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PARARAUCARIA CARRII SP. NOV., ANATOMICALLY PRESERVED EVIDENCE FOR THE CONIFER FAMILY CHEIROLEPIDIACEAE IN THE NORTHERN HEMISPHERE

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A cylindrical permineralized conifer seed cone has been identified from the Officer Member of the Trowbridge Formation, near Izee, in east-central Oregon. The cone is preserved in a Middle Jurassic (Callovian) marine calcium carbonate concretion, associated with araucarian seed cones, conifer twigs and wood, cycad seeds, fern rachides, and lycopodialean remains and was prepared by the cellulose acetate peel technique. The specimen is abraded, 2.8 cm long and 1.3 cm wide, and consists of a cone axis with helically arranged bract/scale complexes, with a large ovuliferous scale and a broad, flattened bract. The bract/scale trace arises as a cylindrical unit from the cone axis, in which the bract and scale traces are separated by ground tissue. The traces separate immediately in the cortex to form a crescent-shaped bract trace and a horseshoe-shaped scale trace with associated sclerenchyma bands that form two triangular bundles toward the distal end of the scale. Ovuliferous scale tissue covers one inverted seed per scale, forming a pocket that contains the seed. Seeds are attached at the chalaza to the inside of the pocket. Seed integuments have an outer epidermis of isodiametric cells with dark contents; one or two layers of palisade cells, occasionally appearing in I-beam configuration; and several inner layers of randomly arranged cells. The nucellus is adnate to the integument, to near the apex, where it forms a cellular mound of tissue. Cylindrical cones with helically arranged bract/scale complexes, bract and scale free to the base, one seed per scale enclosed in a pocket, and triangular sclerenchyma bands are characteristic of the genus *Pararaucaria*, which recently has been placed in the extinct conifer family Cheirolepidiaceae. This third species extends the known range of *Pararaucaria* from the Southern Hemisphere to the Northern Hemisphere and emphasizes that the association of araucarian and pararaucarian conifers extended over a wide geographic area during the Jurassic.

Keywords: Cheirolepidiaceae, Coniferales, Jurassic, Oregon, *Pararaucaria*, seed cone.

Introduction

The extinct conifer family Cheirolepidiaceae Takhtajan was one of the most important components of Mesozoic vegetation (Hirmer and Hörhammer 1934; Alvin 1982; Watson 1988; Axsmith and Jacobs 2005) and was dominant in many forests throughout the Triassic to Cretaceous on several continents (Vakhrameev 1970; Alvin 1982; Watson 1988; Taylor et al. 2009). Although the presence of the family in Mesozoic sediments is most easily recognized by the extremely distinctive pollen genus *Classopollis* Pflug (Traverse 1988), fossils preserved as compressions/impressions and displaying distinctive cuticular characters are well represented in Mesozoic sediments worldwide (Alvin et al. 1978; Taylor et al. 2009). Morphology and cuticular structure of several cheirolepidiaceous species have been thoroughly characterized, and some wood has been described (Alvin 1982; Watson 1988; Clement-Westerhof and van Konijnenberg-van Cittert 1991; Kvaček 2000; Axsmith et al. 2004; Axsmith and Jacobs 2005; Del Fueyo et al. 2008), but only recently has the internal anatomy of the pollen cones (i.e., *Classostrobus crossii* Rothwell, Mapes, Hilton et Hollingworth 2006) and seed cones (i.e., *Pararaucaria patagonica* Wieland emend. Escapa, Rothwell, Stockey et Cúneo 2012; *Pararaucaria delfueyoi* Escapa, Cúneo, Rothwell et Stockey 2013) been discovered.

Pararaucaria patagonica was originally based on seed cones collected from the Jurassic Cerro Cuadrado Petrified Forest of Patagonia (Wieland 1929, 1935). Further studies by Calder (1953) and Stockey (1977) of the original specimens and new material from the same formation provided important anatomical characters for this species, but the affinities of this cone remained in doubt (Archangelsky 1968; Miller 1977; Taylor et al. 2009). Recently, however, cones with more completely preserved outer surfaces were described by Escapa et al. (2012). Evidence that *P. patagonica* had a trilobed ovuliferous scale tip and a pocket of enclosing tissue surrounding the seed, rather than a seed wing, allowed *Pararaucaria* to be recognized as a genus of Cheirolepidiaceae, and this provided the first detailed internal anatomical evidence for seed cones of the family. Most recently, Escapa et al. (2013) have utilized the diagnostic internal anatomical characters of *P. patagonica* to identify a second Jurassic species of *Pararaucaria* from Late Jurassic

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deposits of Argentina (i.e., *P. delfueyoi* Escapa, Cuneo, Rothwell et Stockey 2013).

