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Evidence for an ancient association between leaf mining flies and herbaceous eudicot angiosperms

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ABSTRACT

We describe an early angiosperm and a leaf mine ichnofossil from the Lower Cretaceous Potomac Group of Virginia, USA. The descriptions are based on a fossil leaf that was first reported in 1895 but identified as a fragment of a fossil fern. The new genus and species of angiosperm, *Vernifolium tenuiloba* Jud and Sohn, gen. et sp. nov., was likely herbaceous and is based on a twice odd-pinnatifid leaf with glandular teeth at the tips of the lobes, and minute resin bodies covering the lamina. Leaf architectural features and sedimentological context indicate that this leaf was produced by an herbaceous eudicot angiosperm, possibly associated with Ranunculales. The leaf mine *Phytomyzites wardi* Sohn and Jud, ichnosp. n. is a full depth linear-blotch mine with frass, a trace of puparium inside the blotch mine section, and feeding/oviposition-related puncture marks. The features of the mine are most consistent with those produced by agromyzid flies. This fossil extends the record of agromyzid flies by about 40 myr. Furthermore, data from molecular studies suggests that the ancestral hosts for agromyzid flies are asterids, with several later host-shifts to feeding on Ranunculaceae, but this fossil provides evidence that agromyzid flies or their ancestors were feeding on herbaceous basal eudicots similar to modern herbaceous ranunculids during the Early Cretaceous, prior to the appearance and diversification of asterids.

1. Introduction

Agromyzid flies are globally distributed and include thousands of species that feed on leaf mesophyll as larvae; these are the leaf mining flies. (Spencer, 1972; Scheffer et al., 2007). The diversity of agromyzid flies is shaped largely by evolutionary radiations following host shifts (Spencer, 1990), but the importance of extinction on the phylogenetic structure of modern host associations may be under appreciated (Winkler et al., 2010). Most extant agromyzid flies mine the leaves of herbaceous plants (Spencer, 1990), but some (including members of the early-diverging genus *Agromyza*) specialize on distantly related woody plants (Scheffer et al., 2007; Winkler et al., 2010). This pattern may reflect an ancestral association between leaf mining flies and ancient woody plant lineages followed by more recent radiations on species-rich herbaceous host lineages, or alternatively early agromyzid flies may have diversified primarily on herbaceous hosts, with rare host-shifts to woody plants (Winkler et al., 2010). Fossil evidence of extinct associations with woody Platanaceae and Rutaceae during the Paleocene appears to support to the former hypothesis (Winkler et al., 2010); however, the paucity of fossil mines on herbs could be the result of failure to detect the fossil leaves of herbaceous plants (Winkler et al., 2010).

The taphonomic megabias against herbaceous plants in litter assemblages is well known (Behrensmeyer et al., 2000); however, fine-grained sediment deposited under low-energy conditions on floodplains can preserve herbaceous plants in-situ or nearly in-situ, providing a "snapshot" of floodplain communities (Upchurch and Doyle, 1981; Wing et al., 2011). In the Potomac Group (Gp), these types of assemblages are generally found in local, organic-rich deposits of clay or mud with planar fabric and little or no lamination (Upchurch and Doyle, 1981; Jud, 2014).

Here, we describe an herbaceous eudicot angiosperm with evidence of leaf mining based on a fossil from the Lower Cretaceous (Albian) Potomac Group in Virginia. The preserved leaf architecture indicates a close relationship to eudicot angiosperms, and the mine has a combination of features produced by agromyzid flies. The

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occurrence of an agromyzid fly in the Lower Cretaceous extends the fossil record of the family by ~40 million years ago (Ma) and supports the hypothesis that agromyzid flies have an ancient and ancestral association with herbaceous basal eudicots rather than with Cenozoic woody angiosperms or herbaceous rosids or asterids (Winkler et al., 2010).

2. Methods

Collecting locality. The fossil was collected from a carbonaceous silty clay bed along the bank of the Potomac River.

Stratigraphic position and age. The Mount Vernon locality

The leaf is preserved as an adpression in two pieces and was collected from a light brown clay bed exposed along the Potomac River in Northern Virginia, USA (USGS locality 499), on what was historically the Mount Vernon estate, near Fort Belvoir, Virginia, USA. (38.675N, 77.131W). (Fig. 1). The bed from which the leaf was collected belongs to pollen zone IIB of the Potomac Group (Patapsco Formation) (Brenner, 1963; Doyle and Hickey, 1976; Doyle and Robbins, 1977) (Fig. 2). Previous work showed that pollen and spore flora at the Mount Vernon site is more than 50% angiosperm pollen and includes diverse tricolpate grains indicative of eudicot angiosperms (Doyle and Hickey, 1976). Pollen zone IIB is now thought to correspond to the middle-upper Albian (Hochuli et al., 2006). Ward (1895) reported on three collections from this site that include fossils of ferns, gymnosperms, and angiosperms. We re-examined the specimens that were identified as ferns for herbaceous angiosperms and recognized extensive insect damage on one specimen. We examined the specimen using low-angle light under a dissecting scope and photographed the specimen using a Canon EOS digital camera with a 100 mm EF macro lens and a Nikon D70 digital camera with a Macro-Nikkor 65 mm lens. We processed the images with Adobe Photoshop (San Jose, California, USA) and applied whole-image manipulations to improve the contrast between the fossil and the matrix. The leaf architectural

