

AN APTIAN CYCADEOID FROM THE BUDDEN CANYON FORMATION,
ONO QUADRANGLE, CALIFORNIA

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ABSTRACT

We describe a cycadeoid trunk from the Aptian Chickabally Member, Budden Canyon Formation in Ono, California. Our diagnosis of the specimen as a cycadeoid was initially based on the presence of mucilage canals in the pith and the structure of the secondary xylem. This determination was subsequently supported by recognition of the distinctive morphology of the surface of the primary body of eroded cycadeoid trunks. The latter may aid in the identification of otherwise enigmatic Mesozoic fossils. This specimen is the third cycadeoid to be reported from northern California and slightly extends the known geographic range of the group within the state.

Key Words: Aptian, California, Cretaceous, cycadeoid, gymnosperm, trunk.

The cycadeoids (Bennettitales) are an extinct group of seed plants that evolved during the Triassic (248–206 Ma [mega annus]) following the formation of the supercontinent Pangea and the emergence of other seed plant groups, such as Cycadales, Ginkgoales, and Glossopteridaceae (Willis and McElwain 2002). They became extinct by the end of the Cretaceous (~65 Ma). Cycadeoids attained a cosmopolitan distribution in the Mesozoic; growing abundantly in tropical and, to a lesser extent, warm temperate climates (Taylor and Taylor 1993; Willis and McElwain 2002). As a group, cycadeoids appear to have grown in disturbed habitats, particularly on levees (Retallack and Dilcher 1981). Their seeds were small and wind dispersed, commensurate with an early successional status (Tiffney 1986). Cycadeoids ranged in habit from low barrel-shaped or multi-branched shrubs to erect, often thick, sparsely branched trees. Most bore pinnately compound, coriaceous foliage (Tidwell 1998); the petioles were surrounded by lignitic scales at their point of insertion on the trunk; these scales formed the exterior surface of the trunk. Internally, the trunk consisted of a large central pith, limited primary xylem, prominent to poorly developed secondary xylem, and a thick cortical area. The secondary xylem was manoxylic, with files of tracheids separated by medullary rays that were one to three cells wide (Stewart and Rothwell 1993). Leaf traces arose from the primary xylem and passed through the secondary xylem into the cortex and directly out to the leaves. Cycadeoids were generally differentiated from the distantly related Cycads based on their vascular, reproductive, and stomatal structures (Nishida 1994). Cycadeoid stems generally lacked girdling leaf

traces, which are a characteristic feature of most cycads, although they are lacking in the cycad *Antarcticicyas* (Smoot et al. 1985). In addition, cycadeoids commonly had bisporangiate reproductive structures (although those of *Williamsonia* were monosporangiate) with microsporophylls and ovules within the same cone (e.g., Delevoryas 1968; Crepet 1974). By contrast, most cycads are dioecious (Stewart and Rothwell 1993).

Cladistic analyses have placed the Paleozoic medullosans as a possible ancestor to cycadeoids, based on similarities in wood structure and vascular bundle patterns (Nishida 1994; Willis and McElwain 2002). Earlier cladistic analyses suggested that cycadeoids are most closely related to angiosperms and Gnetales (Doyle et al. 1994; Nixon et al. 1994). More recent studies (e.g., Doyle 2006) generally link Gnetales with conifers (but see Hilton and Bateman 2006), while retaining a cycadeoid–angiosperm link. While some studies place cycadeoids as the sister group to angiosperms, reflecting their bisexual, flower-like reproductive structure, the lack of morphological intermediates and the presence of one, rather than two integuments, suggest some distance between the two groups (Willis and McElwain 2002).

While the group embraced a range of morphologies throughout its history, the dominant western North American Cretaceous taxon was *Cycadeoidea*, a genus of squat, barrel-trunked plants (Ward 1900; Wieland 1906–1916; Delevoryas 1968; Rothwell and Stockey 2002); although some specimens originally attributed to *Cycadeoidea* have been segregated into a separate genus, *Monanthesia* (Delevoryas 1959), and other

genera of cycadeoids were present (e.g., Stockey and Rothwell 2003). Cycadeoid fossils from California are exceedingly rare; to date, only two specimens have been reported. Ward et al. (1905) described *Cycadeoidea stantoni* from Colusa County in northern California. Delevoryas (1959) later transferred this specimen to *Monanthesia* based on vascular patterns. In 1998, an amateur fossil collector uncovered a second *Monanthesia* from Vallejo in northern California (Collecting fossils in California 1998). In this paper, we describe a cycadeoid recently collected from Aptian age sediments of northern California. This find extends the geographic range of cycadeoids within California. The specimen also has an unusual mode of preservation, which led its initial discoverer to ally it with arborescent lycopods.