In this article we describe a third species of *Pararaucaria* from a single specimen preserved in Middle Jurassic deposits of east-central Oregon (fig. 1). The flora that includes this seed cone is permineralized in calcium carbonate concretions from the Trowbridge Formation near Izee, Oregon. Whereas the Argentine *Pararaucaria* species occur in a silicate matrix from which nearly all original organic material has been removed, the Oregon species preserves extensive

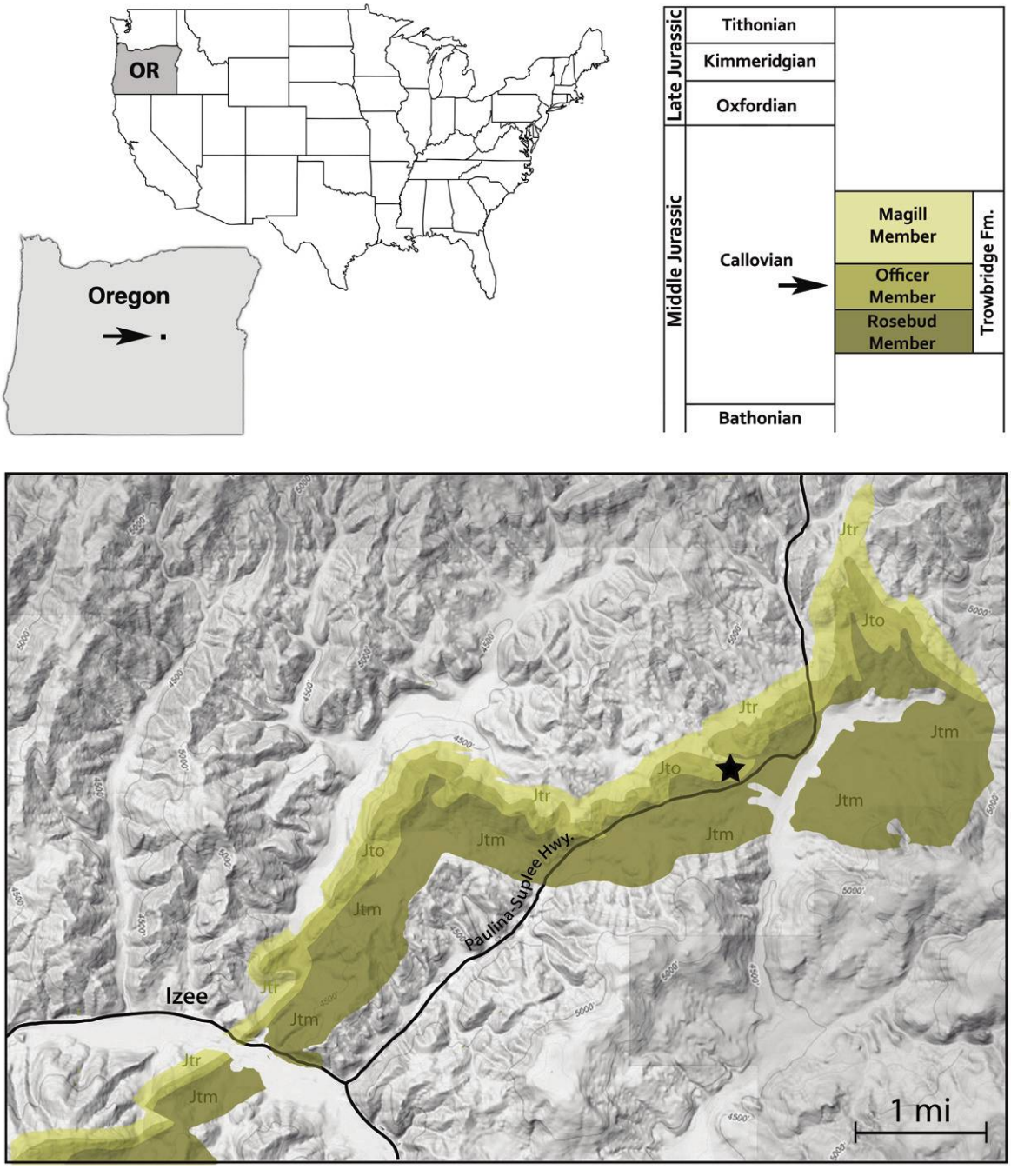

Fig. 1 Geography and stratigraphy of collecting locality. Maps of the United States, with Oregon State (OR) highlighted; of Oregon, with area of locality indicated by the arrow; and of the collecting locality area, with the exposure indicated by the star. Stratigraphic column of the Middle and Upper Jurassic indicates the provenance of the material (at arrow) within the Officer Member of the Trowbridge Formation. Coloring of various members of the Trowbridge Formation coordinates with outcrops of each member on the lower map. Thickness of stages and Trowbridge Formation members not to scale.

organic material within a carbonate matrix. Therefore, specimens from the two sources display complementary suites of anatomical characters that together allow for more thorough characterization of internal anatomy than could be recognized from either preservational mode alone. This new species, *Pararaucaria carrii* Stockey et Rothwell sp. nov., increases the taxonomic diversity of the genus and extends the geographic range of *Pararaucaria* to the Northern Hemisphere.

Material and Methods

One anatomically preserved seed cone was discovered in a calcium carbonate marine concretion removed from a massive black-green mudstone layer near Izee, Oregon. Exposures from which plant fossils were collected are part of the Izee terrane (Silberling et al. 1984, 1987; Blome and Nestell 1992; Orr and Orr 2009) in east-central Oregon. Concretions crop out of the Officer Member of the Trowbridge Formation (fig. 1), Callovian Stage (Dickinson and Vigrass 1965) of the Middle Jurassic (Dorsey and LaMaskin 2007). The locality (fig. 1) is a roadside exposure along the Paulina-Suplee Highway, ~5 mi east of Izee (SE 1/4 sec. 13; T. 17 S, R. 28 E, Grant County, OR; Condon Collection locality no. UO12908). Most concretions at this site are devoid of fossil material and vary up to 1/2 m in diameter. Plant-bearing concretions, however, are often full of conifer wood fragments of at least two types, araucarian cone fragments and dispersed ovuliferous scales, fern rachides, probable cycad seeds, a lycopodiaceous stem, and several other types of small seeds and plant fragments of less certain affinities.

