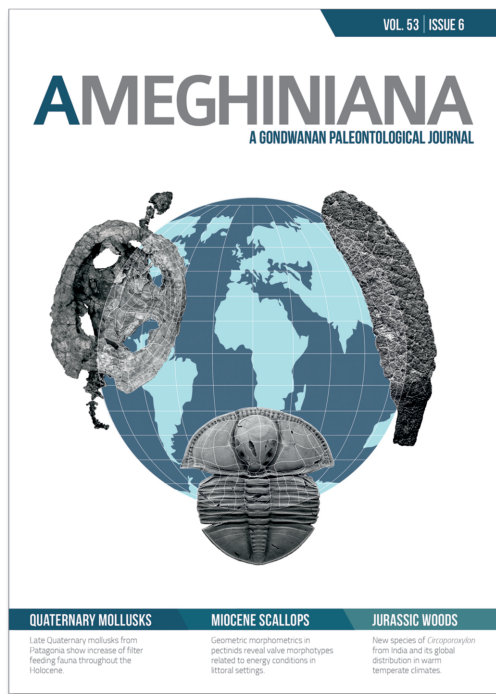




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PINACEOUS WOOD FROM THE LOWER CRETACEOUS (BARREMIAN–EARLY APTIAN) OF CALIFORNIA, USA; LOWER CHICKABALLY MEMBER, BUDDEN CANYON FORMATION

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PINACEOUS WOOD FROM THE LOWER CRETACEOUS (BARREMIAN–EARLY APTIAN) OF CALIFORNIA, USA; LOWER CHICKABALLY MEMBER, BUDDEN CANYON FORMATION

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Abstract. The Budden Canyon Formation is a Cretaceous unit spanning the Valanginian–Turonian interval in northern California. This marine unit includes plant-fossiliferous near-shore sequences, with richest plant fossil occurrences in the Hauterivian–Aptian. The Lower Chickabally Member (Barremian–early Aptian, *ca.* 125 Ma) hosts a rich flora preserved anatomically in carbonate concretions, near the town of Ono. The material is dominated by conifers: wood, foliage, cones and dispersed seeds. We characterize the anatomy of a coniferous trunk. The wood exhibits axial and radial resin canals with thick-walled epithelial cells, distinct growth rings, and conspicuous early to late wood transition. Axial tracheids bear radial uniseriate and opposite biseriate pitting. Rays are uniseriate with biseriate portions, with scarce ray tracheids and taxodioid cross-field pitting. Traumatic resin canals form extensive tangential bands. The axial and radial resin canals indicate pinaceous affinities for the Ono wood, but several characters make it different from most extant Pinaceae. The specimen is most similar to *Picea* Dietrich, from which it differs in cross-field pitting. Among fossil Mesozoic genera, the Ono wood is similar to *Palaeopiceoxylon* Kräusel and *Protocedroxylon* Gothan, and to the *Pinuxylon-Laricioxylon-Piceoxylon* group, but is not entirely consistent with any of these genera. Pinaceous affinity of the Ono wood is consistent with presence in the Budden Canyon Formation of several types of pinaceous foliage and ovulate cones that are, however, not assignable to any extant genus in the family. Together, these indicate the presence in the unit of stem-group Pinaceae that await reconstruction as whole plants.

Key words. Cretaceous. California. Aptian. Barremian. Fossil Wood. Pinaceae.

Resumen. MADERAS DE PINÁCEAS DEL CRETÁCICO INFERIOR (BARREMIANO–APTIANO TEMPRANO) DE CALIFORNIA, EE.UU., MIEMBRO CHICKABALLY, FORMACIÓN BUDDEN CANYON. La Formación Budden Canyon es una unidad cretácica que abarca el intervalo Valanginiano–Turoniano en el norte de California. Esta unidad marina incluye secuencias cercanas a la costa con niveles de plantas fósiles, con la mayor riqueza en el Hauteriviano–Aptiano. La sección baja del Miembro Chickabally (Barremiano–Aptiano temprano, *ca.* 125 Ma), cerca de la ciudad de Ono, porta una rica flora preservada en concreciones de carbonato. El material está dominado por coníferas: madera, hojas, conos y semillas dispersas. En este trabajo se describe la anatomía de un leño de conífera. La madera presenta canales de resina axiales y radiales con células epiteliales de paredes gruesas, los anillos de crecimiento son demarcados y la transición entre leño temprano y tardío es conspicua. Las traqueidas presentan punteaduras uniseriadas y biseriadas en las paredes radiales, de disposición opuesta. Los radios son uniseriados con porciones biseriadas, con escasas traqueidas radiales y los campos de cruzamiento presentan punteaduras de tipo taxodioides. Presenta canales traumáticos de resina formando extensas bandas tangenciales. Los canales axiales y radiales de resina de la madera de Ono indican afinidad con las pináceas, pero varios caracteres la diferencian de la mayoría de las Pinaceae actuales. El ejemplar es más afín a *Picea* Dietrich, de la que difiere en el tipo de campos de cruzamiento. Entre los géneros fósiles del Mesozoico, la madera de Ono es similar a *Palaeopiceoxylon* Kräusel y *Protocedroxylon* Gothan, y al grupo *Pinuxylon-Laricioxylon-Piceoxylon*, pero no es asignable a ninguno de estos géneros. La afinidad a pináceas de la madera de Ono es coherente con la presencia en la Formación Budden Canyon de varios tipos de hojas y conos ovulados de pináceas. Sin embargo, no se puede asignar a ningún género actual de la familia. Estos registros, que podrían ser restos desarticulados que esperan la reconstrucción como planta total, indican la presencia en la unidad del *stem-group* Pinaceae.

