



# A comparison of terpenoid and leaf fossil vegetation proxies in Paleocene and Eocene Bighorn Basin sediments



Aaron F. Diefendorf<sup>a,\*</sup>, Katherine H. Freeman<sup>b</sup>, Scott L. Wing<sup>c</sup>

<sup>a</sup> Department of Geology, University of Cincinnati, PO Box 210013, Cincinnati, OH 45221, USA

<sup>b</sup> Department of Geosciences, Pennsylvania State University, University Park, PA 16802, USA

<sup>c</sup> Department of Paleobiology, Smithsonian Institution, NHB121, PO Box 37012, Washington, DC 20013, USA

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## ABSTRACT

Plant-derived terpenoids, long recognized as biomarkers, can help reveal the major taxonomic groups of land plants present in ancient environments, even if rocks and sediments do not preserve plant macro- or microfossils. Previous studies have used simple di- to triterpenoid ratios to reconstruct floral changes in the geologic past, but few have compared terpenoid ratios with estimates of floral composition from fossils. Further, reconstructions have not taken into account differences in biomarker production (i.e. concentration relative to leaf biomass) between different types of plants. Here, we have examined terpenoids from early Cenozoic fluvial rocks from the Bighorn Basin (Wyoming, USA), where fossil flora has been studied in detail. We analyzed the distributions of diterpenoids, triterpenoids and *n*-alkanes from leaf wax in a total of 43 samples from 15 stratigraphic horizons of late Paleocene (63 Ma) to early Eocene (53 Ma) in age. In nearly all samples, triterpenoids, derived from angiosperms, were significantly lower in abundance than conifer-specific diterpenoids, a finding that contrasted with plant fossil evidence for the same rocks. This suggests that di- to triterpenoid ratios severely underestimate the abundance of angiosperms in paleovegetation. Angiosperms dominated *n*-alkane production among modern plants, and we propose a new paleovegetation proxy based on the ratio of diterpenoids (conifers) to *n*-alkanes (angiosperms), corrected for lipid production estimated from extant vegetation. Using diterpenoids and alkanes, we infer the composition of paleovegetation to be similar to that inferred from plant fossils. Although the approach works well for the Bighorn Basin, we stress the new paleovegetation proxy will need to be evaluated for other time periods, communities, paleogeography and depositional environments with pollen or megafossil data available.

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## 1. Introduction

Characterizing paleovegetation patterns in response to climate shifts is challenging because of the limited or discontinuous preservation of plant fossils such as leaves and pollen in many ancient environments. Plant terpenoids (defense compounds synthesized from the 5 carbon building block, isoprene) are well known biomarkers (Fig. 1) and high level chemotaxonomic indicators. For example, non-steroid pentacyclic triterpenoids are almost exclusively synthesized by angiosperms, whereas tricyclic diterpenoids are characteristic of gymnosperms, specifically conifers (Erdtman, 1963; ten Haven and Rullkötter, 1988; Sukh Dev, 1989; Otto et al., 1997; Otto and Simoneit, 2001; Otto and Wilde, 2001; Hauteville et al., 2006; Keeling and Bohlmann, 2006; Cox et al.,

2007; Diefendorf et al., 2012). Studies have used simple di- to triterpenoid ratios to reconstruct vegetation distribution, but few compared terpenoid abundance ratios to the relative abundance of angiosperms and conifers seen in pollen or megafossils from the same deposits (Bechtel et al., 2003; Nakamura et al., 2010). These earlier studies also did not account for biomarker production, which differs between different plant functional types (angiosperm vs. conifer; deciduous vs. evergreen), as such data have only recently become available (Diefendorf et al., 2012). As a result, there is significant uncertainty as to the value of terpenoid ratios as paleovegetation proxies in ancient sediments where biomarkers have been significantly altered or lost during early diagenesis (e.g. Wakeham et al., 1980).

To investigate the use of terpenoids as proxies for the relative abundance of angiosperms and gymnosperms in paleovegetation, we examined sediments from the Bighorn Basin (Wyoming, USA), where plant fossils provide an independent means of estimating

\* Corresponding author. Tel.: +1 513 556 3787.

E-mail address: [aaron.diefendorf@uc.edu](mailto:aaron.diefendorf@uc.edu) (A.F. Diefendorf).

