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Article abstract

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Leafy branches of *Bothrodendron punctatum* from the Westphalian D (Asturian) of Nova Scotia, Canada

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ABSTRACT

Specimens belonging to the lycopsid genus *Bothrodendron* are identified by distinctive shoots that have small superficial leaf scars. The species are distinguished on the basis of leaf scar shape and ornamentation on their stem surfaces. Of the two Pennsylvanian (upper Carboniferous) species, *Bothrodendron minutifolium* has been found several times with leafy shoots attached, but *Bothrodendron punctatum* has, until now, only been found as large leafless stems. The leafy specimen of *Bothrodendron punctatum* described here from Cape Breton, Nova Scotia, Canada, is therefore the first of its kind to be found and reveals further evidence of the growth patterns and branch shedding of these relatively rare lycopsids.

RÉSUMÉ

Les spécimens appartenant au genre lycopside *Bothrodendron* peuvent être identifiés par leurs pousses distinctives, qui présentent de petites cicatrices foliaires superficielles. Les espèces se différencient par la forme des cicatrices et par l'ornementation de celles-ci sur la surface de la tige. Sur les deux espèces du Pennsylvanien (Carbonifère supérieur), le *Bothrodendron minutifolium* a été trouvé plusieurs fois avec des pousses feuillues encore attachées, mais le *Bothrodendron punctatum* trouvé jusqu'à maintenant ne présentait que de larges tiges dépouillées de feuilles. Le spécimen feuillu de *Bothrodendron punctatum* décrit ici depuis le Cap-Breton, en Nouvelle-Écosse (Canada), est donc le premier en son genre que l'on découvre; il fournit d'autres données de schémas de croissance et de chute de branches de ces lycopsides, qui sont plutôt rares.

[Traduit par la rédaction]

INTRODUCTION

Bothrodendron is characterised by having small leaf scars directly on the stem surface, although the narrow, almost terminal shoots of *Bothrodendron minutifolium* have raised leaf cushions similar to those of *Lepidodendron* (Thomas 1967b). Ligule pit apertures are clearly visible on *Bothrodendron* stems, thereby distinguishing them from the superficially similar stems *Cyclostigma* and *Pinakodendron*, in which they are never seen. The ligulate genus *Lepidobothrodendron* Daber 1959 differs from *Bothrodendron* in having faint cushion outlines enclosing a leaf scar, ligule pit and two external parichnos. (Authorship of and references relating to taxon names are given in Appendix A.).

Some authors, notably Presl (in Sternberg *et al.* 1838), Lesquereux (1870), Kidston (1885) and Hoffman and Ryba (1899) have confused *Bothrodendron* with *Ulodendron*, because the specimen of *Bothrodendron punctatum* first figured

by Lindley and Hutton (1833) has the large oval scars generally known as “ulodendroid” scars. Others took the presence of these large scars to be a criterion of a genus, *Ulodendron*, and it has even been proposed that differences in the ulodendroid scars could be used for species determination (Walkom 1928). Further work has clearly shown that similar large scars are borne by some typical *Lepidodendron* stems, e.g. *Lepidodendron veltheimii* (see Hirmer 1927, fig. 230; Crookall 1964, pl. LXIV, fig. 3; pl. LXXXI, fig. 1; Chaloner 1967, fig. 384) and *Lepidodendron nathorstii* (see Crookall 1964, pl. LXVI, fig. E; pl. LXVII, fig. 1). Some authors have held that these features represent cone abscission scars, others that they are the result of branch abscission. For further discussion see Kidston (1886), Renier (1908, 1910), Watson (1908, 1914), Seward (1910), Lindsey (1915), Crookall (1964) and Jonker (1976).

Nevertheless the distinction between *Bothrodendron* and *Ulodendron* is quite clear, especially since Zeiller (1886a, pl. viii, figs. 1, 1a) figured another specimen of *Bothrodendron*

punctatum from Newcastle-upon-Tyne that W. Hutton (co-author of the species) had given to the Paris Natural History Museum. *Ulodendron* always has persistent leaves attached to diamond-shaped leaf cushions and never exhibits leaf scars. A ligule pit is present at the base of the adaxial surface of the leaves and can often be seen as a narrow ridge extending downwards from the top corner of the leaf cushions. Cuticle preparations of *Ulodendron* and other genera have yielded open-ended tubes of cuticle coming from the inner surfaces of the ligule pits (Auerbach and Trautchohl 1860; Wilson 1925; Thomas 1967a; 1968a, b). Stomata are also present on both leaves and leaf cushions. Pearson (1986) has shown that the permineralized lycophyte stem *Anabathra pulcherrima* has coalified leaf laminae and cuticular features closely comparable to those of *Ulodendron*. For this reason, Pearson included *Ulodendron* as a synonym of *Anabathra*. However, the presence of the ulodendroid scars in *Bothrodendron* is important and relevant to this new specimen, so we will return to this later.