Concretions were sectioned into slabs and studied from anatomical sections prepared by the classical cellulose acetate peel technique (Joy et al. 1956). Microscope slides were prepared using Eukitt (O. Kindler, Freiburg, Germany) mounting medium. Images were captured using a PhotoPhase digital scanning camera (Phase One, A/S, Frederiksberg, Denmark) and processed using Adobe Photoshop, version CS5 (San Jose, CA).

Systematic Description

Order—Coniferales Florin

Family—Cheirolepidiaceae Takhtajan

Genus—Pararaucaria *Wieland emend. Escapa, Rothwell, Stockey et Cúneo 2012*

Species—Pararaucaria carrii *Stockey et Rothwell sp. nov. (Figs. 2–6)*

Specific diagnosis. Cylindrical seed cones at least 2.8 cm long, 1.3 cm wide. Cone axis with helically arranged bract/scale complexes consisting of large ovuliferous scale, subtended by broad, flattened bract; bract and scale separating near base. Scale trace flanked by two frequently connected triangular sclerenchyma bundles within cone axis and basal region of ovuliferous scale. Tissue toward apex of ovuliferous scale forming seed-enclosing pocket. Adaxial pocket-forming tissue thickening distally, thinning toward scale base, terminating near seed micropyle; open toward cone axis. Bract/scale trace diverging from stele as single cylindrical unit enclosing parenchyma but separated from each other by one or two layers of parenchyma cells. Traces separate rapidly to reveal crescent-shaped bract trace and band-shaped scale trace in cortex of cone axis. Bract trace dividing to form several branching bundles accompanied by transfusion tissue distally. Scale trace extending distally as single bundle, dividing distal to seed; vertical division producing small seed bundle, bending back to vascularize seed, and large scale bundle branching repeatedly. One seed per scale, ~5.3 mm long, widest at midregion, ~6.5 mm wide. Integument with outer epidermis of isodiametric cells with dark contents, one or two palisade layers, rarely shrunken into I-beam shapes, and several inner layers of randomly arranged cells. Nucellus adnate to integument up to level of parenchymatous apical region. Seed vascularized at base by cup-shaped zone of tracheids located within nucellar tissue.