Palabras clave. Cretácico. California. Aptiano. Barremiano. Leño fósil. Pinaceae.

THE Lower Cretaceous Budden Canyon Formation is a rock unit of limited extent that is part of the Great Valley Group and represents marine sediments of a Cretaceous overlap sequence that post-dates accretion of the Klamath terranes (Snoke and Barnes, 2006). Today, this unit forms the south-

eastern edge of the Klamath Mountains. Although spatially restricted to a small area in northern California, the Budden Canyon Formation is stratigraphically extensive and spans the Valanginian–Turonian interval (*ca.* 135–90 Ma) (Murphy *et al.*, 1964, 1969; Peterson, 1967; Dailey, 1973; Murphy

and Rodda, 1996; Fernando *et al.*, 2011). The unit consists of marine deposits which include several sequences of near-shore deposits that are plant-fossiliferous.

Previous work in the Budden Canyon Formation has documented a flora of more than 40 taxa (Ward, 1905; Chandler and Axelrod, 1961; Miller, 1975; Stockey and Smith, 2000; Smith and Stockey, 2001). Although most of the material in Ward's (1905) early report consists of carbonaceous compressions and is described as such, some of the figured specimens (especially cones assigned to three *Abietites* species) have proven to be three-dimensionally preserved (Miller, 1975, 1976), highlighting the potential of this unit for anatomical preservation of plant fossils. However, development of this potential begun only a half-century later, when Chandler and Axelrod (1961) provided the first description of anatomically preserved material from the Budden Canyon Formation. The material, preserved in a calcium carbonate nodule and dated to the Hauterivian, represents a permineralized reproductive structure, *Onoana californica*, tentatively interpreted as a fruit of icacinaceous affinities but whose angiosperm affinities have been subsequently questioned (Wolfe *et al.*, 1975). In 1975 and 1976, in a re-investigation of some of Ward's *Abietites* specimens, Miller confirmed anatomical preservation and described them as cupressaceous and pinaceous seed cones, *Cunninghamiostrobus hueberi* (Miller, 1975) and *Pityostrobus shastaensis* and *Pityostrobus ramentosa* (Miller, 1976). Later, Stockey and Smith (2000) described a new species of *Millerocaulis* (Osmundaceae); Smith and Stockey (2001) and Smith *et al.* (2016) further described two more species of pinaceous seed cones (*Pityostrobus californiensis* and *Pityostrobus pluresinosa*), all based on material permineralized in calcium carbonate concretions dated to the middle Aptian–Albian (Smith and Stockey, 2000; Smith *et al.*, 2016).

Recent work in the Lower Chickabally Mudstone Member (Barremian–early Aptian) of the Budden Canyon Formation has revealed a rich and diverse fossil assemblage of anatomically preserved plants permineralized in carbonate concretions *ca.* 125 Ma old (Unger and Tomescu, 2013). The assemblage includes bryophytes, ferns, seed plants, and fungi but is dominated by conifers. The latter are represented mainly by woody fragments and foliage, but cones, dispersed seeds, and larger fragments of tree trunks are

also present. Here we characterize a coniferous trunk from the Lower Chickabally Mudstone Member. The plant is anatomically different from living and previously described extinct conifers, and exhibits characters consistent with pinaceous affinities. This adds the first characterized fossil wood component to the set of pinaceous occurrences previously described (foliage compressions, permineralized cones) or recently observed in this unit (permineralized foliage).

MATERIALS AND METHODS

The Budden Canyon Formation is exposed on a *ca.* 518 km² area on the southern flank of the Klamath Mountains, in northern California. The detailed geology of the unit has been worked out by Murphy (1956, 1975), Murphy *et al.* (1964, 1969) and Dailey (1973), and resulted in a detailed biostratigraphic scheme based mainly on ammonites, bivalves, and foraminifera. A subsequent biostratigraphic study of based on calcareous nannofossils (Fernando *et al.*, 2011) confirmed the results of previous studies and refined the stratigraphy of the unit. The Budden Canyon Formation consists of a clastic succession of marine strata dominantly comprised of mudstone, with some sandstone and conglomerate sequences. The unit ranges in thickness from approximately 2100 m near Gas Point–Ono, to 6705 meters near Budden Canyon–Dry Creek and has been divided into eight members (Murphy *et al.*, 1964, 1969; Murphy, 1975; Murphy and Rodda, 1996); from the base to the top of the unit, these are: Rector, Ogo, Roaring River, Lower Chickabally, Huling, Upper Chickabally, Bald Hills and Gas Point (Fig. 1.1).

