**Position of Ovule Attachment in a Carboniferous Medullosalean Pteridosperm**

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**ABSTRACT**

A specimen of *Alethopteris zeilleri* from Stephanian deposits of Secu, Resiţa Basin of South Carpathians, Romania, provides additional evidence that these medullosalean pteridosperms bore ovules laterally attached to rachises, probably in the proximal part of the frond. *Alethopteris zeilleri* foliage is associated with Pachytesta incrassata ovules with a peculiar taphonomic position.

**Keywords**: palaeobotany, Pennsylvanian, Medullosales, ovules, Romania

INTRODUCTION

The Medullosales were a group of now extinct gymnospermous seed plants that flourished in Pennsylvanian (late Carboniferous) tropical wetlands, growing in both clastic and peaty substrates (DiMichele et al. 2006). Remains of their foliage can be found in the deposits of both lowland paralic and “upland” intramontane wetland basins, albeit with different species in the different basin types (Cleal 2008). Moreover, direct evidence of their ovules, in particular where on the plant they were attached, is extremely limited. The traditional view was that the ovules were directly attached to the vegetative fronds (e.g. Siddle 1981) but when this model was tested (Seyfullah & Hilton 2009) the supporting empirical evidence was found to be weak. This is a major problem as position of ovule attachment is regarded as a key character in phylogenetic studies of early seed plants (e.g. Crane 1985, Doyle & Donoghue 1992, Hilton & Bateman 2006).

Although organic attachment of ovules would be the “gold standard” evidence for solving this problem, some indirect evidence has recently come to light. Specimens from the Middle Pennsylvanian Sydney Mines Formation of Cape Breton, Canada documented by Cleal et al. (2010) suggested that *Alethopteris*-bearing medullosalean plants bore ovules on specialised fertile fronds lacking vegetative lamina. As pointed out in that paper, however, although the regular arrangement of the ovules relative to the axes was strongly suggestive, direct connection between them could not be confirmed; it seemed that compression and coalification during fossilisation may have just slightly pulled the ovules away from the rachis. However, in the present paper we document another specimen, this time from Romania, which appears to corroborate the Canadian evidence.

The specimen originated from the Upper Pennsylvanian Reşiţa Formation (Bucur 1991, 1997) of the Reşiţa Basin, belonging to the Getic Nappe, in the southern Carpathian Mountains, Romania. It was collected from the sterile dump of Secu, a former coal mining locality close to Reşiţa town, Caraş-Severin County in the Banat historical province of Romania (Fig. 1). The Reşiţa Formation is a continental unit yielding several coal seams which were extracted in Secu and Lupac, in the northern part of the Reşiţa Basin (Năstăseneanu 1987, Năstăseneanu et al. 1973, Petrescu et al. 1987, Popa 2001, 2005, 2009, Popa & Psenicka 2010). The Reşiţa Formation includes three members (the Doman, Lupacu Bătrân and Lupac members), but in the eastern part of the Reşiţa Basin, where Secu occurs, they cannot be differentiated (Fig. 1). The age of the Reşiţa Formation in Secu is Westphalian D – Stephanian B (Popa 2005). The sterile dump of Secu is particularly rich in well preserved fossil plants and arthropods (Androne et al. 2000, Popa 2005, 2009, Jarzembowski 2008), a future Site of Special Scientific Interest (SSSI).

**MATERIAL AND METHODS**

The hand specimen yielding the plant material belongs to the historical collections of the University of Bucharest, Laboratory of Palaeontology. Its collector is unknown and...
Cleal & Popa has the inventory number LPBU0607, also bearing an older inventory number (1028). The old label indicates that the hand specimen possibly belonged to the TCA (Trustul de Cărbuni Anina) collection, a historical collection belonging to the Anina Coal Mine, Caraș-Severin County, Romania. The specimen is represented by a fine, carbonaceous sandstone slab full of fragments of *Alethopteris zeilleri* (Ragot ex Remy) Wagner, two *Pachytesta incrassata* Brongniart ex Renault and several fragments of *Cordaites principalis* (Germar) Geinitz (Fig. 2). The adpressions are well preserved but they yield no cuticles. The material was photographed with a Panasonic Lumix DMC-L10 with Olympus Digital Macro 35 mm lens, mounted on a Kaiser copystand with Ike lateral lights (Popa 2011).

