

## A NEW SPECIES OF *PITYOSTROBUS* FROM THE LOWER CRETACEOUS OF CALIFORNIA AND ITS BEARING ON THE EVOLUTION OF PINACEAE

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A single cylindrical, abraded cone specimen has been found associated with ammonites of the Lower Cretaceous Budden Canyon Formation near Ono, California. The specimen was embedded in bioplastic and sectioned using the cellulose acetate peel technique. The pith is composed of parenchyma and scattered sclereids and is bounded by a ring of resin canals. The secondary xylem of the cone axis, with a ring of small-diameter resin canals, is continuous. The cortex is composed primarily of parenchyma with an outer sclerotic zone 10–16 cells thick and has 27–30 dilating resin canals. Vascular traces to the ovuliferous scale and bract diverge separately from the vascular cylinder and are accompanied by a single resin canal from the pith that is positioned between the arms of the horseshoe-shaped ovuliferous scale trace. The bract trace is terete, accompanied by two lateral resin canals from the cortical axial system, and enters the free part of the bract. The ovuliferous scale is almost completely sclerotic, with resin canals both abaxial and adaxial to the vascular strands. A large interseminal ridge is present between the two winged seeds on each scale. This cone represents a new species of *Pityostrobus* and is described as *Pityostrobus californiensis* sp. nov. A phylogenetic analysis using morphological data from the ovulate cones of all the extant and fossil taxa of Pinaceae, as well as those of *Cryptomeria japonica*, *Sciadopitys verticillata*, and *Pararaucaria patagonica*, was done. Relationships of the fossil species of *Pityostrobus*, *Obirastrabus*, and *Pseudoaraucaria* to the living taxa of Pinaceae were assessed. The idea that *Pityostrobus* represents an artificial assemblage of pinaceous taxa is supported by the analyses. The genus *Obirastrabus* cannot be distinguished from *Pityostrobus* species, while *Pseudoaraucaria* species appear as a clade. The difficulty of basing fossil taxa purely on cone characteristics is discussed in light of the analyses.

**Keywords:** Cretaceous, *Obirastrabus*, Pinaceae, *Pinus*, *Pityostrobus*, *Pseudoaraucaria*.

### Introduction

An extensive fossil record of pinaceous conifers demonstrates that the Pinaceae, like the angiosperms, were undergoing extensive radiation during the early Cretaceous. While the extant genera *Pinus* L., *Abies* Mill., *Picea* A. Deitrich, *Larix* Mill., *Pseudolarix* Gordon, and *Tsuga* Carr. have been identified from Tertiary deposits, only the genus *Pinus* is known from the early Cretaceous (Alvin 1960; Miller 1976a, 1977a; Wehr and Hopkins 1994; Falder et al. 1998). Large numbers of fossils have been described from the Cretaceous that cannot be assigned to living genera of Pinaceae. Among these are *Pseudoaraucaria* Fliche (1896) with six described species and *Pityostrobus* Nathorst emend. Dutt (1916) with ca. 24 species based on ovulate cones. While *Pseudoaraucaria* is generally believed to be a natural genus, *Pityostrobus* is probably an unnatural assemblage, with each described taxon appearing quite distinct and with characters as different as those distinguishing modern genera (Miller 1976a; Stockey 1981; Falder et al. 1998). These differences prompted Ohsawa et al. (1992) to place two Upper Cretaceous permineralized pinaceous cones in the genus *Obirastrabus*, breaking with taxonomic tradition. The Pinaceae appear in a basal position among extant con-

ifers in recent phylogenetic analyses using both morphological and molecular characters (Hart 1987; Chaw et al. 1997, 2000; Stefanović et al. 1998; Bowe et al. 2000). Some fossil evidence has been included in an a posteriori discussion of cladistic relationships of the Pinaceae (Wang et al. 2000), but the sampling of fossil taxa is so incomplete that the study does little to resolve relationships within the family. There have been several attempts to order large numbers of fossils with living taxa in a phylogenetic context and to seek natural groupings within and between *Pityostrobus*, *Obirastrabus*, and *Pseudoaraucaria* (Alvin 1988; Ohsawa 1997; C. N. Miller, Jr., unpublished data; C. R. Robison, unpublished data). In this article we describe a new species of *Pityostrobus* based on a permineralized ovulate cone from the Lower Cretaceous of California. It is the twenty-fifth cone of this general pinaceous type thus far described. Using a revised version of C. N. Miller's Pinaceae data matrix (unpublished), we interpret our cone and the species of *Pityostrobus*, *Obirastrabus*, and *Pseudoaraucaria* in relation to living Pinaceae using cladistic analyses in an attempt to identify monophyletic groups within this plexus of pinaceous conifers.

### Material and Methods

The single cone specimen was collected from section 33, T30N, R7W, of the Ono quadrangle in northwestern Califor-

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nia, along Wilson Creek, 1500 m east of the bridge on Bland Road. Dark mudstones with a few interbedded sandstone and limestone lenses make up the Wilson Creek section. The cone was collected from the Upper Chickabally Member of the Lower Cretaceous, Budden Canyon Formation, ca. 21 m above the base of the Huling (Tongue) Member (fig. 1). Associated ammonites date the cone as middle Aptian age, Bedoulian stage (Murphy et al. 1969; Murphy 1975).

The abraded, calcitic, permineralized cone was embedded in bioplastic and cut transversely into two parts. After peeling, the basal part was cut longitudinally and re-peeled using the cellulose acetate peel technique (Joy et al. 1956). Slides were prepared using Eukitt (O. Kindler, Freiberg, Germany) mounting medium.

The specimen was compared to living and fossil taxa of Pinaceae using the University of Montana Conifer Reference Collection, now permanently housed at the University of Alberta (UAPC-ALTA). Slide preparations of the following fossil taxa were reexamined to code the characters: *Pseudoaraucaria arnoldii* Miller et Robison, *Pityostrobus hallii* Miller, *Pityostrobus mcmurrayensis* Stockey, *Pityostrobus milleri* Falder et al., *Pityostrobus pubescens* Miller, and *Pararaucaria patagonica* Wieland. Other taxa were coded using a revised data matrix provided by Charles N. Miller, Jr. (unpublished data), based on his personal examination of fossils from various collections, with the rest of the data obtained from the literature.

Numerical cladistic analyses used a matrix of 33 characters and 46 taxa including all of the species of *Pityostrobus*, *Obirastrabus*, and *Pseudoaraucaria*, with the extant genera of Pinaceae as place holders. Where characters varied across the genus, polymorphic coding was used. This makes the assumption that each living genus is monophyletic, something supported in recent molecular studies (Wang et al. 2000) and classification schemes (Farjon 1998). Also included in the analyses was *P. patagonica*, which has been suggested to have affinities to the Pinaceae (Stockey 1977). *Cryptomeria japonica* (L. f.) D. Don and *Sciadopitys verticillata* (Thunb.) Siebold et Zucc. of the Taxodiaceae were used as outgroups as clear rep-

resentatives of other conifer families (Hart 1987; Takaso and Tomlinson 1991; Stefanović et al. 1998).

Cladistic analyses were conducted using the heuristic search option of PAUP\*, version 4.0b3 (Swofford 2000) with TBR branch swapping and Multrees on and 50 random addition replicates with Maxtrees set to 200, auto-increasing by 100. To minimize a priori assumptions about the relative value of characters, all characters (appendix) were equally weighted and all multistate characters were unordered. Two other analyses using the same search conditions were done using this data, one without the fossil genera *Pityostrobus* and *Obirastrabus* and one with only extant taxa of Pinaceae. Bootstrap analysis was performed for each analysis using the same search conditions as above (with 100 bootstrap replicates), one random addition replicate for each bootstrap replicate, with Maxtrees set to 10,000.

