Biogeography of Pleistocene conifer species from the Ziegler Reservoir fossil site, Snowmass Village, Colorado

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A B S T R A C T

Pleistocene biogeography of conifer species is poorly known in much of western North America. We conducted morphological studies on 201 conifer cones and cone fragments recovered from Pleistocene sediments at the Ziegler Reservoir fossil site (2705 m) near Snowmass Village, Colorado. The basin, formed ~155–130 ka, contains fossil-bearing lacustrine, palustrine, and colluvial sediments spanning approximately 85 ka. Using a suite of morphological characters, particularly cone-scale bracts, we differentiated species of *Abies*, *Picea*, and *Pseudotsuga*. All fossil *Abies* specimens were assignable based on bract morphology to *Abies concolor*, which is currently absent from central Colorado (nearest populations are 160 km southwest of the site). *A. concolor* occurs only in sediments of MIS 5d and 5c. *Pseudotsuga menziesii* and *Picea engelmannii* cones occurred in sediments corresponding to MIS 5e, 5d, 5c, and 5a. A fourth conifer species, occurring in sediments of MIS 5e, 5d, 5c, and 5a, is difficult to assign to any extant species. Bract morphology is similar to *Picea pungens*, which grows near the site today, but scale morphology is unlike *P. pungens*. These fossils may represent ancestral *P. pungens*, an extinct variant, or an extinct sister species.

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Introduction

Knowledge of Pleistocene vegetation and plant biogeography of western North America before the Last Glacial Maximum (LGM, ~ 20 ka) is almost entirely based on pollen data (Heusser and King, 1988; Baker, 1989; Whitlock and Bartlein, 1997; Anderson et al., 2000). Pollen sequences, although informative and readily obtained from a variety of depositional settings, have two fundamental limitations. First, pollen is widely dispersed in the atmosphere. Pollen assemblages, therefore, usually represent a regional integration of vegetation lacking spatial precision (Bradshaw and Webb, 1985; Jackson et al., 1997; Seppa and Hicks, 2006). Second, pollen cannot be identified beyond the genus level in most settings, and sometimes not even beyond the family level. This taxonomic smoothing limits the understanding of biogeographic history and may mask important changes in species-level dynamics (Webb, 1988; Jackson et al., 1997; Birks and Birks, 2000), including species extinction (Jackson and Weng, 1999).

Plant macrofossils are not transported as far as pollen grains, and frequently allow species-level identification. By providing information about flora and vegetation immediately adjacent to a site, plant macrofossils allow local patterns to be distinguished from regional ones, which can be particularly helpful in regions of steep elevational gradients or landscape diversity (Dunwiddie, 1987; Jackson and Booth, 2007). Species identification of plant macrofossils can also provide more precise paleoenvironmental, biogeographic, and ecological information than pollen (Jackson et al., 1997; Birks and Birks, 2000; Weng and Jackson, 2000). Finally, some taxa are absent from or strongly underrepresented in pollen assemblages (e.g., *Pseudotsuga*, *Populus*), whereas macrofossils can document local populations (Miller and Thompson, 1979; Baker et al., 1986, Jackson et al., 1986, Weng and Jackson, 1999).

Ovulate cones of *Picea* and other conifers have been found in many Quaternary deposits (Baker et al., 1980; Jackson et al., 1986, 1997, Givens and Givens, 1987; Warner and Chmielewski, 1987; Miller, 1988; Jackson and Givens, 1994). Because taxonomy of conifers relies heavily on ovulate cone morphology (Florin, 1954; Hart, 1987; Farjon, 2010), such occurrences provide unique opportunities for understanding biogeographic history of individual conifer species (Jackson et al., 1997). However, detailed morphological studies of Quaternary conifer cones are few. In many studies, fossils are simply binned into species categories based on gross morphology or simple length measurements. Although useful in paleoecological and biogeographic studies, much of the potential information in the fossils remains unutilized, and errors in identification can result. For example, Pleistocene conifer cones from the Tunica Hills region (Louisiana/Mississippi) were repeatedly identified as *Picea glauca* based on gross morphology (Brown, 1938;

Delcourt and Delcourt, 1977; Givens and Givens, 1987), but detailed morphological and morphometric studies revealed that the cones belonged to a now-extinct species, *Picea critchfieldii* (Jackson and Weng, 1999).

Recovery of 201 ovulate cones, cone fragments, and dispersed cone-scales from the Ziegler Reservoir fossil site (ZRFS) near Snowmass Village, Colorado provided a unique opportunity for species-level identification of conifers growing in the vicinity of the site, and to better understand the poorly known Pleistocene biogeographic history of several Rocky Mountain forest tree species. In this study, we report results of detailed morphological and morphometric studies of the ovulate-cone materials from the ZRFS, identifying conifer species based on cone, cone-scale, and bract morphology. We discuss ecological and biogeographic implications of our findings, in context of other fossil records from the ZRFS and from contemporary records from the North American interior.

Site description

History of the excavation

In October 2010, bones of a Columbian mammoth were unearthed during the enlargement of Ziegler Reservoir near Snowmass Village, Colorado. Subsequent fossil recovery was coordinated by the Denver Museum of Nature and Science (DMNS) and proceeded for two weeks while construction remained active. Most cone specimens collected in 2010 were exposed by passing D6 bulldozers, rendering stratigraphic control imprecise. All fossil specimens, including conifer cones, were assigned a field number including general site information on lithology and specimen location. The fossil conifer cone specimens were collected in plastic bags in the field and later transferred to jars filled with distilled water and stored at 10°C at DMNS. Approximately 30 conifer cones were recovered in 2010.