**DESCRIPTION**

The specimen shows a 0.4 m long, straight, longitudinally striate rachis, 40 mm wide in its most proximal part. In the proximal part the rachis there is a medial, longitudinal ridge, but this rapidly changes into a longitudinal tear, dividing it into what seem to be 14 mm and 16 mm wide strips. Towards the most distal preserved part of the specimen, these two strips of rachis are 40 mm apart (Fig. 2). Numerous pinna fragments are preserved in association with this main rachis, but no unequivocal evidence of attachment was seen. These pinna fragments have linguiform pinnules, broadly attached to the rachis, up to 15 mm long and 6 mm wide (Fig. 3b, c), with a strong midvein and thick, broadly arched lateral veins. These pinnae correspond to the fossil-species *Alethopteris zeilleri* as documented by Wagner (1968).

On the right-hand side of the distal part of the main rachis, a large ovate ovule, 90 mm long and 35 mm wide; it is widest just below the middle of the ovule. In the proximal part of the ovule, there is a swollen area, 30 mm long and 25 mm wide, probably representing the sclerotesta. The tissue surrounding this sclerotesta is flattened and may be interpreted as the sarcotesta. The chalazal end of the ovule lies next to the thick rachis but organic connection is difficult to unequivocally verify (Fig. 3a).
DISCUSSION

Although there is no pinnate foliage definitely attached to this rachis, the presence of only Alethopteris zeilleri pinnae in such profusion is highly suggestive. Moreover, as pointed out by Cleal et al. (2010) such large ovules have only ever been found in association with the Alethopteris zeilleri / A. pseudograndinioides Zodrow & Cleal complex of foliage species. The Romanian ovule is at the lower end of the size range of the anatomically-preserved species Pachytesta incrassata, which Cleal et al. (2010) argued probably originated from the same plants as produced Alethopteris zeilleri foliage.

It is of course always possible that the occurrence of large ovules very close to thick medullosalean rachises seen in both the Romanian and Canadian specimens is coincidental; in both cases the ovules may just have fallen in the sediment adjacent to the rachises by chance. In our view, however, this would seem unlikely, especially given that in both cases the ovules lie with their chalazal ends next to the rachis, as would be expected if the ovules were originally attached. These specimens indicate that the ovules were laterally attached to wide rachises; at least in these medullosaleans ovules were not borne terminally to pinnae, replacing terminal pinnules, but were laterally attached to rachises. The possible presence of vegetative pinnae would suggest that these were not specialised fertile fronds that only bore ovules, but were indistinguishable from the vegetative fronds except for the presence of ovules.

The most convincing attempts to reconstruct the Alethopteris frond architecture have been by Laveine (1986) and Laveine et al. (1992), who showed that they could be more than 7 m long, with a bifurcate pinnate architecture (sensu Laveine 1997). Given the width of the rachis in the Romanian specimen it seems most likely that it originated from a proximal position within the frond. The presence of abundant pinna fragments may indicate that it was from above the main dichotomy of the primary rachis near the base of the frond.

When trying to establish whole organism reconstructions of extinct plants, we would ideally use evidence of clear organic connection to establish relationships between different organs. Especially in adpression fossils, however, such evidence is likely to be elusive as the processes of compression will tend to pull plant parts apart even if they were still attached when entering the sediment. We must therefore sometimes look at evidence of close association between organs, especially where it can be documented in repeat occurrences such documented in the present paper.
CONCLUSION
Although not clearly preserved in anatomical connection, the taphonomic position of the reproductive and vegetative structures preserved in the specimen LPU0607 show a rare situation hinting that Alethopteris zeilleri and Pachytesta incassata were produced by the same biological species of plant, but also to the idea that this type of medullosalean pteridosperm bore ovules within the proximal part of their fronds.

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LITERATURE CITED