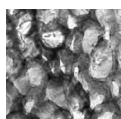


The epidermis of cyclopteroid *Laveineopteris bohémica* (Medullosales) from the Middle Pennsylvanian Radnice Member, Czech Republic

ZBYNĚK ŠIMŮNEK & CHRISTOPHER J. CLEAL



The cyclopterids of the medullosalean *Laveineopteris bohémica* are most similar to those of *Laveineopteris loshii*, and clearly distinct from those of *Laveineopteris rarinervis* and *Laveineopteris tenuifolia*. The evidence supports the view that *L. bohémica* is a fossil-species of foliage of a distinct group of plants favouring the higher elevation wetlands of Variscan Euramerica. • Key words: *Cyclopteris*, Radnice Member, Pennsylvanian, Bolsovian, cuticular analysis, Kladno-Rakovník Basin.

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Laveineopteris Cleal *et al.*, 1990 is a fossil-genus of medullosalean pteridosperm foliage that grew widely in the Early and Middle Pennsylvanian tropical wetlands of Euramerica. It includes both large, bifurcate semi-pinnate fronds (*sensu* Laveine 1997) and much smaller, entire leaves or foliar segments known as cyclopterids. According to Shute & Cleal (2002), cyclopterids had the anatomical and morphological characteristics of shade leaves and were either attached to monopole saplings or epiphyllously to the basal parts of the bifurcate semi-pinnate fronds; the former cyclopterids were usually significantly larger than the latter. Laveine (2005) has in contrast argued that cyclopterids were merely modified pinnae attached to the proximal parts of the main frond, but this overlooks the quite different epidermal anatomy of the cyclopterids compared with the pinnate fronds, and the position of attachment of the cyclopterids (for a further discussion of the relationship between these cyclopterids and the pinnate foliage, see Cleal & Shute 2012). Cleal & Shute (2003) showed that the epidermal anatomy of the cyclopterid foliage is of considerable taxonomic importance in this genus as the cuticles of the pinnate foliage tend to be relatively characterless.

A recent systematic study of the imparipinnate neuropteroid foliage of the Radnice Member in the West and Central Bohemia Coal Basin described cuticles from most of the *laveineopterid* foliage found there (Šimůnek &

Cleal 2011). At the time, however, we did not have available the cuticles from cyclopterids of one of the species, namely *Laveineopteris bohémica* (Ettingshausen) Šimůnek. Subsequently, a suitable specimen has come to light and the present paper documents its cuticles.

Material and methods

The hand specimen (Fig. 1) originated from the Ronna mine, Kladno, in the Kladno-Rakovník Basin in the Central Bohemian Region of the Czech Republic. The specimen was found by a private collector J. Haldovský and donated to the Czech Geological Survey, where it is stored under No. ZŠ 466. It was found in strata of the Radnice Member and is thus early Bolsovian in age in the Heerlen Regional Chronostratigraphy (Wagner 1977), probably approximating to an early Moscovian age in the IUGS Global Chronostratigraphical Scheme (Heckel & Clayton 2006).

The cuticles were prepared by Z. Šimůnek using standard methods involving maceration in 40% Schulze Solution and then bleached using 10% KOH solution (Barthel 1962, Cleal & Zodrow 1989, Kerp 1991, Kerp & Krings 1999). The cuticles were either mounted in glycerine jelly with stain added (safranin, Bismarck brown, malachite green or neutral red) for light microscopy, or mounted on a stub and coated with gold for SEM.

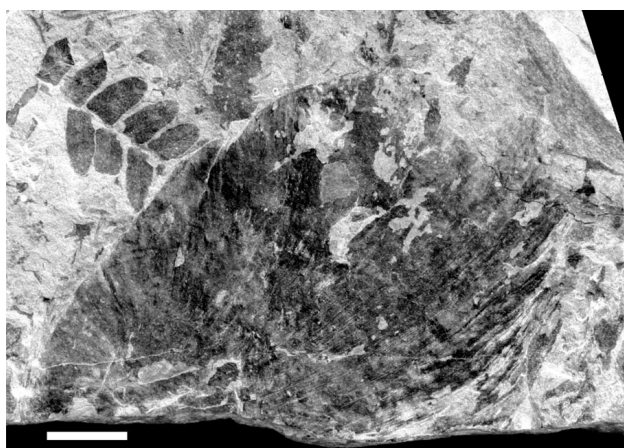


Figure 1. Hand specimen of *Laveineopteris bohémica* (Ettingshausen) Šimůnek, including both pinnate foliage, and the cyclopterid from which the cuticles were prepared. Ronna mine, Kladno; Radnice Member (Bolsovian Substage). Jan Haldovský Collection, Czech Geological Survey, No. ZŠ 466. Scale bar = 10 mm.