Plant-fossiliferous near-shore marine deposits occur at several levels in the unit, with the richest plant fossil assemblages concentrated in the Hauterivian–Aptian interval (Murphy, 1956; Murphy *et al.*, 1969; Stockey and Smith, 2000). In the North Fork Cottonwood Creek area, the 50 m thick Huling Member, comprised of thinly bedded sandstones and conglomerate, separates the Lower Chickabally and Upper Chickabally Mudstone Members (Fernando *et al.*, 2011). The Lower Chickabally Mudstone Member, a wedge-shaped unit with an average thickness of 100 m that increases in a southwest direction, is dominated by mudstones containing limestone nodules.

Plant material, preserved as carbonaceous compressions or permineralized in carbonate concretions along with

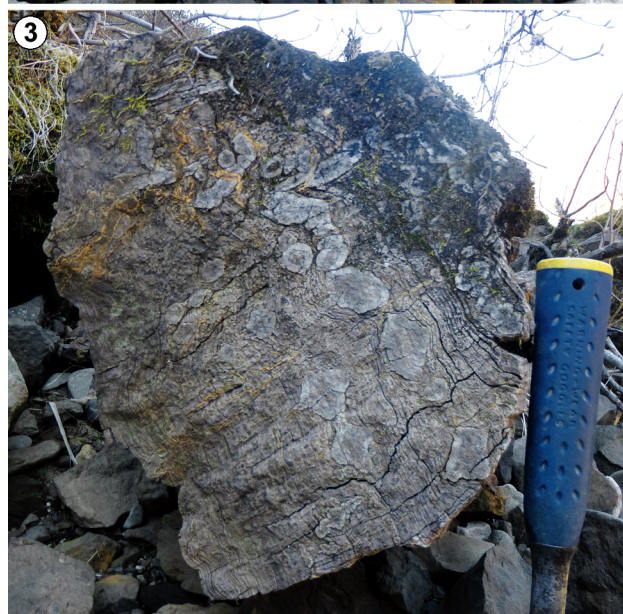
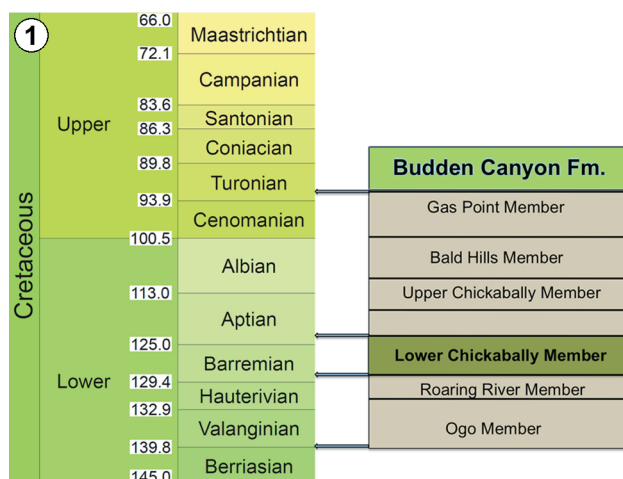


Figure 1. 1, Stratigraphy and age of the Budden Canyon Formation and its subunits. 2, 3, Permineralized pinaceous Ono trunk before sectioning; growth rings are conspicuous in 3, running roughly top left to bottom right, as are several invertebrate burrows with circular and ovoid outlines, filled with calcium carbonate aggregates. Total length of hammer = 28 cm; rubber handle length = 15.2 cm.

marine invertebrates, is present throughout the Lower Chickabally Member in varying concentrations. The material presented here was collected from the upper section of the Lower Chickabally Member, close to the contact with the Huling Member, where mudstones alternate with sandstone; based on this position, the age of the material is close to the Barremian/Aptian boundary, *ca.* 125 Ma. The fossiliferous layers are exposed in the banks of North Fork Cottonwood Creek, 1.5 km southeast of Ono, California (40° 27' 51" N; 122° 36' 32" W).

The wood described here is a trunk fragment permineralized by calcium carbonate and was studied using the cellulose acetate peel technique (Joy *et al.*, 1956). Slides were prepared using Eukitt, a xylene-soluble mounting medium (O. Kindler GmbH, Freiburg, Germany). Micrographs were taken using a Nikon Coolpix E8800 digital camera on a Nikon Eclipse E400 compound microscope. Images were processed using Photoshop (Adobe, San Jose, California, USA). All specimens and preparations are housed in the Humboldt State University Paleobotanical Herbarium (HPH), Arcata, California, USA.

DESCRIPTION

The trunk fragment is 31 cm in diameter and 44 cm long (Fig. 1.2–3). Growth rings are distinctly visible and the transition from early to late wood is gradual but conspicuous (Fig. 2.1). Axial tracheids exhibit polygonal outlines in cross section and intercellular spaces are absent. The tracheids are 1906–3783 μm long and have densities of 756–1079 per mm^2 . The radial width of tracheids is 37–69 μm in the early wood and 18–28 μm in the late wood (Fig. 2.4); cell walls of the late wood tracheids are relatively thin. No unequivocal axial parenchyma was observed.

