Review of Palaeobotany and Palynology 200 (2014) 82–96

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Permineralized *Alethopteris ambigua* (Lesquereux) White: A medullosan with relatively long-lived leaves, adapted for sunny habitats in mires and floodplains

Anne Raymond [a,*], Matthew Wehner [b], Suzanne H. Costanza [c]

[a] Dept. of Geology & Geophysics, Faculty of Ecology and Evolutionary Biology, Texas A&M University, College Station, TX 77843-3115, USA
[b] Dept. of Geology & Geophysics, Texas A&M University, College Station, TX 77843-3115, USA
[c] Harvard Botanical Museum, 26 Oxford Street, Cambridge, MA 02138, USA

ARTICLE INFO

Article history:
Received 2 January 2013
Received in revised form 11 July 2013
Accepted 12 July 2013
Available online 22 July 2013

Keywords:
Alethopteris
Pennsylvanian
paleoecology
mire
leaf economics

ABSTRACT

Permineralized *Alethopteris ambigua* (Lesquereux) White occurs in the Kalo Formation (Moscovian, Pennsylvanian) of Iowa. The following characteristics distinguish *A. ambigua* from other permineralized *Alethopteris* species: narrow pinnule width, a deeply sunken midrib having a round cross-section, deep midline depth, and a thick lamina that is not enrolled. Both the new permineralized *Alethoptheris* from the Kalo Formation and adpressed *A. ambigua* (Lesquereux) White have 'pecopteroid' pinnules with lamina that are linked at the base. Because the midrib of *A. ambigua* is round in cross-section, the widest part of the midrib lies below the midrib–lamina junction. In adpression this configuration would produce the 'midrib flanges' found in adpressed *A. ambigua* from Missouri. Three *Alethopteris* species with narrow pinnules and pecopteriod insertion have been extensively synonomized by previous workers: *A. ambigua* (Lesquereux) White, *Alethopteris friedelii* P. Bertrand, and *Alethopteris lesquereuxii* Wagner. Together with *Alethopteris leonensis* Wagner, these four species form a morphological continuum similar to other alethoperid morphological continua (e.g. the *Alethopteris densinervosa*, *Alethopteris ingbertensis*, *Alethopteris lonchitifolica*, *Alethopteris missouriensis*, *Alethopteris westphalensis* continuum). Nonetheless, because their permineralized forms can be readily distinguished, we favor retention of both *A. ambigua* (Lesquereux) White and *A. lesquereuxii* Wagner.

Most permineralized mire alethopterids, with the exception of *Alethopteris* sp. from the Lewis Creek deposit (Kentucky, U.S.A.), have anatomical features consistent with foliage that grew in sunny, wet or humid habitats, including thick photosynthetic lamina, thick cuticle and enrolled edges. Most permineralized mire neuropterids, with the exception of *Laveineopteris rarinervis* from the Illinois Basin, have anatomical features consistent with foliage that grew in shady, wet or humid habitats, including thin photosynthetic lamina, and thin cuticle. In seed-ferns with broadly attached pinnules and compound leaves, lamina thickness/pinnule width (LT/MaxW) is a proxy for leaf mass per area (LMA), and indicates the relative economic cost and longevity of medullosan foliage. Measures of LT/MaxW for mire medullosans suggest that most mire alethopterids produced metabolically-expensive, long-lived fronds, whereas most mire neuropterids produced metabolically-cheap, short-lived fronds.

1. Introduction

Alethopteris ambigua (Lesquereux) White is an extinct medullosan seed fern frond from the Pennsylvanian, originally identified from North America (White, 1899). Although few medullosan pinnules can be identified with specific growth habits, most medullosans were small to medium sized trees (5 to 10 m) with a sheath of adventitious aerial roots at the base of the stem and persistent leaf bases (Wnuk and Pfefferkorn, 1984; Zodrow, 2007; Falcon-Lang, 2009). The number of frond insertions per unit length on medullosan trunks ranged from two to four fronds per meter to over 14; successive fronds were produced at angles of approximately 120° around the trunk (Pfefferkorn et al., 1984; Wnuk and Pffefferkorn, 1984; Zodrow, 2007). The size of *Alethopteris missouriensis* fronds may have been 4.2 m wide and 6 m long (Laveine, 1986; Laveine and Oudoire, 2009). The fronds reported by these authors came from siliciclastic deposits and probably grew on siliciclastic soil; *Alethopteris* trees growing in mires on peat substrates may have had smaller fronds due to the stress of growing in waterlogged soil and the low nutrient content of peat (Mitsch and Gosselink, 1993).