Descriptive nomenclature for the cuticles and epidermal anatomy follows Cleal & Shute (2012).

Systematic position

A more complete account of the taxonomy of *Laveineopteris bohémica* can be found in Šimůnek & Cleal (2011). Suffice it to say that it is conspecific with the specimens described from Upper Silesia by Gothan (1913) as *Neuropteris nicolausiana* Gothan and as *Neuropteris nikolausii* from Saar-Lorraine by Bertrand (1930) – these are merely orthographic variants of the same species name –, and the specimens from West and Central Bohemia described by Havlena (1953) as *Neuropteris attenuata* Lindley & Hutton. It is unknown from the lowland, paralic basins of the Variscan Foreland.

Description of cyclopterid cuticles

What is here interpreted as the upper (adaxial) surface was thickly cutinised (Figs 2A, B, 3A). The upper epidermis consisted of rounded to polygonal cells, mostly 25–40 µm in size, with the positions of the anticlinal walls marked by thickly cutinised intercellular flanges. The cells in the

intervein areas tended to be isodiametric; those along the veins were slightly elongate and arranged in longitudinal rows. The lower (abaxial) epidermis was more thinly cutinised (Fig. 2C–F) and consisted of irregular polygonal cells, with thinly but distinctly cutinised anticlinal walls. In the intervein area the cells were isodiametric, 40–60 µm in size; along the veins, the cells were elongate, 60–80 µm long and 25–35 µm wide.

Stomata were restricted to the intervein areas of the lower epidermis (Fig. 2C, E). The guard cells were slightly sunken, 15 µm long and *ca* 2 µm wide, and surrounded by two or sometimes three or four thickly cutinised lateral subsidiary cells, *ca* 20 µm long and 10 µm wide. The stomata were aligned approximately parallel to the veins. Stomatal density was *ca* 40 per mm²; Stomatal Index *ca* 4.5.