## Results

### Systematics

#### Order—Coniferales

#### Family—Pinaceae

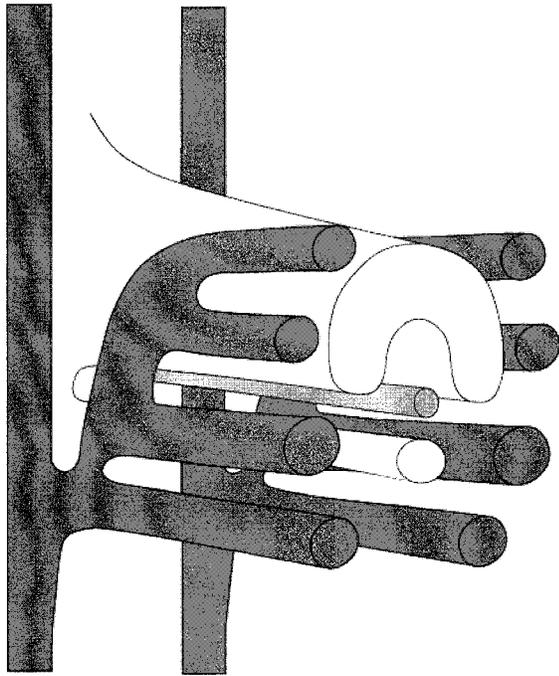
#### Genus—*Pityostrobus* Nathorst 1897 emend. Dutt 1916

#### Species—*Pityostrobus californiensis* Smith et Stockey sp. nov.

**Diagnosis.** Ovulate cone, 6.5 cm long and 3.3 cm in diameter, cylindrical. Cone scale complexes helically arranged. Pith, 3–4 mm in diameter, parenchymatous with scattered sclerenchyma and peripheral ring of 28–37 resin canals (fig. 2). Vascular cylinder continuous, 0.5–1.0 mm, 27–43 tracheids, thick. Secondary xylem with 13–18 small-diameter resin canals. Cortex 1.7–2.5 mm in diameter, with 27–30 dilating resin

Lower Cretaceous	Budden Canyon Formation	Member	Age (Stage)		Guide Fossils
		Upper Chickabally Member	Albian		<i>Brewericeras hulenense</i> <i>Leconteites leconti</i>
		Huling Member	Clansayes	<i>Ammoceratites reesidi</i> <i>Ammoceratites gardneri</i>	
			Bedoulian	<i>Eotetragonites wintunius</i>	
	Lower Chickabally Member		Barremian	<i>Shastrioceras</i> sp.	

Fig. 1 Stratigraphic occurrence of *Pityostrobus californiensis* sp. nov. (asterisk) and associated ammonites (modified from Murphy et al. 1969).



**Fig. 2** Diagram showing distribution of resin canals (dark) and vascular system to cone scale complex. Resin canal from pith is gray; axial canals are black.

canals, mostly parenchymatous with sclerenchymatous outer zone 10–16 cells thick. Traces to ovuliferous scale and bract arising separately from vascular cylinder, with one resin canal from pith; ovuliferous scale trace abaxially concave; bract trace terete. Bract up to 10 mm long, triangular in cross section, with two lateral resin canals, separating from ovuliferous scale at margins. Ovuliferous scale at least 15 mm long, oriented at right angles to axis stele; resin canals both abaxial and adaxial to vascular strands. Two winged seeds per scale, ca. 3 mm long and 3 mm wide, wings at least 6 mm long. Thin layer of ovuliferous scale tissue attached to interseminal ridge encloses seeds and forms seed wing.

*Holotype.* CAS 68491 California Academy of Science, San Francisco.

*Stratigraphy.* Upper Chickabally Member, Budden Canyon Formation.

*Age.* Lower Cretaceous; Aptian age; Bedoulian stage.

#### Description

*General features.* The cone is cylindrical, measuring 6.5 cm long and 3.3 cm in diameter (fig. 3.1). The cone is nearly entire. Its surface is abraded, preventing a complete description of external characters but leaving numerous resin canals visible externally (fig. 3.2). Cone scale complexes are helically arranged and diverge at right angles to the cone axis (figs. 3.3, 3.5).

*Cone axis.* The pith of the cone axis is 3–4 mm in diameter and only partially preserved (figs. 3.3–3.5). It is composed of parenchyma and scattered sclereids (fig. 4.3). In transverse section a ring of 28–37 resin canals, 0.1–0.3 mm in diameter, is

found bordering the pith and primary xylem. Longitudinal sections show that these resin canals are in the pith since they are separated from the primary xylem by several parenchyma cells (figs. 3.4, 3.5).

The secondary xylem forms a continuous cylinder (fig. 3.4), interrupted occasionally by pith tissue extending into the ovuliferous scale. The xylem is 0.5–1.0 mm (27–43 tracheids) thick, and only one growth increment is present (fig. 3.4). A ring of 13–18 small-diameter resin canals is present near the outer edge of the secondary xylem (fig. 3.4). The secondary xylem of the cone axis stele contains uniseriate vascular rays and tracheids with uniseriate, circular bordered pits (fig. 4.2). Probable phloem is present in small patches of thin-walled cells outside the secondary xylem cylinder (fig. 3.4).

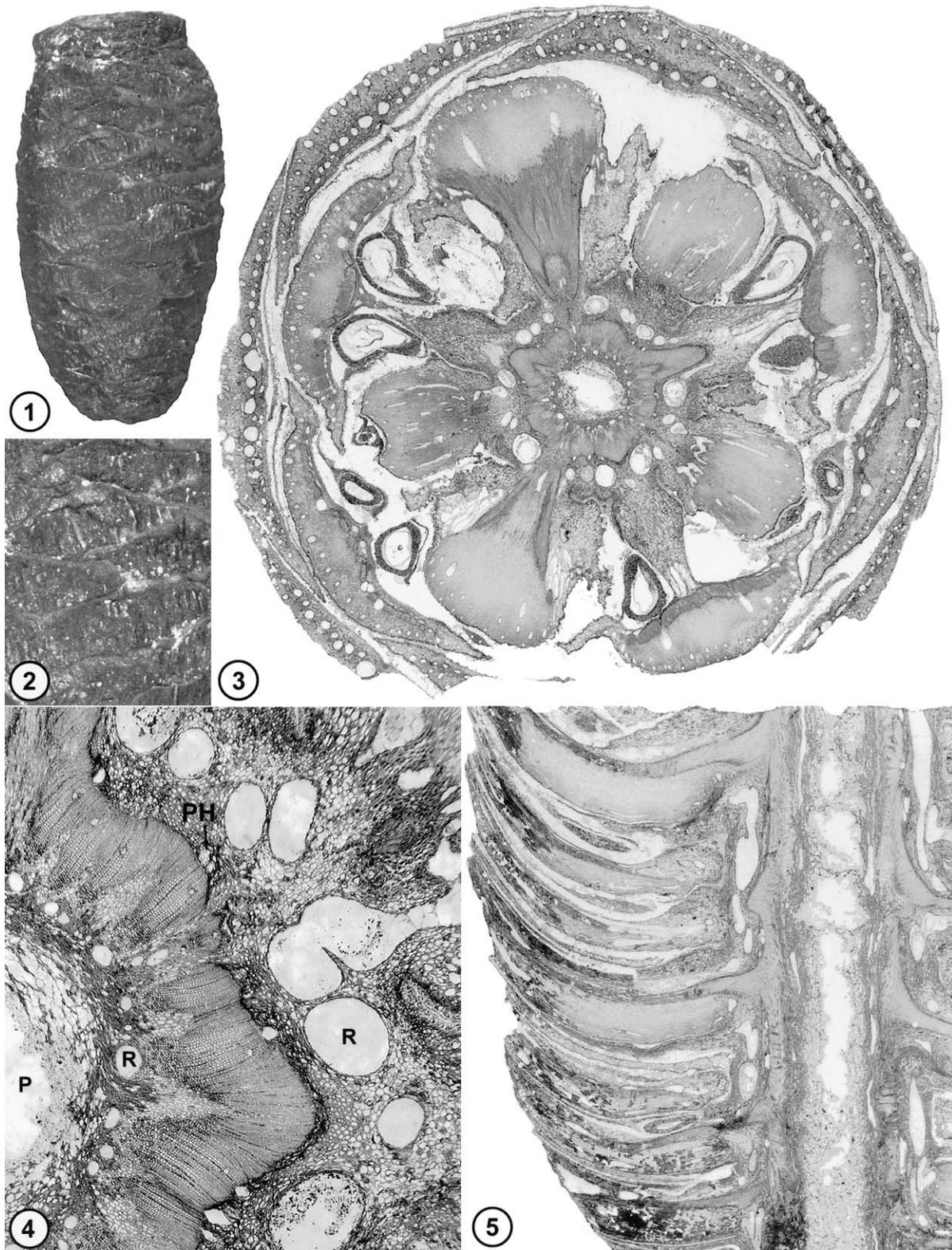
The cortex is 1.75–2.5 mm in diameter, mostly parenchymatous with an outer sclerenchymatous zone 10–16 cells thick (figs. 3.4, 3.5). A ring of 27–30 dilating resin canals, 0.3–1.7 mm in diameter, occurs in the cortex close to the vascular cylinder (figs. 3.3–3.5, 4.1, 4.5).