Most *Alethopteris* species are only known from adpressions, that is, compressions or impresssions of the frond and pinnules. Adpressions preserve pinnules primarily in two dimensions, without internal anatomy, although cuticles may reveal the epidermal anatomy (Greenwood, 1991). In contrast, permineralized pinnules and fronds preserve the

* Corresponding author.
E-mail addresses: raymond@geo.tamu.edu (A. Raymond), nwgeologist@gmail.com (M. Wehner), costanza@oeb.harvard.edu (S.H. Costanza).

0034-6667/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.revpalbo.2013.07.001

three-dimensional shape of pinnules as well as internal anatomy, enabling us to distinguish between ecophenotypic and species-level variation in pinnules that have a similar size and shape, but which differ in their cellular anatomy. Five species of permineralized *Alethopteris* have been found in coal balls and silicified peat from Pennsylvanian and earliest Permian deposits of Euramerica. Two of these have been identified as *Alethopteris sullivantii* and *Alethopteris lesquereuxii* (Leisman, 1960; Baxter and Willhite, 1969; Reihman and Schabilion, 1976). Cleal and Shute assigned pinnules from the Duquesne (Illinois) and Calhoun (Ohio) Coals (Kasimovian, Pennsylvanian) to *Alethopteris pennsylvanica* (Mickle and Rothwell, 1982; Cleal and Schute, 2012). A fourth, found only in the Lewis Creek coal of Kentucky, has not been assigned to an adpression species (Cichan and Taylor, 1981). Permineralized *Alethopteris* pinnules also occur in the Grand Croix (Late Pennsylvanian) and Autun (Early Permian) silicified peat deposits of France (Franks, 1963; Doubinger et al., 1995; Galtier, 2008). These pinnules were originally identified as *Alethopteris aquilina* by Franks (1963) and Galtier (2008); however Cleal and Schute (2012) assigned the Franks (1963) pinnule from Autun to *Alethopteris zeilleri*.

In this paper, we report a new permineralized *Alethopteris* from the Kalo Formation (mid Moscovian) of Iowa, U.S.A., which we assign to *Alethopteris ambigua* (Lesquereux) White (herein referred to as *A. ambigua*) based on the size and shape of the midrib and lamina. We discuss the taxonomy of Late Pennsylvanian *Alethopteris* taxa with narrow, perpendicular pinnules: *A. ambigua*, *Alethopteris lesquereuxii* Wagner, *Alethopteris friedelii* P. Bertrand, *Alethopteris leonensis* Wagner, and *Alethopteris lonchitica* Schlotheim *ex* Sternberg. We also consider the implications of pinnule shape and anatomy for medullosan paleoecology,

2. Materials and methods

The *Alethopteris ambigua* pinnules used in this study come from two coal balls (HU 64711 and HU 64865), collected from the Williamson No. 3 Mine in Lucas County, Iowa, U.S.A. (Fig. 1). Coal balls from the Williamson No. 3 Mine contain the diverse cordaitean assemblage, indicating that the mine belongs to the Kalo Formation (Pennsylvanian, mid-Moscovian, or late Atokan–early Desmoinesian: Raymond et al., 2010). The Williamson No. 3 Mine exploited one of the two, informally named coal seams in the Kalo Formation, either the Cliffland coal or the Blackoak coal, but we do not know which one (Pope et al., 2002; Raymond et al., 2010, Fig. 2). Mr. F. O. Thompson collected coal balls from Iowa mines between 1928 and the early 1940s, and donated them to the Harvard Botanical Museum where they form part of the Thompson–Darrah collection.

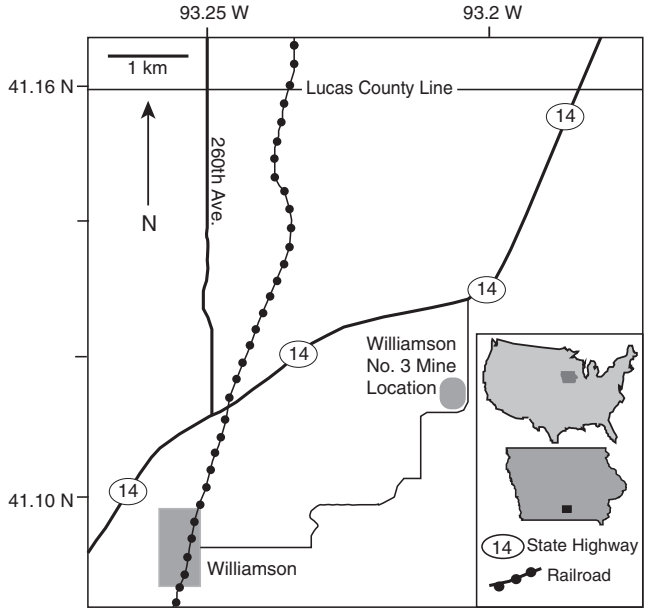

Fig. 1. Location of the reclaimed Williamson No. 3 Mine in Lucas County, Iowa. The inset map of the United States shows Iowa in dark gray; the inset map of Iowa shows Lucas County in black.