Stratigraphy and age. Officer Member, Trowbridge Formation, Callovian Stage, Middle Jurassic.

Holotype hic designatus. Oregon State University paleobotanical specimen preserved in P1 H bottom (bot) and P1 I_1 top, plus peels, and slides prepared from that specimen. Permanent repository, Museum of Natural and Cultural History, Condon Museum, Paleontology Collections specimen no. F-55431, University of Oregon, Eugene.

Etymology. The specific epithet *carrii* is proposed in honor of Gregory Carr of Hillsboro, Oregon, North American Research Group, in recognition of his many contributions to the discovery of Oregon fossils and collection of paleobotanical material.

Description

General Features

The single cone specimen is cylindrical in shape, 2.6 cm long and 1.3 cm wide, and the original saw cut was in an oblique section (fig. 2*A*, 2*B*). The cone axis, bearing helically arranged bract/scale complexes, each bearing a single seed (figs. 2*A*, 2*B*, 3*A*–3*C*), is exposed in oblique section in figure 2*A*, 2*B*. The outer cone surface is significantly abraded such that dimensions originally were larger than the specimen preserved, and, undoubtedly, this cone was transported some distance prior to burial and preservation. Despite the abrasion, internal tissue preservation is generally good.

Cone Axis

The cone axis is woody, ~3.75 mm wide, with a single growth increment and a continuous secondary xylem cylinder, surrounding a narrow pith, interrupted only at the point of trace departure (fig. 2*A*–2*C*). The pith of the cone axis is 0.75 mm in diameter and contains parenchyma with dark-colored cell walls and scattered golden-colored sclereids with very thick cell walls and small lumina (fig. 2*C*, 2*D*).