Pitting on radial tracheid walls consists mostly of uniseriate bordered pits, but biseriate opposite pitting is also present. Pits are circular with round-elliptical included apertures, and border striations and notches are absent (Figs. 2.6–7, 3.7–8). Early wood pits have diameters of 19–28 μm and aperture diameters of 4.8–12 μm , whereas pits of the late wood tracheids have diameters of 13–18 μm and 3.6–7.2 μm apertures. Tangential pitting is absent to very rare; thorough scanning of tangential sections has revealed only two putative pits. Crassulae and helical thickenings were not observed on tracheid walls.

Rays are uniseriate and biseriate portions occur on the rays only in association with resin canals. Ray height is 3–22 cells and 120–663 μm , and their density is 19–31 per mm^2 (Fig. 2.2, 5). Rays are comprised mostly of procumbent

parenchyma and ray tracheids are scarce. The latter have smooth to possibly slightly dentate walls; helical thickenings are absent (Fig. 2.10). Ray parenchyma are 124–205 μm long, 16–41 μm tall and 13–28 μm wide. They have

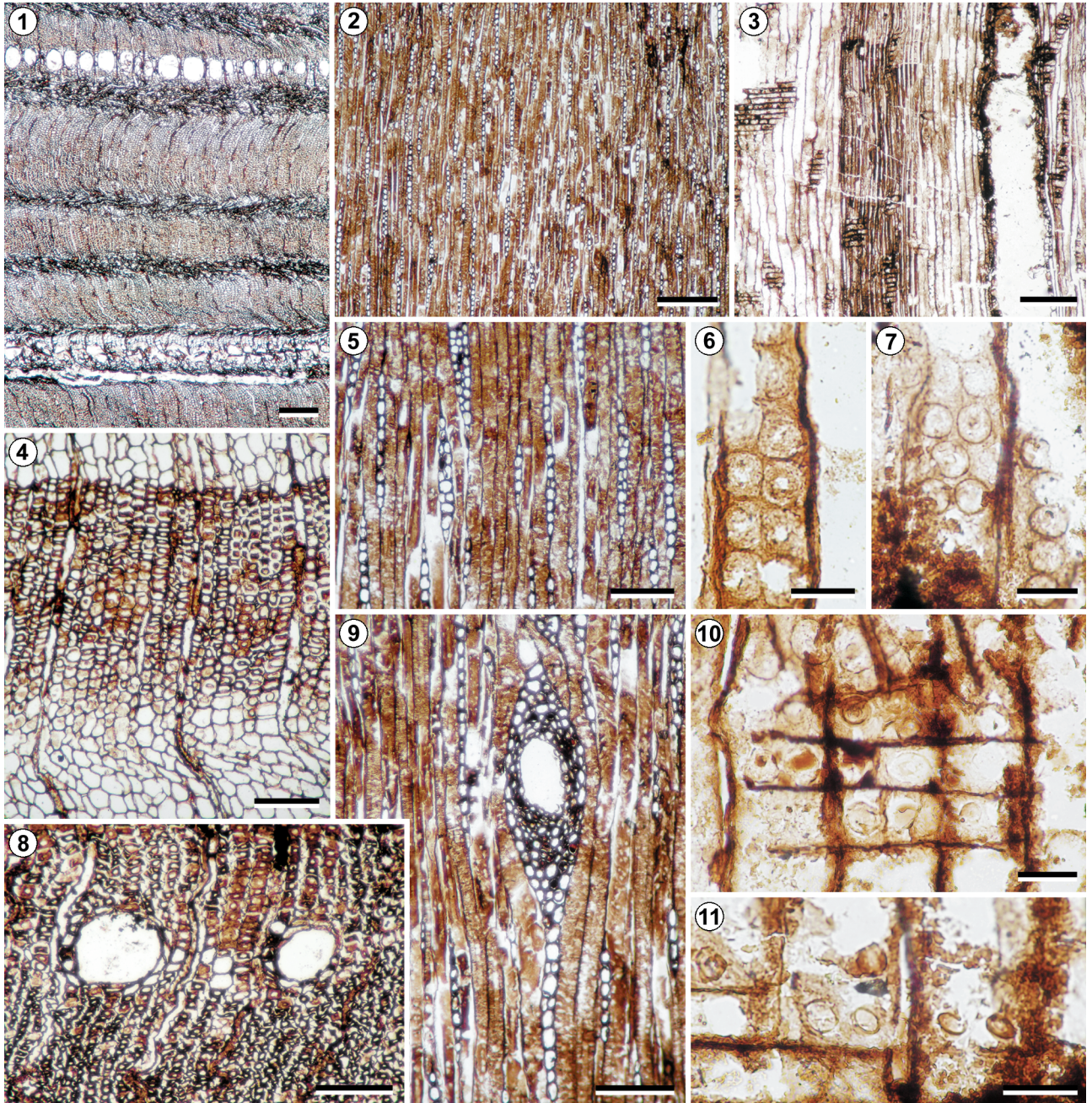


Figure 2. Ono pinaceous wood. 1, Cross section; two tangential bands of traumatic resin canals are present, as well as areas of compressed wood; HPH 233 A #0. 2, Tangential section; HPH 218 A2 #0. 3, Radial section; note traumatic resin canal at right; HPH 218 A(1)side #0. 4, Cross section with growth ring boundary; HPH 218 Btop #0. 5, Tangential section; three xylem rays with biseriate portions, one ray multiseriate due to a radial resin canal; HPH 218 A2 #0. 6, 7, Radial section; tracheid pitting, biseriate opposite bordered pits; HPH 218 A(1)side #0. 8, Cross section; axial resin canal; HPH 233 A #0. 9, Tangential section; radial resin canal; HPH 218 A2 #0. 10, Radial section; ray tracheid and pitting; HPH 218 A(1)side #0. 11, Radial section; cross-field pitting; HPH 218 A(1)side #0. Scale bars= 400 μm (1); 300 μm (2); 30 μm (3, 6–7, 10–11); 150 μm (4–5, 8–9)