The coal ball containing the best preserved permineralized *Alethopteris ambigua* pinnules (HU 64711) was originally sectioned and peeled for floristic studies. Its original shape appears to have been spherical with a diameter of 8–9 cm. Three slices approximately 1 cm thick remain in the Thompson–Darrah collection. Because of the orientation of the *Alethopteris* frond relative to the coal ball slices, most of the pinnules revealed in the surfaces of this coal ball are cross-sections, which range in orientation from oblique to orthogonal. We supplement this material with *A. ambigua* pinnules from HU 64865, also from the Williamson No. 3 Mine. Peels of HU 64865 have cross-sections of *A. ambigua*, and a single *A. ambigua* pinnule occurs on one of the broken surfaces of this coal ball.

Approximately 40 pinnules of *Alethopteris ambigua* occur on the cut surfaces of HU 64711. Our quantitative data come from 22 orthogonal cross-sections from the middle of the pinnule, and six partial paradermal sections and exposed pinnules. Pinnules in HU64865 are either fusainized or more decomposed than those in HU 64711, and were not used to determine the size and shape of *A. ambigua*.

We use six measurements to characterize the shape of *Alethopteris ambigua* from orthogonal cross-sections, and to compare permineralized *A. ambigua* to other permineralized *Alethopteris* species (Fig. 3): 1, pinnule width between the margins of the lamina as found in coal balls, referred to here as edge-to-edge width (EEW); 2, pinnule width of the pinnule at its widest point (MaxW); 3, depth of the midrib below the upper surface of the lamina, at the highest convexity or at the crest of the vault for vaulted pinnules, referred to here as sunkenness (S); 4, midrib width (MidW); 5, depth of the midrib plus lamina, referred to here as midline depth (MidD); and 6, lamina thickness (LT). If possible, we chose EEW and MaxW to be parallel lines; however, because the cross-sectional shape of *A. ambigua* may not be symmetric, this was not always possible (Fig. 3a). We identify sections as orthogonal using the following criteria: 1, the ratio of the lamina width on both sides of the midrib is close to 1:1, generally less than 1:1.2); and 2, the top of the vaulted lamina has either one or no lateral veins perpendicular or nearly perpendicular to the midrib (Fig. 3). Because the cross-sectional shape of *A. ambigua* pinnules varies from base to tip, small deviations in orthogonality contribute to slightly asymmetric cross-sections, in which EEW and MaxW are not parallel.

We use pinnules in paradermal section and on a broken surface of HU 64865 to determine the minimum length and insertion angles of permineralized *Alethopteris ambigua* pinnules (6 to determine the minimum length, 4 to determine insertion angles). We compare the width and length of our permineralized pinnules to the width and length of pinnules from specimens of *A. ambigua* Lesquereux White identified by White or Lesquereux, in the collections of the National Museum of Natural History (Supplementary Data Appendix 1).

We compare permineralized *Alethopteris ambigua* to other permineralized species of *Alethopteris*, using published descriptions, supplemented by shape measurements made on populations of permineralized *Alethopteris* pinnules. Our *Alethopteris lesquereuxii* and *Alethopteris sullivantii* samples consist respectively of 32 and 6 pinnules from the Lovilia deposit of Iowa, which is equivalent in age to the Houchin Creek (No. 4) Coal of the Illinois Basin and the Bevier Coal of Kansas (Brotzman, 1974; Peppers, 1996: Fig. 2). Although the *A. sullivantii* population is small, the large size of these pinnules readily distinguishes this species from other permineralized species of *Alethopteris*.

Our *Alethopteris pennsylvanica* sample consists of 13 pinnules from the Berryville locality of the Calhoun Coal of Illinois (Fig. 2). This species, which also occurs in the Dusquesne Coal of Ohio, is clearly distinct from other permineralized *Alethopteris* species (Mickle and Rothwell, 1982). However we note that the width of adpressed *A. pennsylvanica*