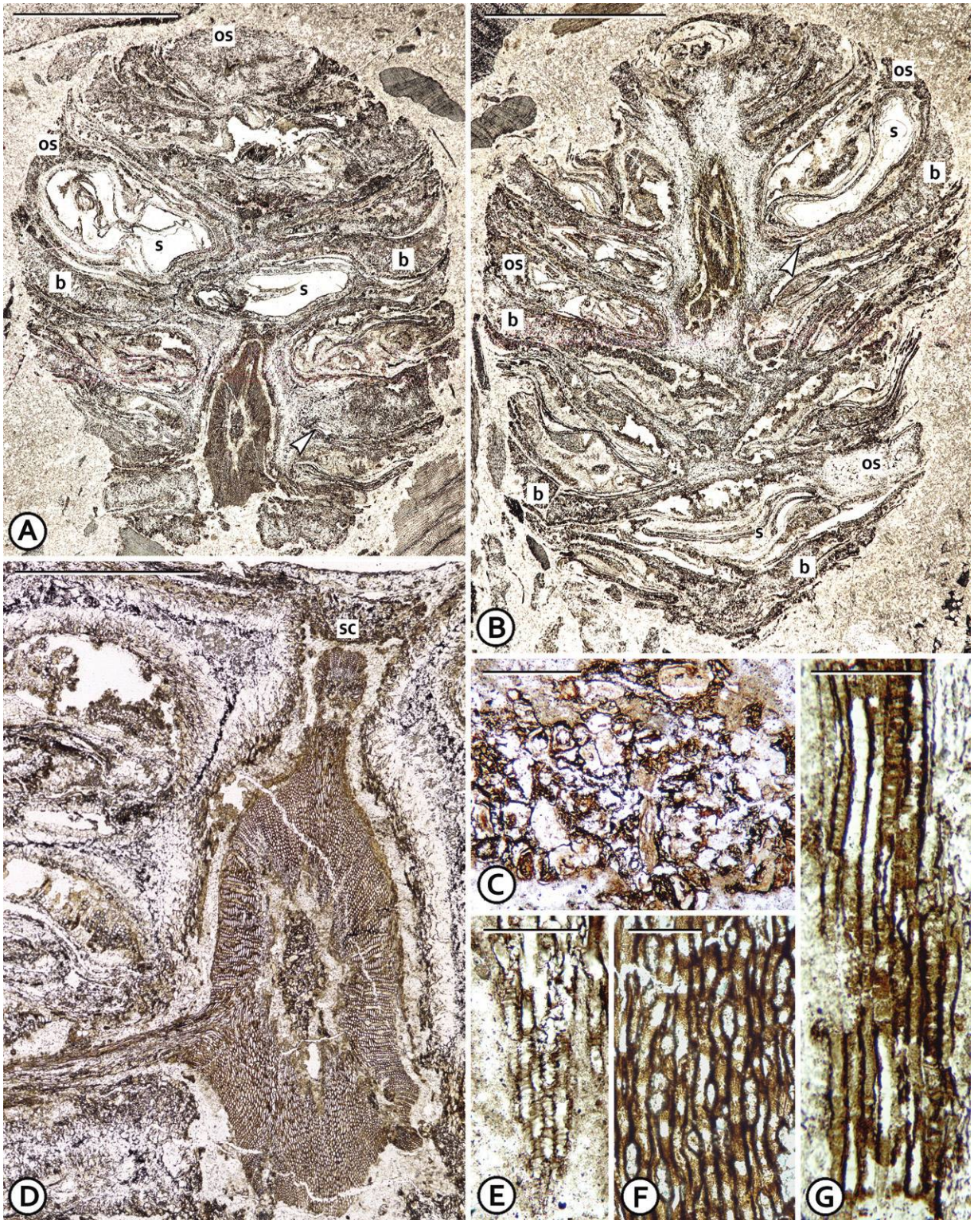

Fig. 2 *Pararaucaria carrii* Stockey et Rothwell sp. nov. Holotype (Oregon State University Paleobotanical Collections specimen P1). *A*, Oblique section showing overall features of cone, including numerous helically arranged bract/scale complexes (i.e., bract [b] subtending ovuliferous scale [os]) diverging from woody axis and each with one seed (s) per complex. I_1 top, no. 9, × 6. Scale bar = 5 mm. *B*, Overall view of cone from opposite face seen in fig. 1*A*. H bottom (bot), no. 6, × 6.5. Scale bar = 5 mm. *C*, Cross section of pith cells, including dark-walled parenchyma and scattered sclereids with golden thick walls. I_1 top, no. 18, × 90. Scale bar = 200 μm. *D*, Oblique section of cone axis showing pith surrounded by cylinder of xylem. Note bract/scale complex traces diverging as single unit in which parenchyma separates bract and scale

The vascular cylinder of the cone axis is 2.0 mm in diameter (fig. 2*D*). Small-diameter primary xylem elements with scalariform secondary wall thickenings have been identified adjacent to the pith (fig. 2*E*). The secondary xylem cylinder is 0.5 mm thick, and the wood lacks resin canals (fig. 2*D*). Secondary xylem tracheids are 18–25 μm in diameter and bear uniseriate, circular bordered pits on their radial walls (fig. 2*G*). Because of the oblique nature of the original saw cut, tangential sections of the wood are available only from the bases of diverging bract/scale traces, and those show uniseriate rays one to three or four cells high (fig. 2*F*). The phloem zone is represented by a gap in tissue preservation, and the cortex is not generally well preserved (fig. 2*D*). Cells in both the inner and outer cortex, where preserved, are parenchyma and large numbers of scattered sclereids, with no resin canals evident. Sclerenchyma cells become prominent at the point of trace departure to the bract/scale complexes (fig. 2*D*).

Bract/Scale Complexes

The bract/scale complex consists of a large ovuliferous scale that is subtended by a broad, flattened bract (figs. 2*A*, 2*B*, 3*A*–3*C*, 6). Traces to the bract/scale complex diverge from the stele as a single cylindrical unit enclosing a small central zone of parenchymatous ground tissue (fig. 2*D*, *top*). However, within that unit the bract and scale traces are separated by one or two rows of parenchyma cells. The bract and scale traces diverge from each other rapidly in the inner cortex, forming a semicircular or crescent-shaped bract trace and a horseshoe-shaped ovuliferous scale trace (figs. 2*B*, 4*A*). The ovuliferous scale trace rapidly assumes a band shape as it extends farther out into the cortex (figs. 2*B*, 4*B*, 4*C*). Within the cone axis and the basal region of the ovuliferous scale, the ovuliferous scale trace is flanked by two (fig. 4*B*) frequently connected (figs. 2*D*, 4*C*) triangular sclerenchyma bundles (fig. 4*A*–4*C*). These sclerenchyma bundles are closely associated with and often partially surround the ovuliferous scale trace as it departs from the axis stele (figs. 2*B*, 2*D*, 4*B*, 4*C*).

