and 25  $\mu\text{m}$  broad. Anticlinal walls straight, periclinal walls smooth. Ligule pits globular, about 340  $\mu\text{m}$  long.

*Eskdalia varia* (Radc.) comb. nov.1960 *Prelepidodendron varium* Radczenko, p. 18, pl. 4 (figs. 1, 1a, 2-4).1972 *Tomiodendron varium* (Radczenko); Meyen, p. 150, pl. 1 (fig. 2), text-fig. 2.1962 ?*Lepidodendropsis hirmeri* A. R. Ananiev and Mikhailova, p. 222, pl. C-32 (fig. 5).*Eskdalia igrischense* (A. R. Ananiev) comb. nov.1957 *Sublepidodendron igrischensis* A. R. Ananiev in Ananiev and Graizer, p. 999, figs. 2-4.1974 *Pseudolepidodendron igrischense* (A. R. Ananiev); V. A. Ananiev.

*Acknowledgements.* We would like to express our gratitude to the Royal Society for sponsoring B.A.T. under the Cultural Exchange Scheme administered by the Royal Society and the Academy of Sciences of the U.S.S.R.; to the Geological Institute of the Academy of Sciences, Moscow, for their hospitality and the use of their facilities; and to the staff of Dr. Meyen's laboratory for their help. The photomicrographs were taken on a Zeiss Photomicroscope III purchased by a grant from the Royal Society and some of the S.E.M. work was made possible by a grant from the Central Research Fund of the University of London. These grants we warmly acknowledge.

## REFERENCES

- ANANIEV, A. R. and GRAIZER, M. I. 1957. On the flora of the Devonian/Carboniferous boundary beds in Minussinke depression. *Doklady Akademii Nauk SSSR*, **116**, 997-1000. [In Russian.]
- and MIKHLOVA, YU. V. 1962. In KHALFIN L. L. (ed.). Biostratigraphy of the Palaeozoic of the Sayan-Altai Mountain Area, 3. Upper Palaeozoic. *Trudy Sibir. nauch. issled. inst. geol., geofiz. i miner. syr.* **21**, 3-569. [In Russian.]
- ANANIEV, V. A. 1974. To the study of the lower Carboniferous of Angaraland. In ANANIEV A. R. (ed.). *Geologiya i poleznye iskopaemye Sibiri. Vol. 1 Stratigrafiya paleontologiya (materialy konferentsii)*, 16-18. Tomsk Univ. Press. [In Russian.]
- AUERBACH, J. and TRAUTSCHOLD, H. 1860. Ueber die Kohlen von Central-Russland. *Nouv. Mém. de la Soc. Impér. de Moscou*, **13**, 1-58.
- BODE, H. 1929. Zur Kenntnis der Gattung *Porodendron* Nathorst (non Zalesky). *Palaeontographica*, **72**, 125-139.
- CHALONER, W. G., in BOUREAU, E. 1967. *Traité de Paléobotanique. II, Bryophyta, Psilophyta, Lycophyta*, Masson et Cie, Paris.
- DARRAH, W. C. 1952. The materials and methods in palaeobotany. *Palaeobotanist*, **1**, 145-153.
- EICHWALD, E. 1860. *Lethea Rossica, ancienne période*, 1,657 pp. Atlas, pt. 1 (1859).
- GÖEPPERT, H. 1861. Über die Kohlen von Malowka in Zentral-Russland. *Sber. bayer Akad. Wiss. (math-nat.)*, **1**, 199-209.
- JENNINGS, J. R. 1972. A new lycopod genus from the Salem Limestone (Mississippian) of Illinois. *Palaeontographica*, **B**, **137**, 72-84.
- KIDSTON, R. 1883. Report on Fossil Plants, collected by the Geological Survey of Scotland in Eskdale and Liddesdale. *Trans R. Soc. Edinburgh*, **30**, 531-550.
- 1903. The Fossil Plants of the Carboniferous Rocks of Canonbie, Dumfriesshire and of parts of Cumberland and Northumberland. *Ibid.* **40**, 741-833.
- KOLODEZNIKOV, K. E. 1982. *Devonian and Lower Carboniferous of the western part of the Vilyui syncline*, 101 pp. Nauka, Moscow. [In Russian.]
- KRÄUSEL, R. and WEYLAND, H. 1949. *Gilboaphyton* und die Protolepidophytales. *Senckenbergia*, **30**, 129-152.
- LACEY, W. S. 1962. Welsh Carboniferous plants. I. The flora of the Lower Brown Limestone in the vale of Clwyd, North Wales. *Palaeontographica*, **B**, **111**, 126-161.
- LEMOIGNE, Y. and BROWN, J. T. 1980. Révision du genre *Lycopodiopsis* B. Renault, 1890. *Geobios*, **13**, 555-577.
- MENSAH, M. K. and CHALONER, W. G. 1971. Lower Carboniferous lycopods from Ghana. *Palaeontology*, **14**, 357-369.
- MEYEN, S. V. 1972. Are there ligula and parichnos in Angaran Carboniferous lepidophytes? *Rev. Palaeobot. Palynol.* **14**, 149-157.
- 1974. Vegetative shoot morphology of the Angara Carboniferous lepidophytes. *Paleont. Zhurn.* **3**, 97-110. [In Russian.]
- 1976. Carboniferous and Permian lepidophytes of Angaraland. *Palaeontographica*, **B**, **157**, 112-157.
- NATHORST, A. G. 1914. Zur fossilen Flora der Polarländer, Teil I, Lief. 4. *Nachträge zur Paläozoischen Flora Spitzbergens*, 110 pp.
- PASHKEVICH, U. G., DRYAGINAL, L., PETERSON, L. N. and SUKHAREVA, L. G. 1978. Miospores of the late Palaeozoic plants of Middle Siberia. In OSHURKOVA, U. V. (ed.). *Applications of an information retrieval system in palaeopalynology for the solution of some taxonomical and stratigraphical problems*, pp. 50-156. Yakutsk State University. [In Russian.]
- RADCZENKO, G. P. 1960. New early Carboniferous lepidophytes of South Siberia. *Novye vidy drevnikh rastenii i bespozvonochnykh SSSR*, **1**, 15-28. [In Russian.]
- RASSKAZOVA, E. S. 1962. Fossil flora of the Katskaya suite of the Tunguska basin. *Trudy Geol. Inst. Akad. Nauk SSSR*, **67**, 3-56. [In Russian.]
- THOMAS, B. A. 1967. *Ulodendron* Lindley and Hutton and its cuticle. *Ann. Bot.* **31**, 775-782.
- 1968. A revision of the Carboniferous lycopod genus *Eskdalia* Kidston. *Palaeontology*, **11**, 439-444.
- and MEYEN, S. V. (in press). *Tunguskadendron borkii*: gen. et sp. nov. A new Angaran lepidophyte. *Palaeontographica*.
- and PURDY, H. M. 1982. Additional fossil plants from the Drybrook Sandstone, Forest of Dean, Gloucestershire. *Bull. Br. Mus. nat. Hist. (Geol.)*, **36**, 131-142.
- WILSON, J. A. R. 1931. Some new facts about the structure of the cuticles in the Russian Paper-Coal and their bearing on the systematic position of some fossil Lycopodiales. *Proc. R. Soc. Edinburgh*, **51**, 104-115.