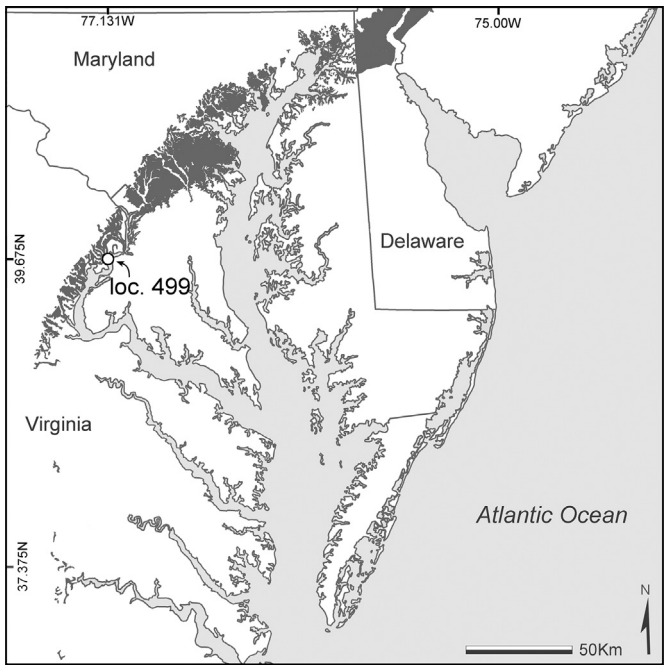

Fig. 1. Map of Lower Cretaceous Potomac Group outcrop in Virginia and Maryland, USA. The Mount Vernon locality is indicated by an arrow on the western bank of the Potomac River.

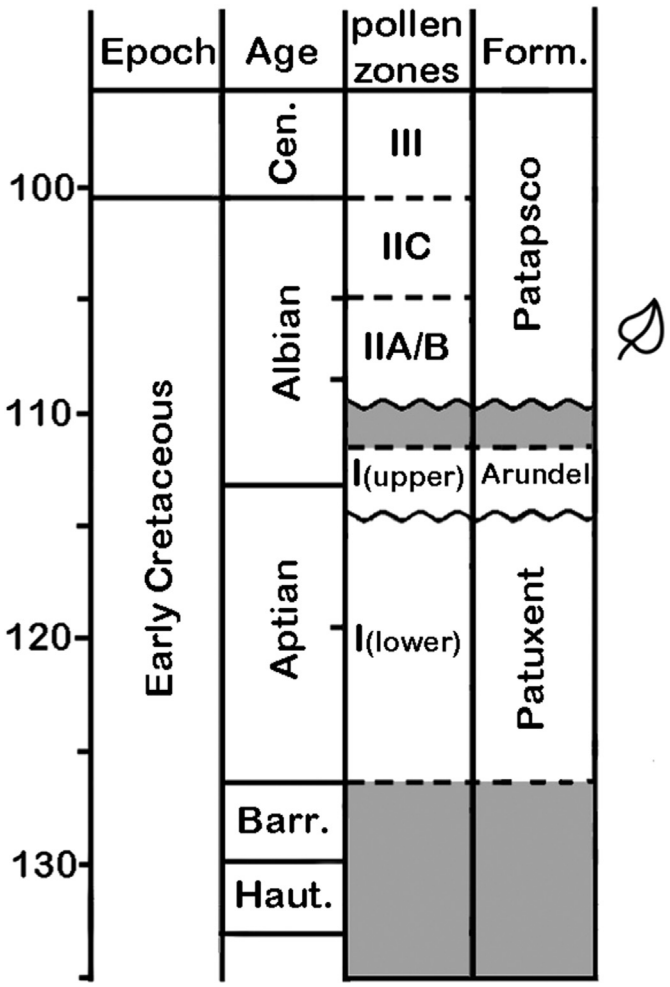

Fig. 2. Age of the lower part of the Potomac Group (modified from Doyle, 1992; Hochuli et al., 2006; dates on the left are from Gradstein et al. (2012). The Mount Vernon locality is in the Patapsco Fm, or the upper part of pollen zone IIA/B, indicated by the leaf icon. Abbreviations: Barr. = Barremian age, Haut. = Hauterivian age.

character definitions used are based on those outlined in the Manual of Leaf Architecture (Ellis et al., 2009) with some of modifications (Jud and Hickey, 2013). The leaf mine trace was observed and photographed using an Olympus SZX12 stereomicroscope accompanied with image capture system and an Image-Pro 6.1 (Media Cybernetics) platform. The leaf mine was illustrated using Adobe Illustrator CC (Adobe systems). The morphological terms for the leaf mine follow Hering (1951) and Winkler et al. (2010).

3. Systematics

3.1. The host plant

Clade Angiosperms
Group Eudicots
Order cf. Ranunculales Jussieu ex Berchtold & J. Presl, 1820.
Family *incertae sedis*

Genus *Vernifolium* Jud and Sohn, gen. nov.

Vernifolium tenuiloba Jud and Sohn, sp. nov. Fig. 3

Diagnosis. Leaves simple, petiolate. Blade a microphyll, twice odd-pinnatifid, wider than long (l:w ratio ~ 1:2); primary lobes in sub-opposite arrangement, secondary lobes alternate; sinuses