FURTHER OBSERVATIONS ON THE UPPER CARBONIFEROUS PTERIDOSPERM FROND *MACRONEUROPTERIS MACROPHYLLA*

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ABSTRACT. A large specimen of *Macroneuropteris macrophylla* clearly shows the overtopped branching of the primary rachis branches in the upper part of the frond. This is the first unequivocal evidence of the distal architecture of this species to be published and confirms the reconstruction proposed by us in an earlier paper.

IN an earlier paper published in this journal (Cleal *et al.* 1996) we proposed a reconstruction of the Upper Carboniferous pteridosperm frond *Macroneuropteris macrophylla* (Brongniart) Cleal, Shute and Zodrow, 1990. This was based on some large specimens in the Department of Palaeontology, The Natural History Museum, London, which clearly showed the proximal and middle parts of this frond. However, the distal part of the frond was represented only by two relatively poor specimens, one of which had suffered considerable taphonomic distortion (our previous pl. 2, fig. 1); the other was broken just above what we interpreted as the main overtopped branch and was poorly preserved (pl. 3, fig. 2). Our proposed reconstruction of this part of the frond thus had to be speculative, based partly on this inadequate material and partly on some poorly illustrated specimens figured by previous authors.

As stated in an endnote to our previous paper, while working on a totally unrelated project at the Sedgwick Museum, one of us (CJC) discovered a large, well preserved specimen, clearly showing the distal portions of two primary pinna branches, which probably represents the apical part of a single frond of this species. This is the first specimen to show unequivocally the architecture of this distal part of the frond of *M. macrophylla*, and allows us to complete the reconstruction of this important species.

MATERIALS AND METHODS

The specimen is stored in the Sedgwick Museum, University of Cambridge, UK, under catalogue number M.1449. It was collected in 1905 by the then curator, E. A. N. Arber, and is recorded as having originated from the Radstock 'Series' (i.e. Formation) at Camerton in Somerset. It is thus late Westphalian D in age.

The specimen had some large chisel marks on the surface, presumably resulting from earlier attempts to prepare the specimen. Whilst not directly affecting the frond fragments themselves, they were ugly distractions to the final photograph. Fortunately, the Palaeontology Conservation Unit of The Natural History Museum were able to obscure these marks, prior to photography by the museum's Photographic Studio. The photograph was taken under cross-polar illumination.

The descriptive terminology used in this paper is the same as that used in Cleal and Shute (1995) and Cleal *et al.* (1996). In order that the specimen could be illustrated whole with the least reduction in size, it is shown in Plate 1 rotated clockwise by 90°. However, in the description below, the specimen will be assumed to be in its more usual orientation, and right-hand and left-hand will be represented in Plate 1 by lower and upper.

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DESCRIPTION

The specimen shows the near-terminal portions of two bipinnate pinna fragments, the left-hand one (as shown in Pl. 1) 163 mm long, the right-hand one 180 mm long. From their relative positions we interpret these fragments as parts of the two primary pinna branches of a single bipinnate frond.

In the left-hand fragment, the primary rachis branch is *c.* 3 mm wide in its most proximal part. This branch produces two secondary pinnae, one on either side. The right-hand (inward-facing) secondary pinna is preserved for a length of 112 mm, the left-hand pinna for 65 mm, but both are incomplete. The angles of attachment are 40° and 50°, respectively, and the secondary rachis offset is 26 mm; where each secondary pinna is attached, the primary rachis branch is kinked. At 53 mm above the right-hand secondary pinna, the primary rachis branch divides as an asymmetrical dichotomy at an angle of 65°. The right-hand branch of this asymmetrical dichotomy is 103 mm long and complete; the left-hand branch 70 mm long and incomplete.