*Cone scale complex.* Like most non-*Pinus* members of the Pinaceae, vascular traces to the ovuliferous scale and bract diverge separately and are not united at their origin from the cone axis stele. Traces to the cone scale complexes diverge at right angles to the cone axis. The ovuliferous scale traces are abaxially concave (horseshoe-shaped) in cross section, 1.5–2.5 mm high and 1.5 mm wide (fig. 2; fig. 4.1, 4.5). A resin canal originating from the pith is present between the arms of this trace and above the bract trace of each cone scale complex (fig. 2; fig. 4.1, 4.5).

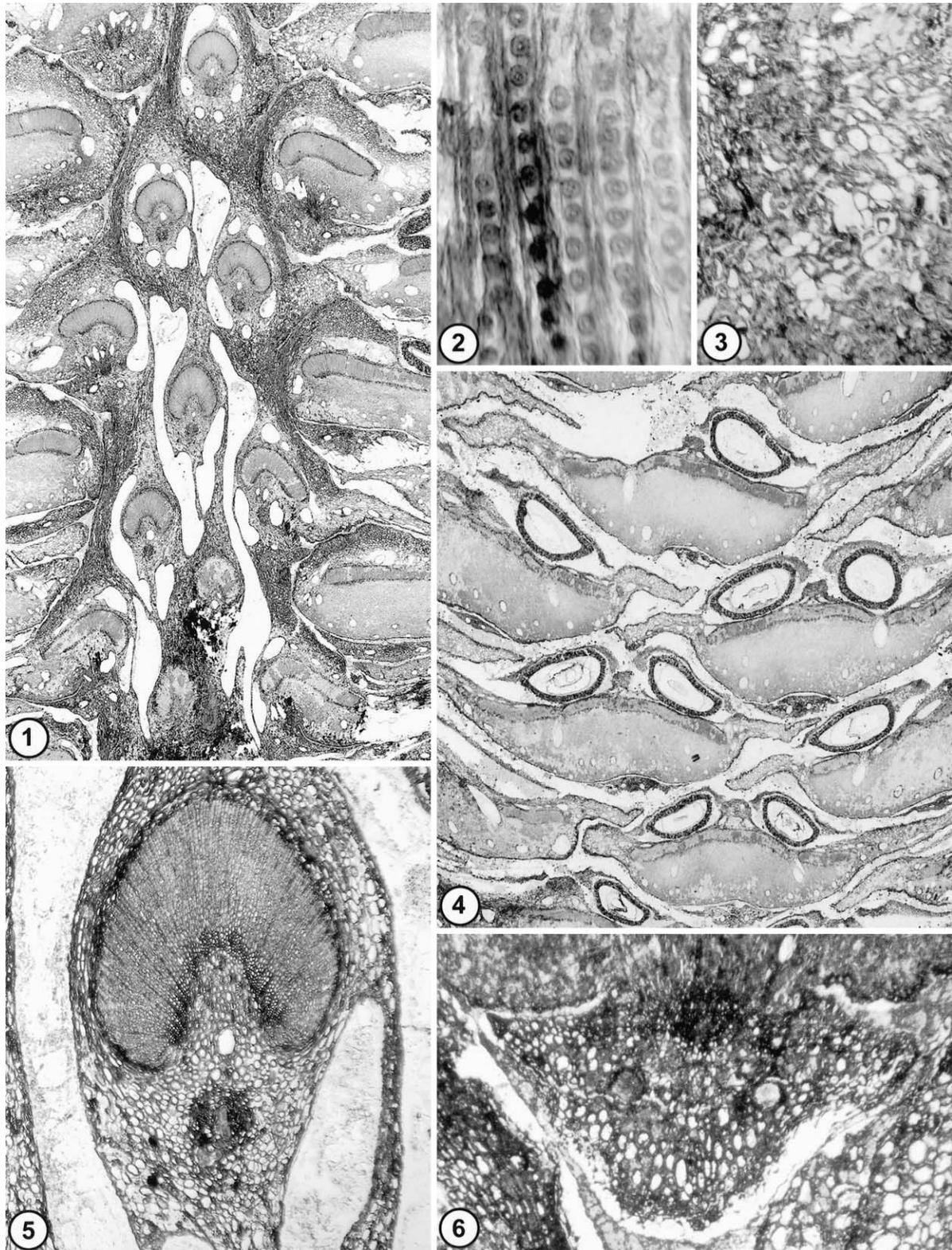
The resin canal system to the cone scale complex is made up of canals from both the cortical system as well as from the pith. In the inner cortex, on either side of the bract trace, the axial resin canals of the cortex branch, giving rise to two canals that soon divide to form a vertical series in the outer cortex going to the ovuliferous scale and the two resin canals of the bract (figs. 2, 4.6). The vertical canals branch distally into two abaxial and four adaxial resin canals associated with the ovuliferous scale trace (fig. 4.1). Farther into the scale these canals divide to form two abaxial series, one adaxial series, and 3–5 resin canals in the interseminal ridge (figs. 5.2, 5.3).

Bracts are up to 10 mm long, 3 mm wide at the base, and triangular in cross section; they lack a basal lobe and separate from the ovuliferous scale at the margins first (fig. 4.6). The terete bract trace, with a centrally located 70–100- $\mu$ m-wide (one to two cells) vascular ray, is accompanied by two lateral resin canals for most of its length and enters the free part of the bract (fig. 4.4, 4.6).