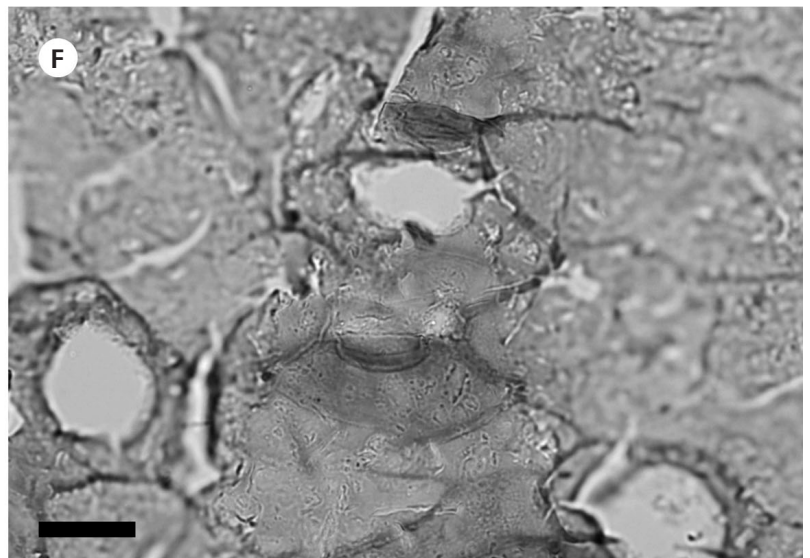
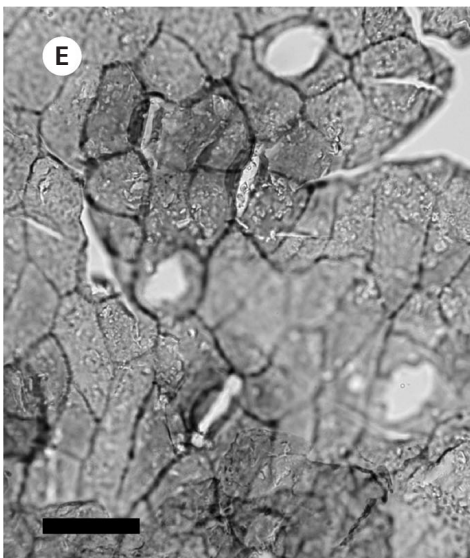
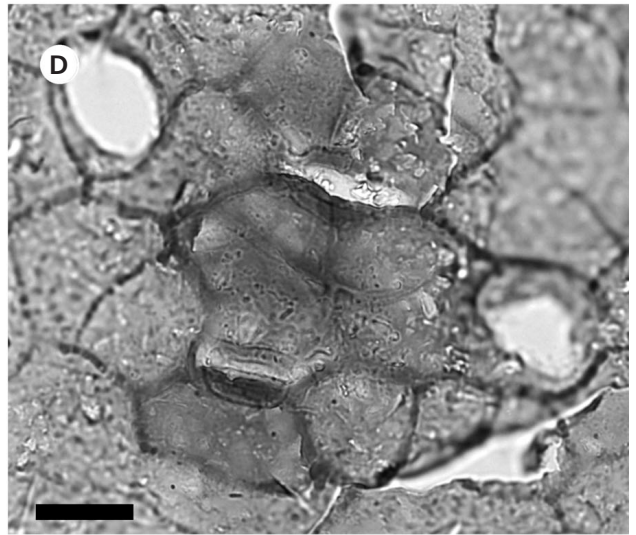
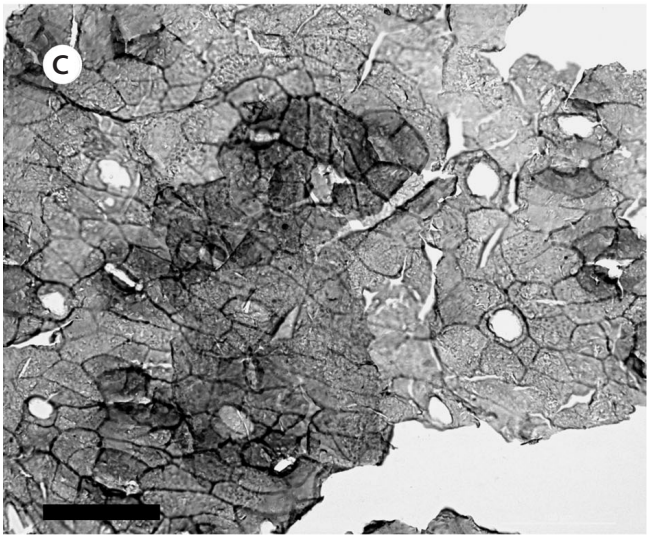
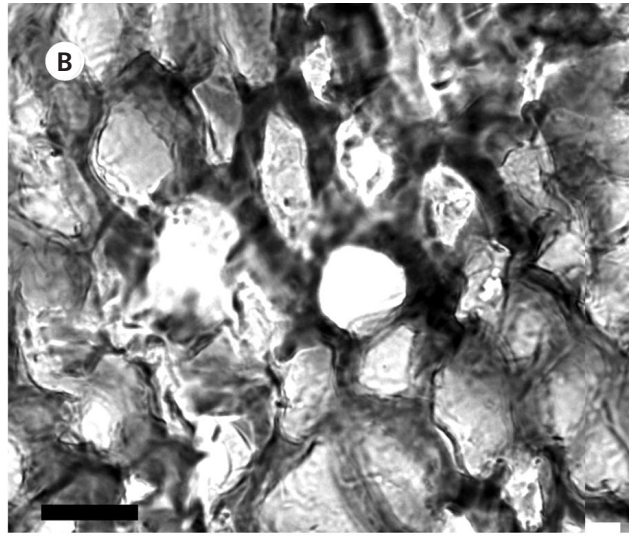
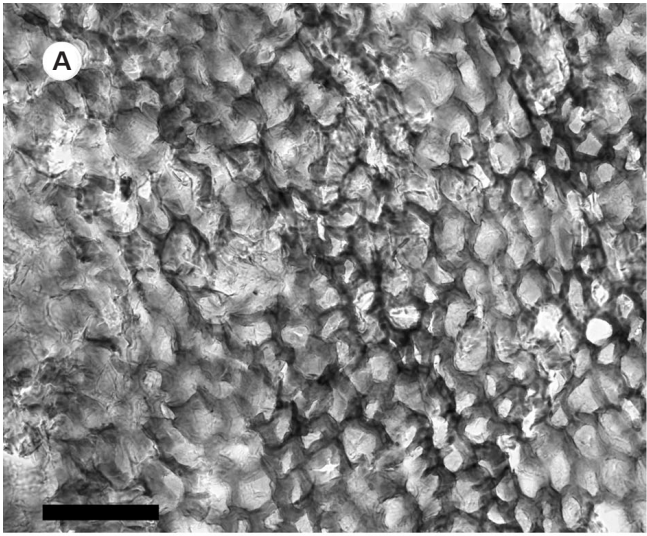
No hairs were preserved attached to either epidermis. On the upper epidermis there were very occasional cells with the periclinal wall uncutinised (Fig. 2B). On the lower surface circular to oval structures with a distinct rim, 20–30 µm in size, occurred in the central part of an epidermal cell (Figs 2C–F, 3B). In some cases these structures represented a complete hole in the cuticle (*e.g.* Fig. 2D, upper left; Fig. 2F, lower left), whereas in others the structure was partly covered by a thin cuticular membrane (Fig. 2F, lower right). There were *ca* 45–50 of these structured holes per mm² on the lower surface of the cyclopterids.