The right-hand pinna fragment also has an asymmetrical dichotomy, but shows less of the frond above this dichotomy but more below it than the left-hand fragment. The primary rachis branch is 133 mm long below the dichotomy and is 5 mm wide in its most proximal part. Three secondary pinnae are attached to the right-hand (outwards facing) side of the primary rachis branch, two to the left-hand side; none is completely preserved and so their length cannot be determined. On both sides of the primary rachis branch, the secondary rachis spacing is 45 mm. The secondary rachis offset (*sensu* Cleal *et al.* 1996, table 1) is 22–26 mm. Where the more proximal of the two pinnae is attached, the line of the primary rachis branch is only slightly deflected, but at the next three attachment points there is a much greater deflection. The most proximal secondary rachis is attached at 65° to the primary rachis branch, the next three at 57°, and the fifth at 45°. The primary rachis branch eventually divides at about 95° in an asymmetrical dichotomy.

The lateral pinnules are linguaeform, sub-falcate or sub-triangular in shape. Those attached to the secondary pinnae are up to 27 mm long and 7 mm wide, and spaced at about 7 mm intervals. Four or five pinnules are intercalated between adjacent secondary rachises along the primary rachis branches; they vary from 7 mm long and 7 mm wide, to 36 mm long and 11 mm wide.

Only one apical pinnule is preserved, which is lanceolate, 20 mm long and 10 mm wide.

DISCUSSION

This specimen confirms that the primary rachis branches in the distal part of *Macroneuropteris* fronds show a gradual transition from laterally attached to overtopped branches, culminating in an asymmetrical dichotomy. This confirms the reconstruction of the *Macroneuropteris* frond proposed by Cleal *et al.* (1996), but for which the then available specimens showing the distal part of the frond were equivocal on the architecture.

Our original paper estimated the length of most fronds to be *c.* 0·8 metres between the main dichotomy of the primary rachis and the apex (the DAD dimension). However, we noted that two of the specimens (V.63416(a) and V.3073) seemed to have been parts of much smaller fronds, whose DAD was estimated to be nearer 0·4 metres. The main dimensions of the Sedgwick Museum specimen (primary rachis branch width 3–5 mm, secondary rachis spacing 45 mm, secondary rachis offset 22–26 mm, maximum pinnule length 27 mm) are very close to those of V.63416(a), suggesting that it came from a frond of similar DAD. Assuming that the two pinna branches in the Sedgwick Museum specimen were from the same frond and are more-or-less in place, it is possible to use their relative positions to get another estimate of the frond length, by extrapolating the primary rachis branches back to where they would have met (with an adjustment for the slight curvature of these rachis branches just above the dichotomy as proposed in the Cleal *et al.* 1996 model). This produces a frond with a DAD of about 0·4 m, which fully agrees with the estimate obtained from secondary rachis spacing and pinnule size.

EXPLANATION OF PLATE 1

Macroneuropteris macrophylla (Brongniart) Cleal, Shute and Zodrow, 1990; Sedgwick Museum, M.1449; two pinna fragments, probably representing the apical part of a single frond; Camerton, Somerset; Radstock Formation (upper Westphalian D); ×0·6.

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The *M. macrophylla* specimens that we have studied to date therefore seem to have originated from fronds varying in size, with DADs of 0·8 m and 0·4 m. The smaller examples might have been the young leaves that had not fully expanded, although they do not seem to differ in texture from the fragments of larger fronds, which might have been expected if they were juveniles. Alternatively, they could be sun-leaves, a suggestion which could be tested by looking at their stomatal density compared with the larger leaves; cuticles are not preserved in Radstock fossils, but they are known for this species from the Sydney Coalfield in Cape Breton (Cleal and Zodrow 1989).

Combined with the evidence described in our earlier paper, we can confirm that the *Macroneuropteris* frond fits with the bifurcate semi-pinnate type of architecture described by Laveine (1997) that occurred in many trigonocarpalean fronds, including *Neuropteris* (Brongniart) Sternberg (e.g. Zodrow and Cleal 1988) and *Laveineopteris* Cleal, Shute and Zodrow (e.g. Laveine 1967). It points to the close relationship between these genera, although the evidence of the cuticles (e.g. Cleal and Zodrow 1989) still points to them being kept taxonomically separate.

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