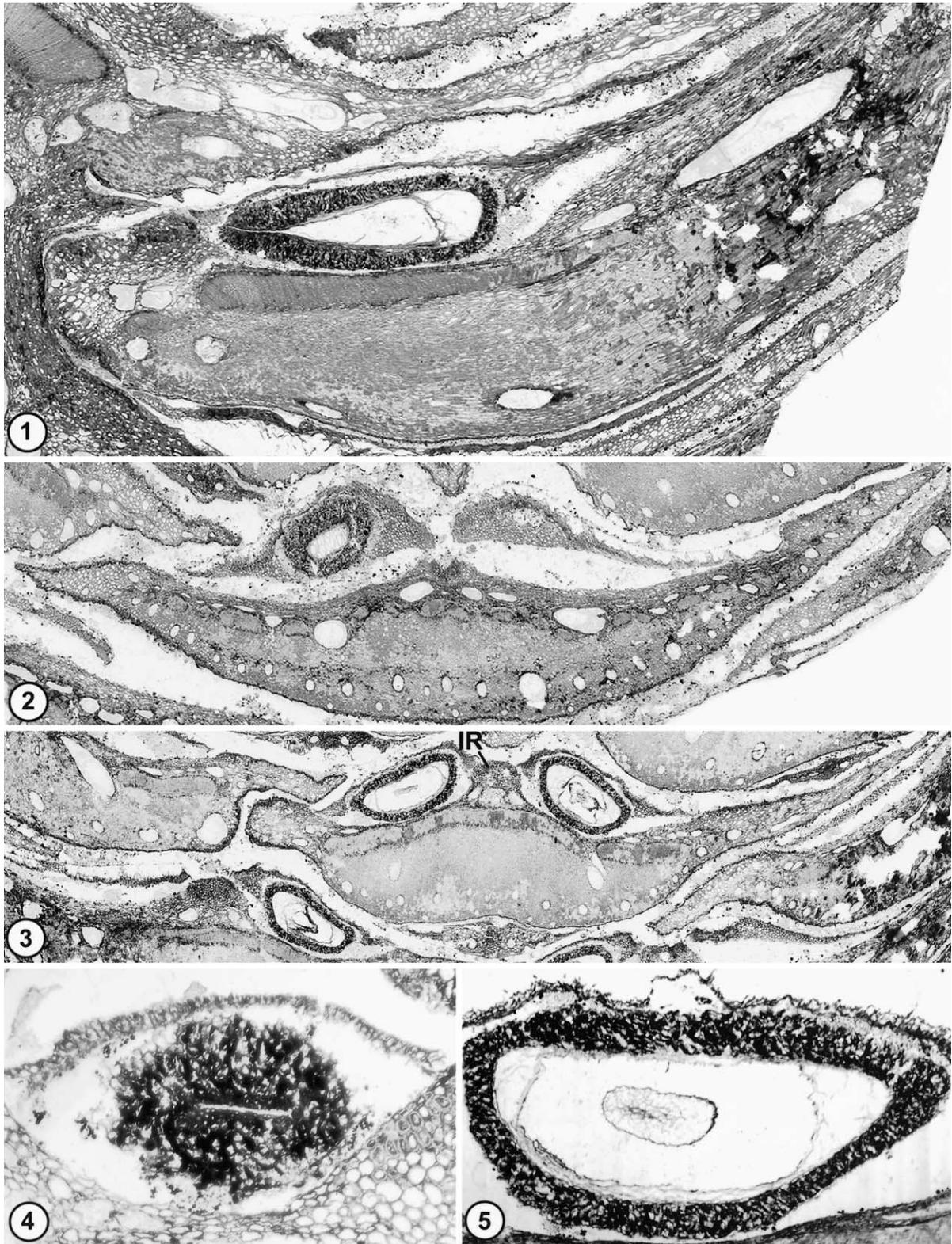
Ovuliferous scales are at least 15 mm long, from 6 mm wide at their base to at least 15 mm wide farther out, and are 5 mm thick at the base, thinning to 3 mm thick at the apex; however, their surfaces were abraded prior to burial and their scale tips were lost (figs. 3.1–3.3, 3.5). Scales have a thick band of sclerenchyma fibers abaxial to the vascular tissue (figs. 3.3, 3.5, 4.4, 5.1, 5.2). Distally, the xylem in the ovuliferous scale breaks up into 17–21 strands, sometimes with a resin canal between adjacent strands (fig. 5.2). The tissue adaxial to the scale trace vasculature is parenchymatous, extending up between the two seeds as the interseminal ridge (figs. 4.4, 5.3). This interseminal ridge measures 1.0–1.5 mm high and 1.0–2.5 mm wide and extends to the top of the seeds but does not



**Fig. 3** *Pityostrobus californiensis* sp. nov. Holotype CAS 68491. Fig. 3.1, External view of cone.  $\times 1$ . Fig. 3.2, External view of abraded cone surface with exposed resin canals in ovuliferous scales.  $\times 2$ . Fig. 3.3, Transverse section of cone axis showing helically arranged cone scale complexes, solid secondary xylem cylinder, and two seeds per scale. A #5  $\times 4$ . Fig. 3.4, Transverse section of cone axis showing pith, xylem, phloem, and cortex with numerous resin canals. A #70  $\times 18$ . Fig. 3.5, Radial longitudinal section of cone showing cone scale complexes arising at right angles to cone axis. B side 1 #192  $\times 4$ . P = pith, PH = phloem, R = resin canal.



**Fig. 4** *Pityostrobus californiensis* sp. nov. Holotype CAS 68491. Fig. 4.1, Tangential longitudinal section of cone showing transverse section of traces to cone scale complexes and associated resin canals. Note resin canals originating from pith in abaxial concavities of ovuliferous scale traces. B side 1 #87 × 6. Fig. 4.2, Secondary xylem tracheids with uniseriate circular bordered pits. B side 1 #195 × 359. Fig. 4.3, Parenchymatous pith with scattered sclereids. B side 1 #163 × 44. Fig. 4.4, Tangential cone section showing bracts, ovuliferous scales with interseminal ridges, and resin canal distribution at level of seed body. B side 2 #47 × 6. Fig. 4.5, Transverse section of horseshoe-shaped ovuliferous scale trace with resin canal in abaxial concavity and terete bract trace. B side 1 #87 × 29. Fig. 4.6, Transverse section of bract showing lateral separation from ovuliferous scale and two resin canals. B side 1 #42 × 40.



**Fig. 5** *Pityostrobus californiensis* sp. nov. Holotype CAS 68491. Fig. 5.1, Longitudinal section of ovuliferous scale with adaxial, winged seed, micropyle facing cone axis. B side 1 #140 × 15. Fig. 5.2, Transverse section of ovuliferous scale showing pattern of distribution of resin canals near chalazal end of seeds with thick wing tissue. A #5 × 9. Fig. 5.3, Transverse section of ovuliferous scale showing interseminal ridge with resin canals. B side 2 #47 × 9. Fig. 5.4, Slitlike micropyle in seed. B side 1 #11 × 27. Fig. 5.5, Transverse section of seed with internal tissues, probably nucellar in origin. These tissues are attached to integument at seed chalaza. B side 1 #11 × 43.

overarch them. The interseminal ridge is continuous with the adaxial ovuliferous scale tissue that surrounds the seed body.

**Seeds.** Two inverted, winged seeds occur on each adaxial scale surface, with slit-shaped micropyles facing the cone axis (figs. 5.1, 5.4). Seed bodies measure 3 mm wide and ca. 3 mm long, with a prominent sclerotesta composed of thick-walled sclereids 32.5–58.5  $\mu\text{m}$  in diameter. They are enclosed by a layer of ovuliferous scale tissue that extends to form the seed wing distally and separates from the rest of the scale surface. Near the chalazal end of the seed, this tissue becomes thicker before it thins distally (fig. 5.1, 5.2). Seed wings are at least 6 mm long and thin distally to one to two cells thick. The inner tissues of the seeds have been obscured by the presence of what appear to be numerous fungal hyphae in the nucellus (figs. 5.1, 5.5). Several seeds show what appear to be cellular embryos in the center (fig. 5.5); however, after serial sectioning, these structures appear to be proliferated nucellar tissue that is attached to the integument at the chalazal end of the seed.