Bothrodendron punctatum and *Bothrodendron minutifolium* are the only two species known from Pennsylvanian (late Carboniferous) floras. The two species can be easily distinguished from each other on the basis of leaf-scar and stem-surface characters. *Bothrodendron punctatum* has oval leaf scars up to 2 mm long with ligule pits contiguous with the top of the leaf scar. The stem surface is covered with fine, sinuous, vertical striations, and the epidermis has uniformly elongated epidermal cells and evenly scattered stomata. In contrast, the oval leaf scars in *Bothrodendron minutifolium* are laterally elongated and the ligule pit apertures are just separated from the leaf scars. The stem surface is divided into small areas by fine, irregular, undulating horizontal grooves. These areas contain groups of small punctae in horizontal rows that correspond to the stomata seen in cuticle preparations. The epidermal cells form files running obliquely from one stomatal group to another (Thomas 1967b; Jennings 1979). There is thus no basis at all for Renier's (1910) view that *Bothrodendron punctatum* and *Bothrodendron minutifolium* are one and the same species.

Bothrodendron minutifolium has small shoots that resemble those of *Lepidodendron* in possessing small leaf cushions. In the lower parts of these shoots narrow strips of bark separate the cushions, but higher up the cushions are adjacent, whereas at the tips the shoots are leafy and no cushions are visible. The surface markings of grooves and punctae on the leaf cushions are like those on the larger stems. Good illustrations of these smaller stems are given by Zeiller (1886b, pl. 74, figs. 4, 4b), Weiss and Sterzel (1893, pl. 1, fig. 3), Kidston (1902, pl. 54, figs. 1–3), Lindsey (1915, pl. 11, figs. 1–2), Hirmer (1927, figs. 352–355), Crookall (1964, pl. 80, figs. 1, 1a), Chaloner (1967, figs. 358–359) and Thomas (1967b, fig. 2). Similar leafy shoots attached to a stem lacking leaf cushions has not been previously recorded for *Bothrodendron punctatum* and here we document for the first time a specimen showing just such an arrangement. The specimen is from the Sydney Coalfield on Cape Breton Island, Nova Scotia, Canada.

Throughout this paper we have used the Heerlen regional chronostratigraphical scheme that is normally used

for Carboniferous sequences in the Canadian Maritimes (see Wagner 1974 for a discussion of the background to this scheme).

DESCRIPTION

Lindley and Hutton (1833) first described *Bothrodendron punctatum* from two specimens, one from the roof of the High Main Seam (Duckmantian Substage) of Jarrow Colliery in County Durham and the other from the Percy Main Colliery, Newcastle-upon-Tyne. The former specimen was figured by Lindley and Hutton (1833, pl. LXXX) and Crookall (1964, pl. LXXIII, fig. 5) and is now in the collections of the British Geological Survey (BGS collection no. 5257). The whereabouts of the latter specimen is unknown.



Fig. 1. *Bothrodendron punctatum* (Nova Scotia Museum, no. 990-281) from the Coal Measures (above the O'Dell/Gardiner Seam from the Pioneer Coal Mine at Sydney Airport) of Nova Scotia, Canada. Scale bar 10 mm.

The new specimen (No. 990-281) is from the Morien Group, above the middle/late Asturian O'Dell/Gardiner Seam from the Pioneer Coal Mine at Sydney Airport, Nova Scotia, Canada. It shows the stem ornamentation characteristic of *Bothrodendron punctatum*. But, unlike any other specimen of this species, it has a main axis with a branching leafy side shoot (Figs. 1–2). The main axis is about 24 mm across and visible on it are very small leaf scars almost circular in outline and about 0.5 mm across in low angle spirals of about 10° and steep spirals of about 60° (Fig. 3). No foliar prints could be seen in any of the leaf scars. The side shoot departs upwards at an angle of about 20° with a decurrent upper surface. The side shoot is about 10 mm across a little way from its broader point of attachment and for the first 20 mm bears no leaves. The surface of this basal portion of the branch is like that of the main stem and does not have small leaf cushions of the type shown in *Bothrodendron minutifolium*. The maximum length shown by the side shoot is nearly 20 cm, although it is not complete. The first dichotomy is about 70° and the next two are 70° and 50° with the axes, by then, having thinned to less than 2 mm across. The leaves are in tight spirals decurrent and then spreading out at angles of $30\text{--}40^\circ$ before curving upwards again. Individual leaves are lanceolate, about 0.6 mm long and about 0.2 mm across at their broadest point. Their apices are shortly acuminate. These leaves are very similar to those of *Bothrodendron minutifolium*, but are less densely packed together on the shoots.