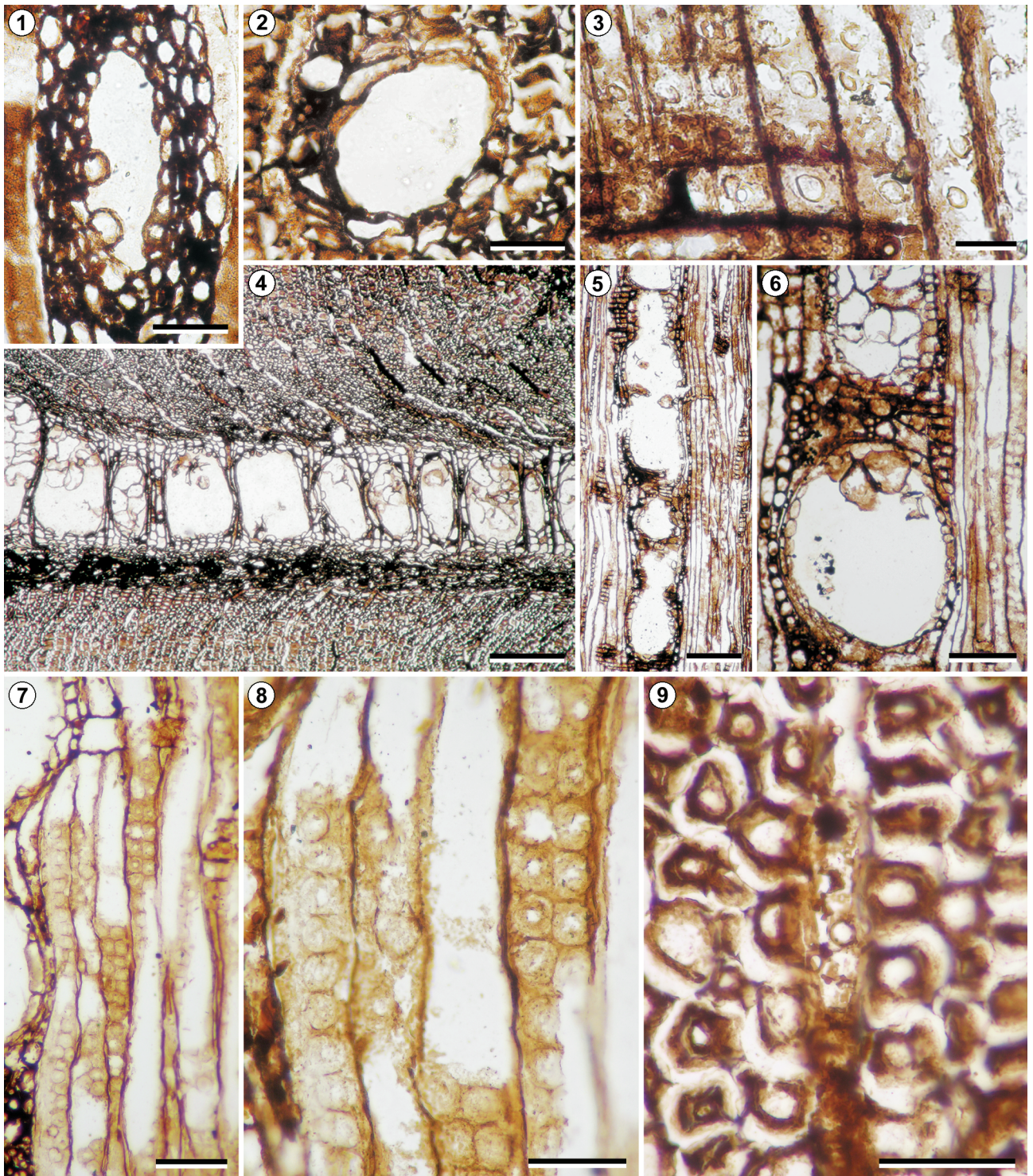


Figure 3. Ono pinaceous wood. **1**, Tangential section; radial resin canal; HPH 218 A2 #0. **2**, Cross section; thick-walled epithelial cells of axial resin canal; HPH 233 A #0. **3**, Radial section; cross-field pitting; HPH 233 A #0. **4**, Cross section; traumatic resin canals with inflated epithelial cells, some tylosed; HPH 233 A #0. **5**, Radial section; traumatic resin canal; HPH 233 A #0. **6**, Radial section; traumatic resin canal partially tylosed; HPH 233 A #0. **7**, Radial section; tracheid pitting, uniseriate and biseriate opposite bordered pits; HPH 218 A(1)side #0. **8**, Radial section; tracheid pitting, uniseriate and biseriate opposite bordered pits (detail of **7**); HPH 218 A(1)side #0. **9**, Cross section; uniseriate ray running vertically at center shows abietineetüpfelung; HPH 218 Btop #0. Scale bars= 50 μm (**1–2**, **8–9**); 30 μm (**3**); 300 μm (**4–5**); 150 μm (**6**); 100 μm (**7**).

smooth terminal walls and smooth to lightly pitted horizontal (transverse) walls (*i.e.*, *abietineetüpfelung*; Fig. 3.9); the presence or absence of indentures could not be determined due to diagenetic alteration. Cross-fields exhibit one to four (usually two) oblique taxodioid pits 4.8–14.4 µm in diameter (Figs. 2.11, 3.3).

Normal axial and radial resin canals are present and diffuse. Viewed in cross section, they are lined with five to nine thick-walled epithelial cells. The axial canals have 77–161 µm diameter lumens and are 91–190 µm in diameter, epithelial cells included (Figs. 2.8, 3.2). Radial canals are 11–112 µm in tangential diameter, 26–334 µm high and are included in 398–998 µm tall rays (Figs. 2.9, 3.1). Large traumatic axial resin canals up to 450 µm in diameter and often fused laterally are numerous. They form long tangential bands that are positioned within the growth rings, most often within the early wood toward the growth ring boundary. The traumatic resin canals are frequently tylosed and their epithelial cells are commonly swollen and thick-walled (Fig. 3.1–2, 3.4–6).

DISCUSSION

Pinaceous affinities and differences from extant genera

Based on the presence of typical axial and radial resin canals, the Ono wood is most similar to the Pinaceae, among the living Coniferales. Extant representatives of all other conifer families characteristically lack resin canals; additionally, many of them exhibit axial parenchyma, which have not been observed in the Ono wood. Comparisons based on data provided by Phillips (1941), Greguss (1955), Ghelmeziu and Suci (1959), Kukachka (1960), Hu and Wang (1984), Schweingruber (1990), Jagels *et al.