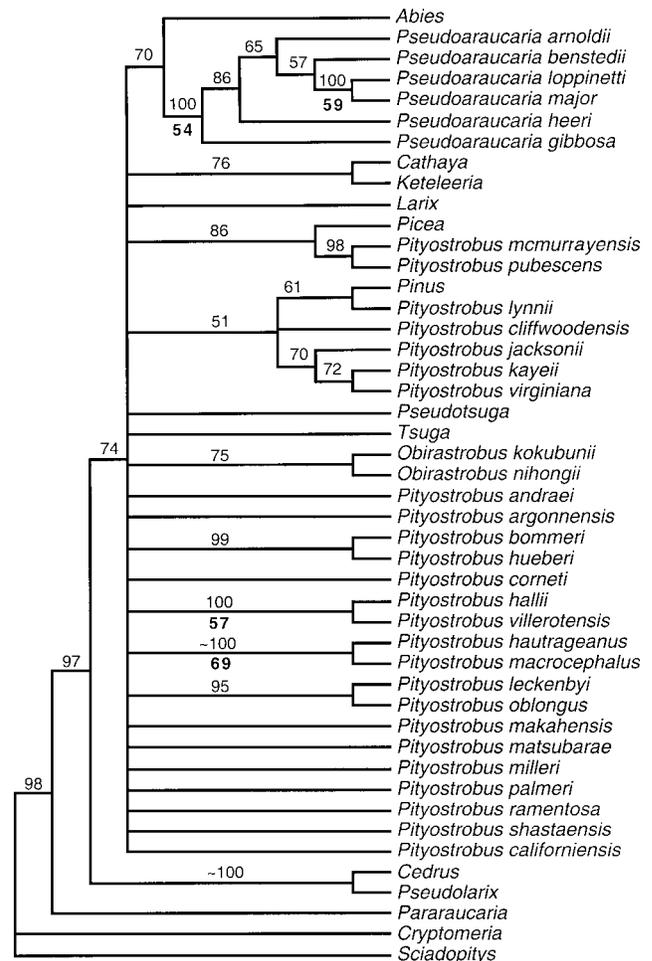
### Phylogenetic Analysis

The results of the analysis using cones of all 46 taxa resulted in 25,243 most parsimonious trees (in 24 islands) with a length of 243 steps (Consistency Index [CI] = 0.449, Retention Index [RI] = 0.550). Maxtrees was hit twice on trees a few steps longer than the shortest trees. The resulting large polytomy (fig. 6) is not surprising because of the large number of taxa compared to the number of characters. It is interesting to note, however, that the species of *Pseudoaraucaria* form a clade found in all 25,243 trees (fig. 6). *Pararaucaria* appears as sister group to a monophyletic Pinaceae (fig. 6). *Pityostrobus hallii* and *Pityostrobus villerotensis* appear as a clade found in all trees (fig. 6). *Pityostrobus hauterageanus* and *Pityostrobus macrocephalus* appear as a clade in nearly all trees (fig. 6). Other species pairs that appear in 95% or more of the trees include *Pityostrobus mcmurrayensis* and *Pityostrobus pubescens*, *P. bommeri* and *P. hueberi*, and *P. leckenbyi* and *P. oblongus* (fig. 6). There is, however, also a clade containing *Cedrus* and *Pseudolarix*.

In 70% of the 25,243 most parsimonious trees, *Abies* appears as a sister group to the *Pseudoaraucaria* clade (fig. 6). In 86% of the most parsimonious trees, *Picea* appears as sister group to the clade containing *P. mcmurrayensis* and *P. pubescens*. In 75% of the trees, the two species of *Obirastrabus* appear as a clade. In 51% of the most parsimonious trees, *Pinus* nests within a clade containing *Pityostrobus lynnii*, *P. cliffwoodensis*, *P. jacksonii*, *P. kayei*, and *P. virginiana* (fig. 6).

In the analysis using only extant taxa, eight most parsimonious trees were found (one island hit) of 105 steps (CI = 0.810, RI = 0.574). The Pinaceae form a single clade distinct from *Cryptomeria* and *Sciadopitys* when the latter taxa are used as outgroups (fig. 7). Relationships among extant Pinaceae are not well supported by the bootstrap analysis. The node connecting extant Pinaceae to *Cryptomeria* and *Sciadopitys* was resolved in 83% of the replicates.

The analysis using all taxa except *Obirastrabus* and *Pityostrobus* resulted in 259 most parsimonious trees (three islands hit) with a length of 138 steps (CI = 0.681, RI = 0.581). *Pseudoaraucaria* spp. again resolve as a clade in 100% of the most parsimonious trees (fig. 8). This analysis does little

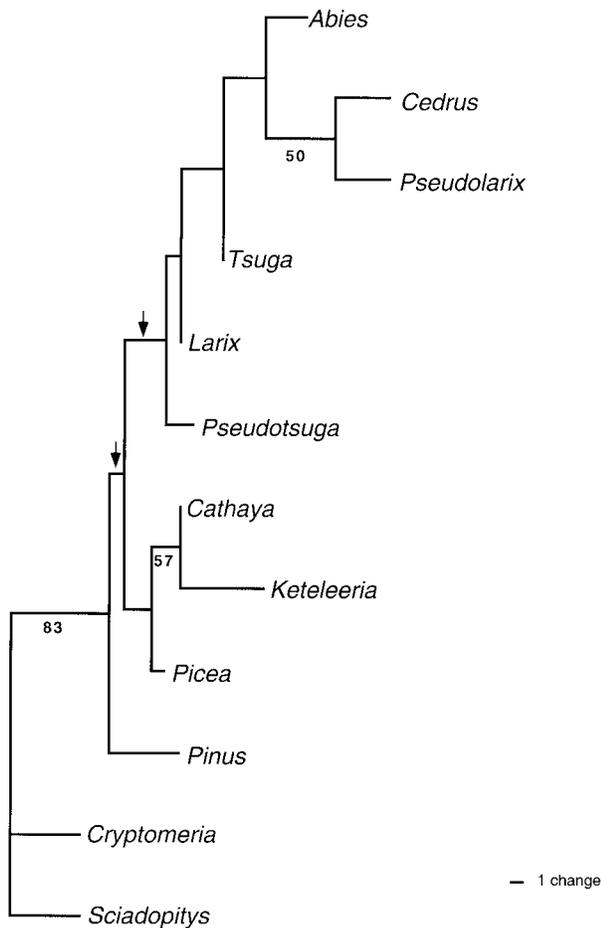


**Fig. 6** Majority rule consensus of 25,243 most parsimonious trees. The tree includes all 46 taxa examined (243 steps, CI = 0.449, RI = 0.550). Note that *Pseudoaraucaria* resolves as a clade. Bootstrap values are indicated in bold below lines. Numbers above lines indicate values from majority rule consensus.

to resolve the large polytomy seen in figure 6, even after the removal of the large number of taxa.

### Discussion

The California cone is clearly pinaceous, based on its cylindrical shape, helically arranged cone scale complexes, enlarged ovuliferous scale, small free bract, and two winged seeds per scale. Although the tips of the ovuliferous scales are not preserved due to abrasion, the structure of the most distal tissues does not appear to be the type that would support an apophysis and umbo, as in *Pinus* cones. The vascular traces to the cone scale complex arise separately from the axis stele, as in non-*Pinus* species of Pinaceae (Miller 1976a; table 1). Secondary xylem of the cone axis forms a continuous cylinder, however, like *Pinus*, *Cathaya*, *Larix*, *Keteleeria*, *Picea*, *Pseudotsuga*, and *Tsuga* and unlike *Abies*, *Cedrus*, and *Pseudolarix* (table 1). Sclerenchyma cells occur in the pith of several Pinaceae, as in our fossil cone, but are lacking in *Cathaya*, *Cedrus*, and *Ke-*



**Fig. 7** Phylogram of one of eight most parsimonious trees (analysis of only extant taxa using ACCTRAN optimization to demonstrate branch lengths; 105 steps, CI = 0.818, RI = 0.574). Arrows indicate those clades not seen on all the most parsimonious trees. Bootstrap values are indicated in bold below lines.

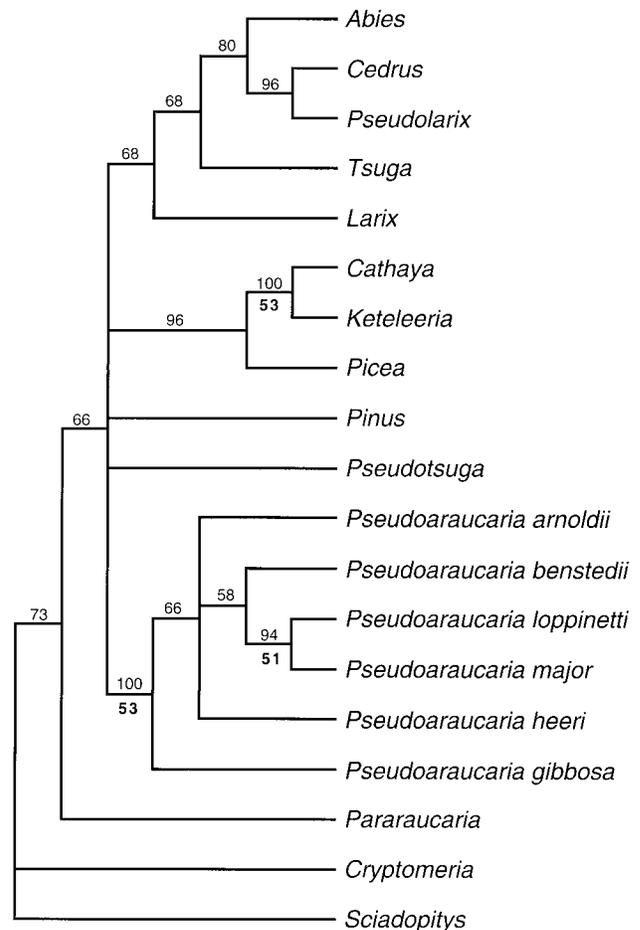
*teleeria* (table 1). The bract is short in our fossil cone, like most pinaceous conifers, the exceptions being the long trifurcating bracts of *Pseudotsuga* and some species of *Abies* and the elongate bracts in some species of *Larix* and *Tsuga* (Silba 1986).