DISCUSSION

As outlined earlier, there has been much debate about the reason for *Bothrodendron* and some species of *Lepidodendron* having the large oval/round scars commonly referred to as ulodendroid scars. These have been thought to be abscission scars of flowers (Rhode 1820), roots (Carruthers 1879), bulbils (Stur 1875), cones (Lindley and Hutton 1833; Thomson 1880) and branches (Watson 1908; Renier 1910; Lindsey 1915; Jonker 1976). The evidence now favours them having been formed through branch abscission, especially since Lindsey (1915) described and illustrated two new specimens of *Bothrodendron minutifolium*, one showing a short stem bearing a mass of dichotomising leafy shoots that has a clean-cut, trumpet shaped base, the other showing a main axis bearing leafy branches that have similar decurrent, trumpet-shaped bases. These specimens suggest that such relatively short branches were lost by shedding along a definite abscission layer. The Nova Scotia specimen of *Bothrodendron punctatum* is similar to the second specimen of Lindsey's *Bothrodendron minutifolium* in having a main axis and a leafy side branch that has a trumpet-shaped base. The implication is that this leafy branch might be ultimately shed to produce an ulodendroid scar.

In contrast to *Bothrodendron minutifolium*, which is relatively widespread in the Pennsylvanian-age macrofloras of Euramerica, *Bothrodendron punctatum* was much rarer and



Fig. 2. *Bothrodendron punctatum*. (a) Area of attachment of the lateral branch and (b) portion of dichotomising leafy shoot. Scale bars 10 mm.