Discussion

We now have detailed evidence of the epidermal anatomy of the cyclopterids of the five *Laveineopteris* species mostly commonly found in Variscan Euramerica (Table 1). They are all broadly similar in epidermal characters: stomata are predominantly on the lower surface and the stomatal density is very low; stomata have well-developed subsidiary cells; and both surfaces have holes that Shute & Cleal (2003) interpreted as pores of active hydathodes. However, *Laveineopteris bohémica* most obviously distinguishes itself from the other taxa by the thickly cutinised upper surface, which appears to lack stomata and at most has only very sparse structured holes.

Laveineopteris bohémica is most similar in its cyclopterid epidermis to *Laveineopteris loshii* (Brongniart) Cleal *et al.*, especially in the structure and distribution of

Figure 2. Cuticles of the cyclopterid of *Laveineopteris bohémica* (Ettingshausen) Šimůnek photographed under plain light. Ronna mine, Kladno; Radnice Member (Bolsovian Substage). • A – upper cuticle (Slide No. 548/3) showing thickly cutinised epidermal cells; scale bar = 100 µm. • B – close up of A, showing epidermal cell with uncutinised periclinal wall; scale bar = 25 µm. • C – lower cuticle (Slide No. 548/2) showing sparse distribution of stomata and structured holes; scale bar = 100 µm. • D – close-up of lower cuticle showing stomata with lateral subsidiary cells and structured holes; scale bar = 25 µm. • E – lower magnification view of D; scale bar = 50 µm. • F – close-up of C showing structured holes, including one partially covered by cuticle; scale bar = 25 µm. All photographs by Z. Šimůnek.