One of the most diagnostic characters used in distinguishing pinaceous cones is the path of the resin canals. Miller (1976a) diagrammed the origin and ramification of the resin canal systems in extant Pinaceae. The genus *Pinus* has a series of resin canals that originate abaxial to the vascular traces of the ovuliferous scale from two axial canals in the cortex. *Cathaya*, *Cedrus*, *Keteleeria*, and *Pseudolarix* have resin canals that are both adaxial and abaxial to the scale trace at their origin, as in our fossil cone. However, the California cone is unique in having an axial resin canal system in the pith that gives rise to a single resin canal that enters the abaxial concavity of the ovuliferous scale at its origin, in addition to abaxial canals that arise from the axial resin canal system in the cortex. Furthermore, the two lateral branches from the cortical axial system branch in the inner cortex, giving rise to four adaxial resin

canals that continue to branch farther out in the scale. Thus, using a combination of characters, it appears that the California fossil cone has a resin canal system that differs from any living taxon.

Traditionally, any permineralized cone showing a plexus of pinaceous characters that did not resemble cones of any living genus was referred to one of two genera, *Pseudoaraucaria* or *Pityostrobus*. While *Pseudoaraucaria* (now containing six species) was considered to be a natural genus (Alvin 1957b; Miller and Robison 1975; Miller 1988), *Pityostrobus* was not (Miller 1976a, 1988; Stockey 1981). Both conclusions are supported here (fig. 6). Cones within *Pityostrobus* were considered to differ from one another as much as those of living genera (Stockey 1981). Ohsawa et al. (1992), breaking with tradition, described a new genus, *Obiraostrobus*, from the Cretaceous of Japan and Saghalien, with two species. Our analysis of the characters (table 1) includes all of the living genera of Pinaceae and the fossil species of *Pseudoaraucaria*, *Obiraostrobus*, and *Pityostrobus*.

The genus *Pseudoaraucaria*, as described by Alvin (1957a, 1957b, 1960) and Miller and Robison (1975), has cones that



**Fig. 8** Majority rule consensus of all taxa except *Obiraostrobus* and *Pityostrobus* (140 steps, CI = 0.664, RI = 0.618). *Pseudoaraucaria* appears as a clade. Bootstrap values are indicated in bold below lines. Numbers above lines indicate values from majority rule consensus.

**Table 1**  
**Pinaceae Ovulate Cone Data Matrix, Taxa and Characters**

	1	11	21	31
<i>Abies</i>	0 (01) 101 (01) 011 (01)	(01) (01) 1011 (01) 110	0117001121	001
<i>Cathaya</i>	0000000010	0010??1011	02?5010020	001
<i>Cedrus</i>	0000101 (01) 10	(01) 010300101	02004 (01) 1121	001
<i>Larix</i>	0 (01) 100 (01) 0 (01) 10	101011 (01) 0 (12) (01)	(01) 1150 (12) 0020	001
<i>Keteleeria</i>	0000000011	(01) 011101111	(01) 222011021	001
<i>Picea</i>	00 (01) 0 (01) (01) 0 (01) 10	(01) 0101010 (12) 0	(01) 12 (57) 4 (12) 0020	001
<i>Pinus</i>	10 (01) 001 (01) (01) 1 (01)	0110100 (01) 10	(01) 0 (03) 5410020	001
<i>Pseudolarix</i>	1010100110	1010?00100	?235610121	001
<i>Pseudotsuga</i>	0110010 (01) 10	(01) 010100010	(01) 115010020	001
<i>Tsuga</i>	0 (01) 10000 (01) (01) 0	(01) 01031 (01) 110	0115010021	001
<i>Pseudoaraucaria arnoldii</i>	0000100011	000010002 (01)	0115531021	011
<i>P. benstedii</i>	?000100?1?	0000?00?10	0?1?131021	011
<i>P. gibbosa</i>	1010100111	0000300?10	0215031020	011
<i>P. heeri</i>	1000100010	0000100110	0112031021	011
<i>P. loppinetti</i>	1000100010	0000100010	111?131020	011
<i>P. major</i>	1000100010	0000100011	1115431021	011
<i>Obirastrabus kokubunii</i>	0000110111	00 (01) 0310020	0235020020	001
<i>O. nihongii</i>	0000010011	0 (01) 10411020	0225020020	001
<i>Pityostrobus andraei</i>	10000?01?1	00101?0????	0005000020	001
<i>P. argonnensis</i>	1010000110	0010130??1	0005010020	001
<i>P. bommeri</i>	0011000000	0010100?01	0002100020	001
<i>P. cliffwoodensis</i>	?000010010	0010??0?10	0035110020	001
<i>P. corneti</i>	0010000110	0011?00111	0235100021	001
<i>P. hallii</i>	0000000010	0110110010	00554?0020	001
<i>P. hautraeanus</i>	1010000110	0000??00?1	0055100020	101
<i>P. hueberi</i>	1010000100	1011100101	0052110020	001
<i>P. jacksonii</i>	1000010000	0010?00?20	00?511002?	?01
<i>P. kayeii</i>	1010010000	0000100010	0005000020	001
<i>P. leckenbyi</i>	0000000???	0110200011	0115 (13) 10021	001
<i>P. lynnii</i>	1000010011	01101100? (01)	000511002?	?01
<i>P. macrocephalus</i>	1010000110	000?1?0?11	00?5000020	101
<i>P. makahensis</i>	0010010011	00101100 (12) 0	0025010021	001
<i>P. mcmurrayensis</i>	0010100000	0010101010	002?210020	001
<i>P. matsubarae</i>	0010000110	0000100010	0235010020	001
<i>P. milleri</i>	1000110011	101013?111	005501002?	?01
<i>P. oblongus</i>	0010000111	0110200010	0125010021	001
<i>P. palmeri</i>	1010011110	0 (01) 00100011	0026410020	001
<i>P. pubescens</i>	0000100000	1010101010	0013420020	001
<i>P. ramentosa</i>	0000000011	1110?00010	022502002?	?01
<i>P. shastaensis</i>	?010010110	0010100011	00?5010020	001
<i>P. villerotensis</i>	0000000000	0110110?10	0035410020	001
<i>P. virginiana</i>	00000?0000	1100?00010	0000010020	001
<i>P. californiensis</i>	0011010111	0010100010	1235020020	001
<i>Cryptomeria</i>	0210000110	00??000020	?344400010	002
<i>Pararaucaria</i>	1010000?12	1010500000	0344601020	00 (01)
<i>Sciadopitys</i>	0200100000	1000100020	0117200010	002

Sources. Data are taken from personal observations using the University of Montana Conifer Reference Collection; Radais 1894; Fliche 1896; Dutt 1916; Seward 1919; Hirmer 1936; Alvin 1953, 1957a, 1957b, 1960, 1988; Calder 1953; Creber 1956, 1960, 1967; Louvel 1960; Miller 1972, 1974, 1976a, 1976b, 1977a, 1978, 1985; Miller and Robison 1975; Robison and Miller 1977; Stockey 1977, 1981; Silba 1986; Crabtree and Miller 1989; Takaso and Tomlinson 1989, 1991; Ohsawa et al. 1991, 1992; Saiki 1992; Miller and Li 1994; Ohsawa 1997; Falder et al. 1998.

are all characterized as having ovuliferous scale traces arising from two lateral strands, a large overarching interseminal ridge, a parenchymatous pad at the chalazal end of the seed, dissected axis steles, and scales that are attached at right angles to the axis stele with a sharply upturned distal portion. While our cone has a large interseminal ridge, it is not overarching, as in cones of *Pseudoaraucaria* (table 1). Furthermore, the

California cone has vascular traces to ovuliferous scales that arise as single horseshoe-shaped strands from the axis stele, unlike the double traces of *Pseudoaraucaria* (table 1). While our cone shows a right angle divergence of the cone scale complexes, as in *Pseudoaraucaria*, there is no sharply upturned distal portion as in *Pseudoaraucaria* species. The fossil cone also lacks a parenchymatous pad at the seed chalaza and stele

dissection. Therefore, we believe that our cone differs significantly from those of the extinct genus *Pseudoaraucaria*.