LOCALITY DESCRIPTION

The specimen was collected by Charles Dailey from Cottonwood Creek, in the Chickabally Member of the Budden Canyon Formation near Ono, California (Sec. 18, T30N, R6W). It was found on the surface, and is presumed to be derived from the immediately surrounding sediments. The Chickabally Member was determined to be of Aptian age (~120 to 112 Ma) by Murphy and colleagues (Murphy et al. 1969; Murphy 1975), who provide a detailed description of the local geology. The upper Chickabally Member is characterized by mudstone with a few sandstone beds and limestone concretions (Murphy et al. 1969).

Marine invertebrate fossils associated with this member include *Potamides diadema*, *Plicatula variata*, *Nucula gabbi*, *Turbo festivus*, and *Tessarolax bicarinata*, all suggestive of a near shore marine environment. Chandler and Axelrod (1961) described the following plant taxa as occurring in the Chickabally member, basing their identifications upon Fontaine (in Ward et al. 1905): *Cladophlebis*, *Ctenopteris*, *Sagenopteris*, *Dioonites*, *Ctenophyllum*, *Cephalotaxopsis*, *Sphenolepidium*, and *Acaciaephyllum*. These attributions are a century old, and have not been re-verified for accuracy of identification or systematic assignment. However, at face value, these comprise three taxa of cycadophyte foliage, two of conifer foliage, and a single angiosperm leaf (Tidwell 1998). Chandler and Axelrod (1961) also described a putative angiosperm fruit from a nearby locality (Sec. 17, T30N, R7W). More recently, new specimens of an osmundaceous fern (Stockey and Smith 2000), a cyatheaceous tree fern (Lanz, Rothwell and Stockey 1999), and a cone of the Pinaceae (Smith and Stockey 2001) have been collected from the same general area.



FIG. 1. This portion of a Cycadeoid stem was uncovered in Cottonwood Creek, near Ono, California. The stem has been strongly eroded so that the majority of preserved tissue is pith. Leaf scars occur in a spiral arrangement, about 50° off the vertical axis.

GENERAL DESCRIPTION

The specimen is a portion of a laterally compressed, silicified, stem that is 4.5 to 5.3 cm long and 4.8×3.2 cm in cross section. The specimen is strongly eroded and is primarily composed of pith tissue (Fig. 1), with small, scattered portions of primary and secondary xylem located on one side. This same side of the fossil is covered with spirally arranged leaf scars. The specimen is assigned number TLLE 65 in the Collection of the Natural History Museum, Sierra College.

Pith

The pith was originally about 3.4 cm in diam. and is poorly preserved in some areas due to cell degradation (Fig. 2). Intruding sediments have occasionally permeated to the center of the fossil, and in one instance, contained a fungal spore. The majority of the preserved portion of the pith consists of thin-walled parenchyma. These cells are roughly equidimensional, averaging 110×105 μm in cross section and 116×98 μm in long section. Scattered throughout the pith are mucilage canals lined by small epithelial cells (109×105 μm) and bearing dark resin within. Overall, these canals are larger in diameter than the parenchyma cells, averaging 248×239 μm in cross section and 405×205 μm in long section (Fig. 3).



FIG. 2. Cross-section of specimen. Primary and secondary xylem occur in the lower left section of the specimen, below the intruded sediment.

Xylem

An approximately 5 mm wide by 1 mm thick area of primary and secondary xylem adheres to one side of the pith. A roughly 200 μm wide zone of poorly preserved cells that are interior to the secondary xylem and distinct in morphology from the pith cells is inferred to represent the place of the primary xylem. Exterior to this are radially oriented strands of alternating secondary xylem and parenchyma. Each xylem band is one to three cells wide, and is composed of dark, lignified cells averaging $28 \times 25 \mu\text{m}$ in cross section. The largest band of secondary xylem (Fig. 4) is 666 μm thick. In between these bands of lignified cells are thin-walled medullary rays. Each ray is one to two cells wide, and is composed of thin-walled parenchyma cells averaging $49.6 \times 40.7 \mu\text{m}$ in cross section. The limited amount of secondary xylem did not permit serial sections or a section in the tangential or radial plane.

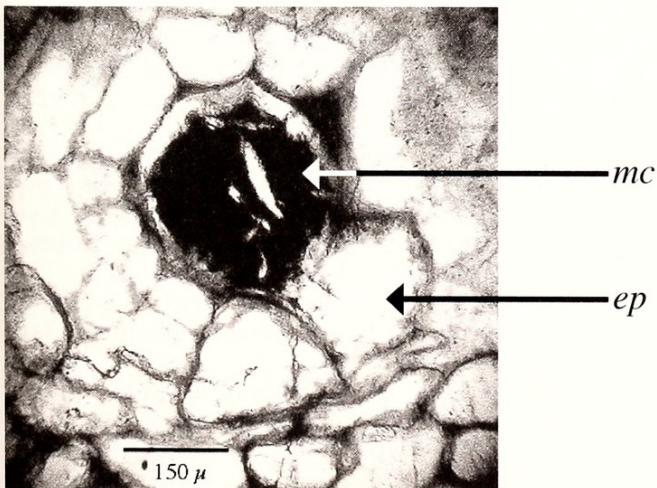


FIG. 3. Cross-section of mucilage canal (mc) surrounded by epithelial cells (ep). Note the dark contents in the interior of the canal.

