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

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The cyclopterids of the medullosalean *Laveineopteris bohemica* 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. bohemica* 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 epiphylously 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 bohemica* (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.

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

A more complete account of the taxonomy of Laveineopteris bohemica 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, parallic basins of the Variscan Foreland.

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.

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