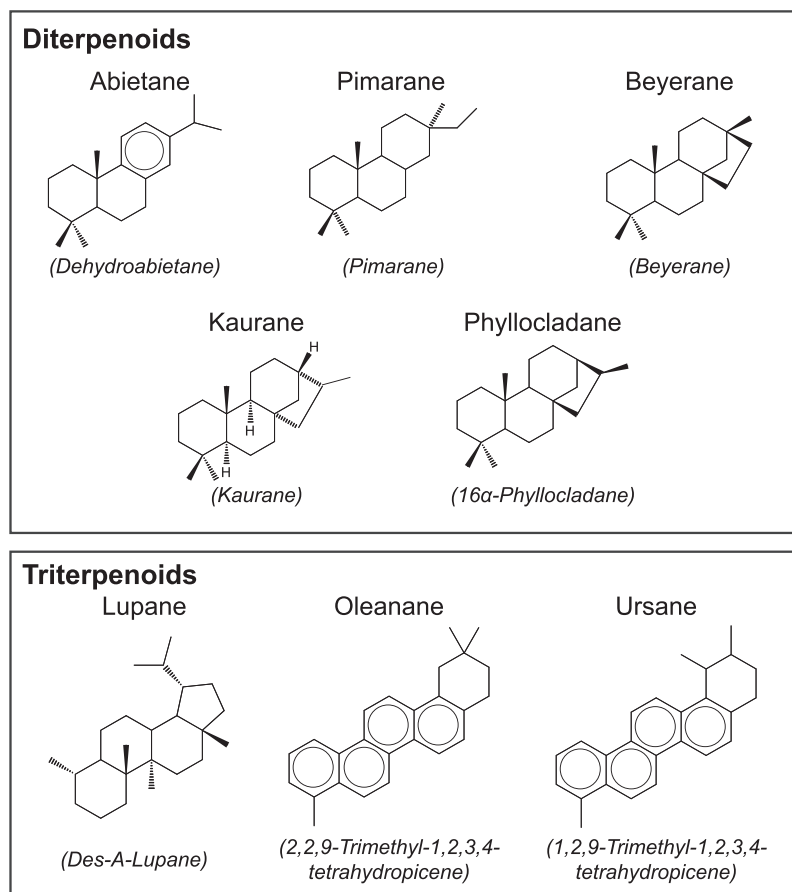


Fig. 1. Di- and triterpenoid classes and commonly found compounds (in italics) from each class found in Bighorn Basin sediments.

the relative abundance of the two groups. Diterpenoids, triterpenoids and leaf wax *n*-alkanes in 43 samples from 15 stratigraphic horizons from the late Paleocene (63 Ma) to early Eocene (53 Ma) were quantified. For the majority of sampling sites, leaf fossil data indicated a mixture of angiosperms and gymnosperms dominated by angiosperms (typically 85–100%).

Simple di- and triterpenoid abundance ratio estimates of paleovegetation and estimates that took into account production differences between plant taxonomic groups and leaf lifespans were not consistent with floral composition predicted from fossils. Angiosperm triterpenoids had lower than expected abundance relative to diterpenoids given the dominance of angiosperms in the leaf flora, and also had low abundance compared with leaf wax *n*-alkanes, which are most common in angiosperms (Diefendorf et al., 2011). The data reveal a preferential loss of triterpenoids and suggest separate controls on di- and triterpenoid preservation. In contrast, after accounting for biomarker production differences, diterpenoid to *n*-alkane ratios gave angiosperm/gymnosperm estimates that agreed with fossil data. Although the diterpenoid and *n*-alkane-based paleovegetation proxy approach works for sites in the Bighorn Basin, we stress it needs to be evaluated for other time periods, paleogeographic and depositional settings, and major plant groups.

## 2. Material and methods

### 2.1. Geological and sedimentological setting

Samples were collected from outcrops of the Paleocene and lower Eocene Fort Union and Willwood formations in the Bighorn Basin, Wyoming, USA (Fig. 2). The basin is a Laramide structural

depression surrounded by mountains uplifted during the Paleocene and early Eocene (Bown, 1980). The Fort Union and Willwood formations are alluvial deposits with a total thickness of ca. 2 km, though thickness and lithology vary markedly across the basin (Gingerich, 1983; Wing and Bown, 1985; Kraus, 1992). The fluvial systems that deposited these two formations are reconstructed as having been anastomosed channels of moderate size, with dynamics controlled primarily by avulsion, i.e. the sudden switching of major channels through the process of crevasse-splay formation and growth (Bown and Kraus, 1987; Kraus, 1996; Kraus and Aslan, 1999). They created a mosaic of environments on the subsiding basin bottom, including active and abandoned channels, alluvial ridge and crevasse-splay deposits, and broad muddy floodplains that varied from well drained to poorly drained (Bown and Kraus, 1981, 1987; Wing, 1984; Kraus, 1996, 1998; Davies-Vollum and Kraus, 2001). Common lithologies include fluvial sandstones, mudstones, minor lignites and carbonaceous shales, and rare freshwater carbonates (Gingerich, 1983). Fort Union sediments are primarily gray-brown with interspersed lignitic and carbonaceous [i.e. organic carbon (OC)-rich] shales (Bown, 1980). The Willwood Formation is dominated by oxidized mudstone paleosols that are variegated red, purple and yellow, but there are also channel sandstones, laterally extensive carbonaceous shales and abandoned channel deposits containing plant fossils and dispersed organic material (Bown, 1980; Kraus and Riggins, 2007).

Samples were collected from eight stratigraphic levels spanning  $10 \times 10^6$  yr of the Paleocene and early Eocene, with the oldest level being ca. 63 Ma and the youngest ca. 53 Ma (Table 1). The age of each bed was calculated by linear interpolation between levels of known age and stratigraphic level within each section (Wing

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