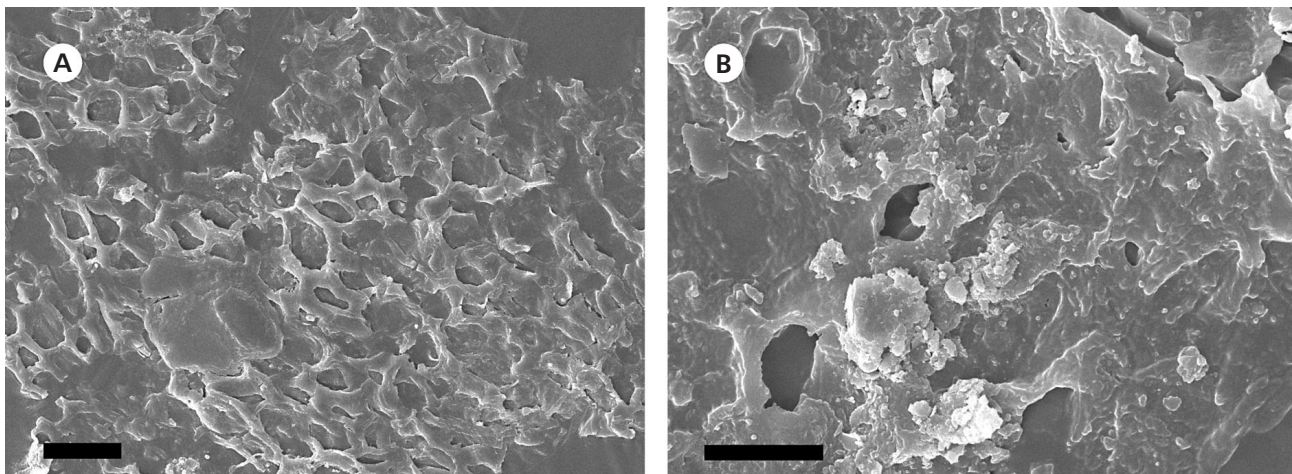


Figure 3. SEM images of cuticles of the cyclopterid of *Laveineopteris bohemica* (Ettingshausen) Šimůnek (SEM Stub No. 63). Ronna mine, Kladno; Radnice Member (Bolsovan Substage). • A – inner surface of upper cuticle showing thickly cutinised anticlinal walls; scale bar = 50 μm . • B – outer surface of lower cuticle showing structured holes; scale bar = 20 μm . All photographs by Z. Šimůnek.

Table 1. Cuticular characters for distinguishing the cyclopterids of the five most commonly found laveineopterid fossil-taxa. Modified from Cleal & Shute (2003, table 1), with new data from Šimůnek & Cleal (2011) and the present paper.

	<i>L. loshii</i>	<i>L. tenuifolia</i> var. <i>tenuifolia</i>	<i>L. tenuifolia</i> var. <i>nordfrancia</i>	<i>L. rarinervis</i>	<i>L. bohemica</i>
Stomatal distribution	Mainly lower surface	Mainly lower surface	Mainly lower surface	Mainly lower surface	Only lower surface
Stomatal density per mm^2 (upper surface)	4–10	Very low	50	15	–
Stomatal density per mm^2 (lower surface)	27–65	25	70	35	40
Stomatal Index (lower surface)	3.6–10.5	5.5–8.5	6.0–6.5	?	4.5
Polar subsidiary cells	Rare	2	2–4	2	None
Lateral subsidiary cells	2–4	2, sometimes with second pair of outer laterals	2–4, sometimes with an outer pair of laterals	2–4	2–4
Cutinisation of subsidiary cells	Thick	Same as normal cells	Same as normal cells	Thick	Thick
Hydathodes (upper surface)	Structured holes (15–25 per mm^2) mainly along veins	Structured holes (35 per mm^2), slightly more dense along veins	Structured holes (25–30 per mm^2), uniformly distributed	Structured holes (20 per mm^2), only along veins	(?)Structured holes, very sparse
Hydathodes (lower surface)	Structured holes (15–25 per mm^2) mainly along veins	Ragged holes (7 per mm^2), uniformly distributed	Structured holes (15–20 per mm^2), uniformly distributed	Structured holes (20 per mm^2), uniformly distributed	Structured holes (40–50 per mm^2), uniformly distributed
Cutinisation of hydathodic epidermal cells	Thick	Same as normal cells	Same as normal cells	Same as normal cells	Same as normal cells

the stomata, which have lateral subsidiary cells with thickly cutinised periclinal walls, and no or only poorly demarcated polar subsidiary cells. However, *L. loshii* can be distinguished by distinctive, thickly cutinised epidermal cells with structured holes (interpreted by Shute & Cleal 2002 and Cleal & Shute 2003, 2012 as active hydathodes) as well as the thick cutinisation of the upper epidermis.

Laveineopteris tenuifolia (Sternberg) Cleal *et al.* var. *tenuifolia*, *Laveineopteris tenuifolia* var. *nordfrancia* (Bertrand) Cleal & Shute) and *Laveineopteris rarinervis* (Bunbury) Cleal *et al.* can all be clearly distinguished from

L. bohemica by the cyclopterid stomata, which normally have distinct polar subsidiary cells, and which occur on both surfaces (albeit more abundantly on the lower surface). The two varieties of *L. tenuifolia* can also be distinguished from *L. bohemica* by the stomatal subsidiary cells not having thickly cutinised periclinal walls.

Stockmans (1933) and Laveine (1967) argued that *Laveineopteris bohemica* and *Laveineopteris rarinervis* were conspecific, but the clear differences in their cyclopterid epidermal structures do not support this view. It instead supports the view of Havlena (1953), Cleal (2008)

and Šimůnek & Cleal (2011) that *L. bohemica* represents foliage of a distinctive medullosalean species of the higher elevation wetland vegetation of Variscan Euramerica.

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