There are two cones of *Obirastrobus* described from the Upper Cretaceous of Hokkaido as *Obirastrobus kokubunii* Ohsawa et al. and *Obirastrobus nihongii* Ohsawa et al. (1992), but they are quite different from the California cone. Both species of *Obirastrobus* have more than two resin canals entering the bract; *O. kokubunii* has four resin canals in the bract, while *O. nihongii* has six or eight (Ohsawa et al. 1992), compared with two resin canals in the bract in the California cone. The scale traces of *O. nihongii* are sometimes united at their origin, unlike those in our cone (Ohsawa et al. 1992). Other differences from the California cone are that the pith lacks resin canals and the secondary xylem has scattered resin canals in the two *Obirastrobus* species (Ohsawa et al. 1992). *Obirastrobus kokubunii* differs from our cone in that the xylem cylinder is dissected by narrow bands of parenchyma and is not continuous, the cortical resin canals do not dilate prior to branching, the scale trace is derived from two lateral strands, and the pith is parenchymatous with no sclerenchyma or resin canals (Ohsawa et al. 1992). Both species of *Obirastrobus* have a resin canal system supplying the bract and scale that is quite different from that of the California cone (Ohsawa et al. 1992; table 1).

Of the three fossil genera, this cone fits best within *Pityostrobus* but differs from all of the previously described species (table 1). The most unique feature of the California cone is the presence of resin canals in the pith. These have only been reported in *Pityostrobus bommeri* Alvin (1953). *Pityostrobus bommeri* differs in a large number of characters from our fossil cone, including a lack of resin canals in the secondary xylem of the cone axis and bract, an absence of sclerenchyma in the cortex and on the adaxial side of the ovuliferous scale, a bract trace that terminates before entering the bract, resin canals that do not dilate in the cortex, an absence of an interseminal ridge, and resin canals that are only abaxial to scale traces at their origin and opposite the seed bodies.

The central vascular ray in the bract trace of *Pityostrobus californiensis*, while it occurs in two species of *Pseudoaraucaria* (Alvin 1957a) and six genera of extant Pinaceae, has not been reported in any other species of *Pityostrobus* (table 1). The large interseminal ridge that does not overarch the seeds has been reported in both *Obirastrobus* species (Ohsawa et al. 1992), *Pityostrobus ramentosa* Miller (1976b) and *Pityostrobus pubescens* Miller (1985), as well as in some species of extant *Picea* and *Larix* (table 1). *Pityostrobus ramentosa* and *P. pubescens* do not have sclerenchyma in the pith, resin canals in the pith or secondary xylem (Miller 1976b, 1985; table 1). In addition, these species have trichomes on the cone axis, bases of bracts, and ovuliferous scales (Miller 1976b, 1985). Traces to the bract and ovuliferous scale are united at their origins in the axis stele in *P. ramentosa*, unlike the separate origins in the California cone (table 1). Therefore, the fossil cone described here differs from all of the known *Pityostrobus* species and is here considered to represent a new taxon, *P. californiensis* Smith et Stockey.

We attempted to look for monophyletic groups among the fossil and living taxa of Pinaceae to determine whether the generic limits of *Pseudoaraucaria* and *Obirastrobus* were diagnosable and whether they could, in fact, be distinguished from

*Pityostrobus* using cladistic analysis. It was also important to determine whether any clusters of characters appeared among the species of *Pityostrobus* that would allow the splitting of what appears to be an unnatural genus into smaller or monophyletic groups. It is widely believed that cones of all of the species of this genus are different enough from those of extant Pinaceae to be considered different genera (Miller 1976a; Stockey 1981); hence, our analysis used genera of extant Pinaceae as placeholders. In our comparisons of *Pityostrobus* species to the genera of extant Pinaceae, it should be noted that the characters used come only from ovulate cones. The analysis of only the extant taxa had poor resolution, indicating that the use of morphological characters of seed cones only to infer phylogenetic relationships among living and fossil taxa may not be possible. Unfortunately, at only a few localities are there pinaceous vegetative organs associated with the fossil ovulate cones. None of these have been found in attachment; nor have taxa been reconstructed as whole plants. Unless such material can be recovered, all that we have are cone characters.

In both the strict consensus and majority rule consensus of all 46 taxa, and the majority rule consensus where the species of *Pityostrobus* and *Obirastrobus* were excluded, the species of *Pseudoaraucaria* form a well-supported clade. This reinforces the idea that *Pseudoaraucaria* may have been a natural genus (Alvin 1957a, 1988; Miller and Robison 1975; Miller 1976a, 1977b). While it has been suggested that this genus may have been involved in the evolution of some of the non-*Pinus* species of the family (Alvin 1988), the similarities of its cones to those of some species of *Pityostrobus* (Miller 1985; Alvin 1988) suggest that both genera might represent the stock from which living taxa may have evolved. While this appears to be the case for *Pityostrobus*, our analyses support the idea that *Pseudoaraucaria* did not give rise to any extant lineages of Pinaceae. As our data matrix suggests (table 1), there is a vast plexus of characters shared by these pinaceous cones. However, it is obvious from these data that the large number of taxa and the smaller number of characters that can be scored for these taxa are a problem for any sort of parsimony analysis. The analysis excluding *Pityostrobus* and *Obirastrobus* allowed a test of relationships of *Pseudoaraucaria* to extant Pinaceae on a much smaller set of taxa in an attempt to alleviate the problem caused by a large taxon to character ratio. The analyses without *Pityostrobus* and *Obirastrobus* are better resolved than those that include these genera, suggesting that these fossil taxa contribute to the formation of the large polytomy seen in the analysis with all 46 taxa. Considering all of the cone data now known, it is not possible to distinguish lines of evolution within these taxa.

The genus *Pityostrobus* has long been thought to represent an artificial assemblage of pinaceous taxa whose relationships within the family may not be easily resolved. That view is supported here. Our cladistic analyses also indicate that the genus *Obirastrobus* is not different enough from the vast majority of pinaceous cones described as *Pityostrobus* to be regarded as a separate genus, unless all *Pityostrobus* species represent separate genera, as suggested by Miller (1976a, 1988). The most significantly different characters of *Obirastrobus* from the majority of *Pityostrobus* species involve those of resin canal distribution (table 1). Ohsawa et al. (1992) point out that the number of branches from the axial system in the cone

cortex and number of resin canals in the bract differ from most species of *Pityostrobus*. During this study, however, we observed a larger number of resin canals in the bracts of cones of *Picea polita* (Siebold et Zucc.) Carrière from Japan. Some cone sections show two, four, six, or even seven resin canals in the bracts of the same cone, suggesting that this may not be a reliable character to use in the separation of new taxa.

Early in studies of permineralized pinaceous cones, Miller (1976a, p. 114) indicated that the genus *Pityostrobus* showed a "strong *Pinus* influence." However, since that time a large number of *Pityostrobus* species have been described. Many of these, like *P. californiensis*, show more similarities to the non-*Pinus* species of the family (Stockey 1981). In examining the extant conifer collection, we were struck by the similarity of cones of the genus *Picea* to some *Pityostrobus*. The presence of a large interseminal ridge in some species such as *P. pubescens* (Miller 1985), *P. ramentosa* (Miller 1976b), and *P. californiensis* and the resin canal distribution in others such as *Pityostrobus oblongus* (Creber 1960; Louvel 1960) indicate that the genus *Picea* may have diverged from certain taxa in this plexus. This further supports the idea that the cones of *Pityostrobus* reflect the evolutionary radiation not only of *Pinus* but of other genera of Pinaceae such as *Picea* and that the genus *Pityostrobus* is not necessarily *Pinus*-centered.