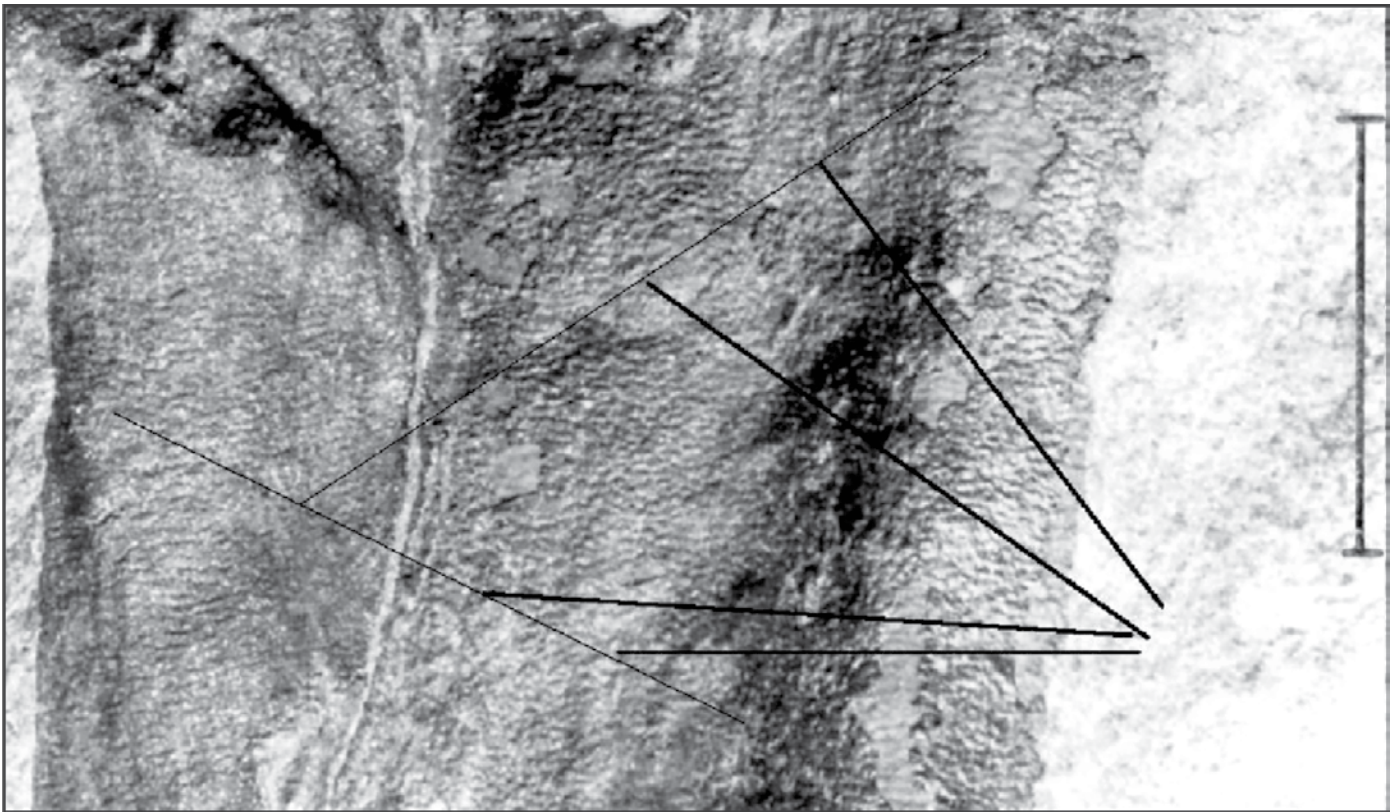


Fig. 3. *Bothrodendron punctatum*. Angles of whorls shown by the narrow lines. Thicker lines indicate the positions of the leaf scars. Scale bar 10 mm.

had a more restricted geographical distribution. Having checked all of the published records listed in the *Fossilium catalogus* (Jongmans 1913; Jongmans and Dijkstra 1969), most are either unillustrated and thus unverifiable, indeterminable stems with ulodendroid scars but not showing the bark surface, indeterminable detached leafy shoots, or simple misidentifications usually of *Bothrodendron minutifolium*. The only verifiable records that we have seen are of Duckmantian age from Britain (Yorkshire, Durham and Ayrshire coalfields; Crookall 1964; Thomas 1967b) and Langsettian age from Nord-Pas-de-Calais (Zeiller 1886b; Weiss in Weiss and Sterzel 1893). To this list may now be added the specimen from the Asturian of Cape Breton. There is also a possible record from the Donets Basin in Ukraine – the type of *Ulodendron schlegelii*. Eichwald (1840) stated that this specimen was very similar to *Bothrodendron punctatum*, distinguished only by the position of the vascular trace in the ulodendroid scar. Although the illustration of the specimen is too poor to show the details of the stem surface, the description mentions punctae arranged in distinct rows, as is normally seen in *Bothrodendron punctatum*. It would seem, therefore, that the plant with *Bothrodendron punctatum* stems was restricted to the very lowland paralic habitats of central and eastern Euramerica, and was absent from the intra-montane basins, or even the slightly more elevated parts of the Variscan Foreland such as Upper Silesia or even the Ruhr.

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Editorial responsibility: Robert A. Fensome

APPENDIX A: TAXONOMIC NAMES MENTIONED IN TEXT, WITH AUTHORSHIP CITATIONS AND REFERENCES.

- Anabathra* Witham 1833 [Internal Struct. Foss. Veg.: 74].
- Anabathra pulcherrima* Witham 1833 [Intern. Foss. Veg.: 74].
- Bothrodendron* Lindley and Hutton 1833 [Foss. Fl. Gr. Brit. 2(1): 80].
- Bothrodendron minutifolium* (Boulay 1876 [Terr. houill. Nord

- Fr.: 39. 1876]) Zeiller 1888 [Compt. Rend. Hebd. Séances Acad. Sci., Ser. 3 14: 180].
- Bothrodendron punctatum* Lindley and Hutton 1833 [Foss. Fl. Gr. Brit. 2(1): 80].
- Cyclostigma* Haughton 1860 [J. Roy. Dublin Soc. 2: 12; an illegitimate junior homonym of *Cyclostigma* Hochstetter ex Endlicher 1844 --- Gen. Suppl. 2: 56].
- Lepidobothrodendron* Daber 1959 [Geologie Beih. (26) 8: 36].
- Lepidodendron* Sternberg 1820 [Versuch Fl. Vorwelt 1(1): 19, 23].
- Lepidodendron nathorstii* Kidston 1885 [Ann. Mag. Nat. Hist. Ser. 5 16: 163].
- Lepidodendron veltheimii* Sternberg 1825 [Versuch Fl. Vorwelt 1(4): 43, tent. 13].
- Pinakodendron* Weiss in Weiss and Sterzel 1893 [Abh. Königl. Preuss. Geol. Landesanst. Ser. 2 2: 61].
- Ulodendron* Lindley and Hutton 1831 [Foss. Fl. Gr. Brit. 1(1): 22].
- Ulodendron schlegelii* Eichwald 1840 [Bull. Sci. Acad. Imp. Sci. Saint-Pétersbourg 3: pl. 3 fig. 4].