* (2001), Baas *et al.* (2004), Esteban *et al.* (2004) and the Gymnosperm Database (2012) reveal five extant pinaceous genera that have resin canals and exhibit similarities with the Ono wood: *Larix*, *Cathaya*, *Pinus*, *Pseudotsuga*, and *Picea*. However, all these genera are different from the Ono wood (Tab. 1). Except for *Larix*, which can have taxodioid pits like the Ono wood, the other genera have piceoid (or pinoid- *Pinus*) cross-field pitting. *Cathaya* has tracheids with round cross section and crassulae in the walls, as well as exclusively uniseriate rays and resin canals with two layers of epithelial cells. *Larix* has radial tracheid pitting up to 4-seriate and crassulae, exclusively uniseriate rays, and resin canals lined with a higher

number of epithelial cells (10–14) than the Ono wood. In *Pinus* the epithelial cells of resin canals are thin-walled and crassulae are present; further, traumatic resin canals forming extensive tangential bands are rarely seen, even in highly traumatic situations (Bannan, 1936). *Pseudotsuga* has frequent helical thickenings of axial tracheids, exclusively uniseriate radial tracheid pitting, and axial parenchyma regularly present. Of the five extant genera, *Picea* is most similar to the Ono specimen, from which it differs by the piceoid cross-field pitting.

Comparisons with fossil conifer wood genera

Of the fossil wood morphogenera documented in the Mesozoic, six are more closely similar to the Ono specimen and warrant comparisons: *Piceoxylon*, *Laricioxylon*, *Pinuxylon*, *Pityoxylon*, *Protocedroxylon* and *Palaeopiceoxylon* (Tab. 2). Aside from similarities in terms of resin canals, all six genera exhibit pitted transverse ray cell walls; whereas *Piceoxylon*, *Pinuxylon*, *Protocedroxylon*, and *Palaeopiceoxylon* have *abietineetüpfelung*, like the Ono wood, the pitting of transverse ray cell walls in *Laricioxylon* and *Pityoxylon* is less well characterized (Harland *et al.*, 2007). However, each of the six morphogenera exhibits some differences from the Ono wood (comparisons based on Gothan, 1910; Thomson, 1914; Seward, 1919; Bannan and Fry, 1957; Tidwell and Thayne, 1985; Nishida and Nishida, 1995; Meijer, 2000; Petrescu and Bican-Brisan, 2004; Bondarenko, 2007; Harland *et al.*, 2007; Philippe and Bamford, 2008; Philippe and Hayes, 2010; Afonin, 2011 and personal communication 2016). For instance, all six genera have crassulae, although these can be absent in *Protocedroxylon*, *Pityoxylon* and *Pinuxylon*. Additionally, *Pityoxylon* has variable cross-field pitting, may exhibit helical thickenings, and the walls of resin canal epithelial cells can be thin.