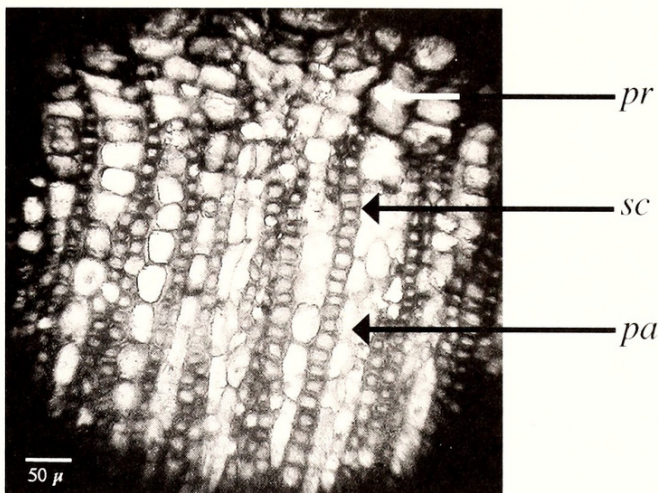


FIG. 4. Cross-section of secondary xylem. Strands of thick walled secondary xylem (sc) alternate with strands of parenchyma (pa). The interface with the primary body (pr) is at the top of the picture.

Leaf Scars

Spiral leaf scars occur on the same side of the specimen as the adherent secondary xylem. Five vertical spirals are present, each with four scars per spiral; the spirals incline at an angle of $49\text{--}50^\circ$ off the vertical axis. Each scar ranges from 10 to 15 mm in length and 2.0 to 3.0 mm in width; a horizontal distance of 5 mm separates the scars. Leaf scars are most prominent in the center of the specimen, fading to either side.

DISCUSSION

This specimen was first presented to us as a possible Mesozoic arborescent lycopod, and indeed the spiral traces show a strong similarity to the traces observed on decorticated specimens of *Lepidodendron*. The structure of the pith, however, argued against this interpretation. Partially decorticated *Cycadeoidea* specimens from the Cretaceous of Maryland illustrated in Plate LXXXIX, Figure 2 of Ward et al.'s (1905) *Later Mesozoic Floras of North America* provide a view of the surface of the primary body, and exhibit a distinctive set of spiraled leaf scars, very much like those on the surface of this fossil. This led us to interpret the specimen as a cycadeoid, a conclusion further supported by the structure of the pith with its slightly elongate mucilaginous canals, and the manoxylic structure of the small amount of secondary xylem preserved.

To date, anatomically preserved cycadeoid trunks have generally been recognized by the structure of their secondary xylem and the direct path of the leaf trace, together with their reproductive organs, if present. Those with external morphology are identified by the distinctive arrangement of the surficial ramental scales and interspersed holes demarcating the

insertion of petioles. Recognition of the distinctive morphology of the exposed surface of the primary body in the Maryland specimens provides another potentially useful character, and one which allows us to ally this otherwise perplexing specimen with the cycadeoids. Recognition of this pattern of leaf traces on the surface of the primary body may aid in the identification of other anomalous Mesozoic stems, and suggests the need to examine previously described Mesozoic lycopsid axes.

Cycadeoid specimens from California are notably scarce. The present specimen is the third known. The first *Monanthesia* species was discovered in 1905 and ninety-four years passed before the second specimen of the same genus was uncovered 170 km south of the first locality. While the present specimen cannot be assigned to a specific genus of cycadeoids, its occurrence extends the range of the Californian cycadeoids by an additional 170 km to the north of the original find. These discoveries suggest that more focused research in this area would be productive.

ACKNOWLEDGMENTS

We are grateful to Charles Dailey for the discovery of the specimen. We thank Julie Broughton for assistance in photographing the specimen and preparing the figures. We thank the editor and an anonymous reviewer for valuable comments on an earlier version of this manuscript.

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Going, Barbara M , Hilton, Robert, and Tiffney, Bruce H. 2007. "AN APTIAN CYCADEOID FROM THE BUDDEN CANYON FORMATION, ONO QUADRANGLE, CALIFORNIA." *Madroño; a West American journal of botany* 54, 167–171.
[https://doi.org/10.3120/0024-9637\(2007\)54\[167:aacftb\]2.0.co;2](https://doi.org/10.3120/0024-9637(2007)54[167:aacftb]2.0.co;2).

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