It becomes obvious when examining the large number of fossil pinaceous cones now available that the Pinaceae were undergoing rapid and extensive radiation during the Cretaceous. Only by reconstructing these conifers as whole plants

can we appreciate and interpret these data in a meaningful context. The smaller numbers of vegetative remains (e.g., Stockey and Nishida 1986) associated with these ovulate cones cannot at this time be linked with certainty to any of the species based on cones. Cladistic analysis utilizing cone characters alone are subject to the problem of a high taxon to character ratio, and fully resolved trees cannot be obtained at this time. Species of *Pseudoaraucaria*, however, do resolve as a distinct clade. In addition, the novel combinations of characters displayed by each species (table 1) allow for the confident identification of new specimens using the data matrix.

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### Appendix

#### Concepts of Characters Used in the Phylogenetic Analysis

- Ovuliferous scale apex. 0 = thinning distally; 1 = thickening distally (or has umbo). Ovuliferous scales of the cones of *Pinus* have an umbo, while most other Pinaceae do not. In fossil cones, scale tips are often abraded, but distal thickening or thinning of ovuliferous scales can usually be seen. The presence of an umbo or a distal thickening ovuliferous scale results in a coding of 1; extensive abrasion resulted in a question mark.
- Bract length. 0 = bract shorter than ovuliferous scale; 1 = bract longer than ovuliferous scale; 2 = bract and ovuliferous scales equal in length.
- Sclerenchyma in pith. 0 = absent; 1 = present. Includes only sclereids or fibers; thick-walled or sclerotic parenchyma is excluded.
- Resin canals in pith. 0 = absent; 1 = present. Canals do not include those in primary xylem; they must be separated by at least a few pith cells from the xylem.
- Secondary xylem of cone axis. 0 = forming a continuous cylinder (or little dissected); 1 = in separate strands. Steles described as "moderately" dissected were coded as continuous since these are usually only interrupted at the point of trace departure.
- Resin canals in secondary xylem. 0 = absent; 1 = present.
- Number of growth increments in secondary xylem of cone axis. 0 = one; 1 = two.
- Sclerenchyma in inner cortex. 0 = absent; 1 = present. The inner cortex may be entirely sclerotic or may contain sclereid nests, fiber nests, or isolated sclerotic cells; all are coded as 1.
- Sclerenchyma in outer cortex. 0 = absent; 1 = present. Includes cones with an outer layer that is completely sclerotic as well as those with isolated sclerenchyma cells or nests (as above).
- Cortical resin canals. 0 = uniform in diameter; 1 = dilated markedly near points of branching; 2 = absent. Cortical canals are usually uniform or somewhat dilated near branching points, and either condition is coded as 0. Those that are significantly dilated code as 1.
- Trichomes on the cone axis, scale, or bract base. 0 = absent; 1 = present. This includes "glandular epidermis."
- Bract and scale traces. 0 = separate at origin; 1 = united at origin. This is viewed in tangential longitudinal sections through the inner cortex of the cone axis.
- Scale trace. 0 = clearly derived from two lateral strands; 1 = derived as single abaxially concave strand. In some ovulate cones, such as those of *Pseudoaraucaria*, *Obiraostrobus kokubunii*, and some *Pityostrobus*, two strands of vascular tissue are initially derived from either side of the gap, and they later fuse together to form an abaxially concave horseshoe-shaped trace. These are coded as 1 for character 13 and 0 for character 14.
- Scale trace. 0 = abaxially concave; 1 = becoming cylindrical after divergence. This is examined in the inner cortex of the cone axis.

15. Resin canals to cone scale complex arising from cortical canals. 0 = as a single branch; 1 = two origins; 2 = three separate origins; 3 = four separate origins; 4 = more than four separate origins; 5 = no resin canals. This number is the total number of branches, from both sides of the scale trace, that are formed as the cortical axial system branches to form the resin canals that will enter bracts and ovuliferous scales.
16. Bract/ovuliferous scale separation. 0 = separates laterally first; 1 = separates medially first; 2 = do not separate. If the middle region of the bract becomes free of the ovuliferous scale first, this is often described as having a medial pouch before separation.
17. Abaxial lobe of bract base (or cone scale complex). 0 = absent; 1 = present.
18. Sclerenchyma in bract. 0 = present; 1 = absent.
19. Resin canals in bract (or accompanying bract trace). 0 = absent; 1 = two; 2 = more than two.
20. Bract trace. 0 = entering bract; 1 = terminating before entering free part of bract.
21. Vascular ray in bract trace. 0 = absent; 1 = present.
22. Resin canals to ovuliferous scale at scale base. 0 = abaxial to vascular tissue; 1 = adaxial to vascular tissue; 2 = both adaxial and abaxial to vascular tissue; 3 = resin canals absent. This character refers to the distribution of resin canals relative to the ovuliferous scale trace only and is determined in tangential longitudinal sections through the outer cortex of the cone axis. Resin canals to the bract are not included in the coding of this character.
23. Resin canals to ovuliferous scale at level of seed body (not under seed wing). 0 = abaxial to vascular tissue; 1 = adaxial to vascular tissue; 2 = both adaxial and abaxial to vascular tissue; 3 = abaxial and adaxial and between vascular bundles; 4 = no resin canals; 5 = abaxial and between vascular bundles.
24. Resin canals to ovuliferous scale distal to seed body (includes under wing and more distal sections). 0 = abaxial to vascular tissue; 1 = adaxial to vascular tissue; 2 = both abaxial and adaxial to vascular tissue; 3 = between vascular bundles; 4 = no resin canals; 5 = abaxial and adaxial and between vascular bundles; 6 = abaxial and between vascular bundles; 7 = adaxial and between vascular bundles.
25. Sclerenchyma in ovuliferous scale. 0 = both abaxial and adaxial to vascular tissue; 1 = abaxial to vascular tissue; 2 = adaxial to vascular tissue; 3 = absent; 4 = abaxial and adaxial and between vascular bundles; 5 = abaxial and between vascular bundles; 6 = adaxial and between vascular bundles. This includes distribution of sclereids and fibers relative to the vascular tissue of the whole ovuliferous scale and not only at scale origins.
26. Intersemlinal ridge. 0 = absent between seeds; 1 = extending less than half of seed diameter; 2 = extending more than half of seed diameter; 3 = extending between and overarching seeds. In *Pseudoaraucaria* cones the intersemlinal ridge overarches the seeds, so that they appear almost embedded in the ovuliferous scale tissue; these are coded as 3. Intersemlinal ridges that are large but not overarching are coded as 2.
27. Scale at right angles to cone axis for length of seed body with sharply upturned distal portion. 0 = absent; 1 = present. Some taxa such as *Pityostrobus pubescens* and *Pityostrobus californiensis* have ovuliferous scales that are at right angles to the cone axis but have a more gradually upturned distal portion. Only those with sharply upturned distal portions are coded as 1.
28. Method of seed release. 0 = by cone spreading; 1 = by scale abscission from cone axis.
29. Seed wings. 0 = absent; 1 = sarcotestal wing(s); 2 = wing formed from ovuliferous scale tissue.
30. Resin vesicles/cavities in integument (seed coat). 0 = absent; 1 = present.
31. Ridged sclerotesta. 0 = absent; 1 = present. These ridges have usually been found on the lower surfaces of seeds (the part in contact with the ovuliferous scale) and are independent of resin cavities in the integument.
32. Enlarged parenchyma pad or cushion at chalazal end of seed. 0 = absent; 1 = present. This structure is in addition to seed wing tissue, which is separate.
33. Number of ovules/ovuliferous scale. 0 = one; 1 = two; 2 = three or more. Although Takaso and Tomlinson (1991) report from one to 12 seeds per scale in *Sciadopitys*, theirs was a developmental study examining even the most apical scales of cones. The usual seed number reported by these authors is eight to nine per scale. This number is usually reported from lower cone scales. Therefore, we have keyed *Sciadopitys* as having greater than three seeds per scale.

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