Pinuxylon, *Laricioxylon*, and *Piceoxylon* show closer similarities to the Ono wood. However, some characters vary within broad ranges in these genera, which allows for partial overlap between these genera and between each of them and the Ono wood. Additionally, they exhibit clear differences from the Ono wood. For instance, *Pinuxylon* can have resin canal epithelial cells with thin walls and piceoid cross-field pitting. *Laricioxylon* and *Piceoxylon* are very similar and the generic concepts overlap to the extent that *Laricioxylon* is often included under *Piceoxylon* (Harland *et al.*,

TABLE 1 – Comparison of *Ono* wood with extant genera; only genera with distinct growth rings and normal resin canals were included (data from Phillips, 1941; Greguss, 1955; Ghelmeziu and Suciu, 1959; Kukachka, 1960; Hu and Wang, 1984; Schweingruber, 1990; Jagels et al., 2001; Baas et al., 2004; Esteban et al., 2004; Gymnosperm Database, 2012).

	<i>Ono</i> wood	<i>Picea</i>	<i>Pseudotsuga</i>	<i>Pinus</i>	<i>Larix</i>	<i>Cathaya</i>
Early to latewood transition	gradual-distinct	gradual	distinct	gradual-abrupt	distinct	gradual
Tracheid cross section	polygonal	mainly polygonal	polygonal	mainly polygonal	polygonal	round
Helical thickenings	absent	present, latewood	present throughout	absent	present, latewood	present
Radial pitting	uniseriate, opposite biseriate portions	uniseriate to biseriate	uniseriate	uniseriate to biseriate	mainly opposite biseriate, up to 4-seriate	uniseriate, biseriate portions
Crassulae	absent	in <i>P. koraiensis</i>	in <i>P. sinensis</i>	present	present	present
Tangential pitting	?present rare	present (some species)	present	present or absent	present	present
Axial parenchyma	not observed	absent-scarce	present, nodular	absent-scarce	scarce, marginal, nodular	scarce, diffuse, nodular
Ray height (cells)	3–22	8–10	4–10	1–30+	10–20	1–20
Ray width	uniseriate, biseriate portions	uniseriate-multiseriate	uniseriate-multiseriate	uniseriate-multiseriate	uniseriate	uniseriate
Ray tracheids	present	present	present	present	present	present
Terminal ray cell walls	?smooth	nodular	nodular	smooth-nodular	nodular	nodular or pitted
Cross field pitting	horizontal row of 1–4 taxodioid pits	mainly piceoid, 2–6	piceoid, 1–6	1–2 large, 2–4 ovoid piceoid, or 1–6 pinoid	2–7 in alternating rows, piceoid or taxodioid	piceoid, 1–7
Epithelial resin canal cells	5–9 thick-walled	8–10 thick-walled	5–7 thick-walled	thin-walled	10–14 thick-walled	2 layers, thick-walled

2007). Although both *Laricioxylon* and *Piceoxylon* can have taxodioid cross-field pitting like the *Ono* wood, they may also exhibit piceoid or cupressoid pitting of the cross-fields.

Protocedroxylon and *Palaeopiceoxylon* also warrant closer comparison. *Palaeopiceoxylon* has araucarioid radial pitting and piceoid cross-field pitting; additionally, helical thickenings may be present, ray tracheids may be absent, and walls of epithelial resin canal cells can be thin. *Protocedroxylon* has araucarioid to mixed radial pitting, variable cross-field pitting, pitted terminal ray cell walls, and lacks ray tracheids. Despite some significant similarities, the *Ono* wood differs from *Protocedroxylon* in several features

(Tab. 2). While a few *Protocedroxylon* species are similar to the *Ono* wood in terms of radial tracheid pitting seriation and arrangement, most species of *Protocedroxylon* differ from it in those characters. Furthermore, while both the *Ono* wood and some *Protocedroxylon* species have traumatic resin canals, *Protocedroxylon* lacks normal resin canals. Additionally, *Protocedroxylon* does not have true ray tracheids, and the terminal walls of ray cells are not pitted as in the *Ono* wood. The occurrence of normal resin canals in *Palaeopiceoxylon* places the *Ono* wood closer to this genus. However, in contrast to the *Ono* wood, *Palaeopiceoxylon* is characterized by piceoid cross-field pitting and by the

TABLE 2 – Comparison of *Ono* wood with fossil genera with documented Cretaceous occurrences, characterized by distinct growth rings and normal resin canals (Gothan 1910; Thomson, 1914; Seward, 1919; Bannan and Fry, 1957; Tidwell and Thayne, 1985; Nishida and Nishida, 1995; Meijer, 2000; Petrescu and Bican-Brisan, 2004; Bondarenko, 2007; Harland et al., 2007; Philippe and Bamford, 2008; Philippe and Hayes, 2010; Afonin, 2011).