In May 2011, DMNS personnel returned to the ZRFS with a systematic plan for collecting fossil specimens and carefully documenting the stratigraphic placement of individual specimens. The DMNS excavation, with a large complement of trained volunteers, proceeded from early May until early July. Many cones were found by the members of the volunteer crew in the course of the excavation, and others were recovered during systematic screening of bulk sediments for small vertebrate bones. The 2011 field season yielded 171 fossil conifer cones, making a total of 201 whole and partial cones recovered from the site.

Geological setting, chronology, and stratigraphy

The ZRFS, ~2705 m above sea level on a ridge between the Brush Creek and Snowmass Creek drainages (Fig. Fig. 1), comprises a 12 ha basin that originated as an ice block depression, dammed on one side by a moraine formed during the Bull Lake glaciation (~155–130 ka) (Pigati et al., 2014–in this volume). The basin was occupied by a lake during much of its history, slowly filling with windblown silts and clays and both allochthonous and autochthonous organic materials. Bedded silts, clays, and colluvium from debris flows were deposited along the steep slopes of the basin margin. Ages of sediments in the basin are estimated to be between ~140 and 55 ka based on cosmogenic dating of moraine boulders, radiocarbon dating, and optically stimulated luminescence (OSL) dating of lake sediments (Mahan et al., 2014–in this volume).

The stratigraphy at the ZRFS can be divided into lake-center and lake-margin sequences. The lake-center sequence consists of 18 distinct stratigraphic units, all representing low-energy deposition in a lacustrine or palustrine environment (Fig. 2). Lake-margin units are characterized by coarse-grained, poorly sorted sediments, including clasts up to 1 m in diameter, that resulted from slumping of the impounding moraine and extend ~50 m toward the basin center. Most fossil cones were found in the coarse-grained, basin-margin sediments, which represent alternating slope washes, debris flows, beaches, and quiet-water deposition. For this study, we follow zones established by Anderson et al. (2014–in this volume) based on changes in the pollen assemblages. This provides the most precise stratigraphic placement possible for most of the conifer cones. Pollen Zone (PZ) 6 includes the Basement Red Pebble and units 3 and 4, has an age of ~141–138 ka, and sits directly on top of glacial till. PZ 5e includes the Basement Silt and units 4–6 (138–129 ka), with multiple alternating layers of organic-rich silt, clay, and sterile silt. PZ 5d corresponds to the Main Floor, Main Floor Red Pebble, Main Silt, and Primary Debris Flow, as well as units 6–8 (129–113 ka). PZ 5c includes the Upper Silt, Beach Silt, and Upper Debris Flow, as well as units 8–12 and the base of Unit 13 (113–100 ka). Unit 10, also known as the Yellow Brick Road (103 ka), is a critical stratigraphic marker-horizon linking the lake-center and near-shore sequences. PZ 5b includes the White Clay and units 13 and 14 (100–87 ka). PZ 5a corresponds to the Upper Red Sand and units 15 and 16 (87–77 ka). Finally, PZ 4 corresponds to units 17 and 18 (77–55 ka).

Methods

We identified the cones by systematically examining and measuring morphological features, comparing them with descriptions and measurements obtained from the botanical literature and from modern reference specimens. For the latter, we used cones obtained from the University of Wyoming Rocky Mountain Herbarium, the University of Wyoming Quaternary Plant Ecology Laboratory collections, the University of Washington Herbarium, and the Arnold Arboretum at Harvard University. These specimens were augmented by additional field collections during summer 2012, which provided larger sample sizes and broader geographic coverage of the species of interest (*Abies amabilis*, *Abies concolor* var. *concolor*, *Abies concolor* var. *lowiana*, *Abies grandis*, *Abies lasiocarpa* var. *lasiocarpa*, *Abies lasiocarpa* var. *arizonica*, *Abies magnifica*, *Picea engelmannii*, *Picea glauca*, *Picea pungens*, *Pseudotsuga menziesii* var. *glauca*, *Pseudotsuga menziesii* var. *menziesii*, *Tsuga heterophylla*, and *Tsuga mertensiana*). Although not all of these taxa are represented in the fossil assemblages at the ZRFS, it was important to include them to assess variation within and among species. Details on the field-collection techniques, as well as metadata for both the herbarium and field collections, are described by Miller (2013).

The lengths and widths of cones, cone scales, and seeds were measured for extant and fossil conifer specimens using a digital caliper. Cone scales for measurement were carefully removed from cones using forceps, and in many cases, seeds were removed directly from the cone scale. Dispersed seeds of modern and fossil cones were also measured. The bracts required greater measurement precision, so they were measured using a Leica dissecting microscope equipped with a Leica digital camera. Digital images for modern and fossil bracts were measured with Leica LAS V3.8 software.

Cone length was measured from the base to the apex. Many fossil cones were broken, so length measurements are treated as minimum estimates. Cone scales were closed in the fossil specimens, so all diameter measurements of modern cones were made on wet cones with closed scales. All cone-diameter measurements were made at the widest portion of the cone. Because *Abies* cones typically disintegrate upon maturing, few fossil or modern *Abies* cones were measured.

For each cone specimen, modern or fossil, 7–10 cone scales were measured, selected at intervals from the cone base to the cone apex. Cone-scale length was measured recorded from the apex of the cone scale to the base, defined as the attachment point to the cone axis. Cone-scale width was measured at the widest point of each scale.

When possible, 7–10 seeds were removed from cone scales of fossil and modern specimens for study. Seed length and width (at widest point) were measured, and the length of the entire seed and wing was recorded from the tip of the seed to the terminus of the seed wing.