Bract and ovuliferous scale separate near the base (fig. 2*A*, 2*B*). The bract, 1.0 cm wide, at least 8 mm long and 1.5 cm thick, is shallowly V-shaped in cross section (fig. 3*C*). The crescent-shaped bract trace passes through the cortex (fig. 4*C*), dividing to form several branching bundles distally (fig. 4*E*). The branching bract traces are accompanied by sclerenchyma and a zone of transfusion tissue distally (fig. 4*E*, 4*F*). Conducting cells of the transfusion tissue (transfusion tracheids) bear alternate, multiseriate, circular bordered pits (fig. 4*F*). Ground tissue of the bract appears to be thick-walled parenchyma with scattered sclereids (fig. 4*E*).

The ovuliferous scale is weathered to the same length as the bract (~8 mm) and is 1 cm wide and 4.5 mm thick near the tip (figs. 2*A*, 2*B*, 3*A*, 3*B*, 6). The ovuliferous scale trace extends from the cortex of the cone axis as a single bundle (figs. 2*B*, 4*A*–4*C*). A vertical division of the ovuliferous scale trace produces a small seed bundle near the base of the seed (fig. 4*D*, arrow), and slightly farther out, the larger scale bundle branches repeatedly distal to the seed to form several strands (fig. 4*D*). The final number of ovuliferous scale bundles could not be determined because of cone abrasion (fig. 6).

In radial sections of the cone, the ovuliferous scale tissue can be seen extending out from the cone axis beyond the seed and then overarching the seed and forming a seed-enclosing pocket (figs. 3*A*, 6). The adaxial pocket-forming tissue thickens over the midregion of the seed, thinning toward scale base, terminating near the seed micropyle, and almost completely enclosing the seed (figs. 2*A*, 2*B*, 3*A*, 6). Seeds often appear to be flattened in cross section (fig. 3*A*, 3*C*) in the central region, where radially aligned cells (secondary ground tissue) are produced within the pocket-forming tissue of the ovuliferous scale (figs. 3*A*, 5*A*). Other cells of the pocket-forming tissue in this central region (adaxial to the secondary tissues) consist of parenchyma and scattered sclereids and are randomly oriented, suggesting that they are primary in origin (fig. 5*A*).

Seeds

The single inverted seed on each ovuliferous scale is ~5.3 mm long and is widest in the midregion where it is ~6.5 mm wide (figs. 2*A*, 2*B*, 3*A*–3*C*) and positioned with the micropyle adjacent to the cone axis (figs. 2*B*, 3*A*, 6). The seed integument consists of an outer epidermis of isodiametric cells with dark contents, one or two palisade layers, rarely shrunken into I-beam shapes (fig. 5*D*), and several inner layers of randomly arranged cells (fig. 5*C*, 5*D*).

The nucellus is typically separated from the integument throughout the length of many specimens. However, in a few seeds the nucellus and integument are adnate up to the level of the parenchymatous apical region (fig. 5*B*, 5*C*). This reveals that the separation in other seeds is probably taphonomic in origin. No pollen has been found associated with the nucellus. The seed is vascularized at the base by a cup-shaped zone of tracheids with scalariform wall thickenings that are located within the nucellar tissue (fig. 5*E*, 5*F*).

Discussion

Systematic Relationships of Pararaucaria carrii

This new seed cone from the Jurassic Trowbridge Formation of Oregon is the first species of *Pararaucaria* (Cheirolepidiaceae)

traces (*left*, *top*). Note adaxial sclerenchyma bundle above diverging bract/ovuliferous scale trace (sc). I_1 top, no. 18, × 17. Scale bar = 2 mm. *E*, Oblique section of cone axis showing scalariform wall thickenings of primary xylem tracheids. I_1 top, no. 22, × 170. Scale bar = 100 μm. *F*, Tangential section of wood showing tracheids and uniseriate rays one to three (or four) cells high. I_1 top, no. 4, × 130. Scale bar = 100 μm. *G*, Radial section of wood showing uniseriate, circular bordered pits on radial walls of secondary tracheids. I_1 top, no. 22, × 200. Scale bar = 100 μm.