	<i>Ono</i> wood	<i>Piceoxylon</i>	<i>Laricioxylon</i>	<i>Pinuxylon</i>	<i>Pityoxylon</i>	<i>Palaeopiceoxylon</i>	<i>Protocedroxylon</i>
Early to late wood transition	gradual-distinct	distinct-abrupt	distinct	±gradual	gradual	gradual-abrupt	gradual or abrupt
Helical thickenings	absent	absent	absent	absent	±present	present or absent	absent
Radial pitting	uniseriate, opposite biseriate portions	uniseriate, opposite biseriate portions	uniseriate, opposite and some alternate biseriate portions	uniseriate, opposite biseriate portions	uniseriate, opposite biseriate portions	uniseriate, opposite biseriate portions, araucarioid	uniseriate, biseriate - tetraseriate, alternate to partly opposite
Crassulae	absent	present	present	±present	±present	present	absent (rare when pitting is opposite)
Axial parenchyma	absent-scarce	marginal, if present	present or absent	present or absent	present, scarce	present or absent	present or absent
Ray height (cells)	3–22	1–31	up to 36	1–45	1–30	1–27	1–54
Ray width	uniseriate, biseriate portions	uniseriate, biseriate portions	uniseriate, biseriate portions	uniseriate, biseriate portions	uniseriate, biseriate portions	uniseriate, biseriate portions	uniseriate, rarely bi-triseriate portions
Ray tracheids	present	present	present, scarce	present	present	present or absent	absent
Terminal ray cell walls	?smooth	pitted-nodular	smooth-pitted	pitted-nodular	pitted	pitted-nodular	pitted
Cross field pitting	horizontal row of 1–4 taxodioid pits	piceoid or taxodioid	rows of 1–4 cupressoid, taxodioid or piceoid pits	1–6 pinoid, 1–4 piceoid or taxodioid	2–4 pits, variable pitting	1–3 piceoid	1–6 pits, simple, pinoid, podocar-poid, cupressoid or taxodioid
Epithelial resin canal cells	5–9 thick-walled	thick-walled	thick-walled	thick- or thin-walled	thick- or thin-walled	thick- or thin-walled	thick-walled

presence of crassulae and helical thickenings (in some species), as well as nodules or pitting on the terminal walls of ray cells.

CONCLUSIONS

The Lower Cretaceous (Barremian–Aptian) deposits of the Budden Canyon Formation, in northern California, host abundant permineralized wood. The specimen described here, collected from an exposure in the vicinity of the town of Ono, is the first type of permineralized wood characterized from the unit. The presence of axial and radial resin canals indicates pinaceous affinities for the *Ono* wood. However, this fossil wood is different from most extant

Pinaceae in several anatomical characters. The *Ono* specimen is most similar to *Picea*, from which it differs in the type of cross-field pitting. Among fossil wood morphogenera, the *Ono* wood is most similar to the *Pinuxylon-Laricioxylon-Piceoxylon* group, as well as to *Protocedroxylon* and *Palaeopiceoxylon*. However, several anatomical differences preclude placement in either *Protocedroxylon* and *Palaeopiceoxylon*. On the other hand, members of the *Pinuxylon-Laricioxylon-Piceoxylon* group show significant overlap in anatomical characters with the *Ono* wood. At the same time, members of this group are not well distinguished taxonomically from each other, as they exhibit overlap in some anatomical characters. Consequently, placement of

the Ono wood in any of these three fossil morphogenera would be arbitrary to some degree, therefore we refrain from it. We also refrain from erecting a new morphogenus, because of what we perceive as a counterproductive inflation of morphotaxa based on fossil wood; e.g., see discussion in Philippe and Bamford (2008). We hope that future work in the Budden Canyon Formation will reveal connections between this pinaceous wood morphotype and other plant parts preserved in the same fossil assemblage, which will allow for inclusion of this type of wood into a whole-plant concept.

Both permineralized foliage and seed cones of pinaceous affinities are present in the Budden Canyon Formation assemblages. Among the several types of coniferous leaves identified in the Budden Canyon Formation, the most abundant is closely similar to extant *Pinus* and *Picea* (Petlewski and Tomescu, 2015). Additionally, the ovulate cones *Pityostrobus shastaensis* and *P. ramentosa*, as well as *Pityostrobus californiensis* and *P. pluresinosa*, all represent extinct Pinaceae. Together, these fossils of clear pinaceous affinities that are not assignable to any of the extant genera in this family, indicate the presence of extinct diversity representing several species of stem-group Pinaceae.

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