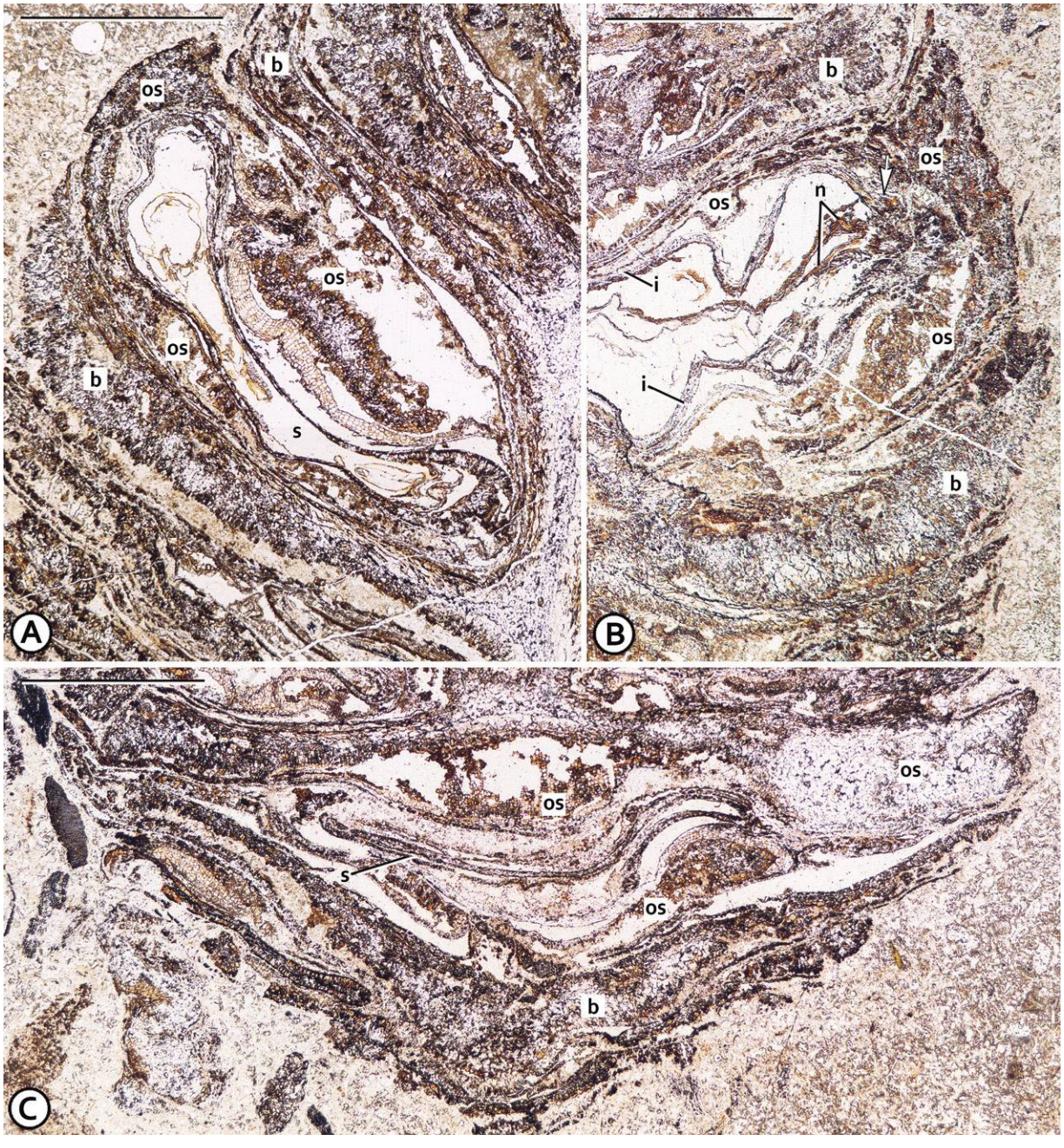

Fig. 3 *Pararaucaria carrii* Stockey et Rothwell sp. nov. Holotype (Oregon State University Paleobotanical Collections specimen P1). *A*, Oblique tangential section of cone (axis at right) showing bract/scale complex with bract (b) and ovuliferous scale (os) separating near base and inverted seed (s) enclosed by overarching ovule-enclosing scale tissue (os; distal to seed). Note that ovule-enclosing tissue is inflated adjacent to midregion of seed and contains both randomly arranged isodiametric cells with dark contents and radially aligned cells of periderm-like tissue. H bottom (bot), no. 22, × 17. Scale bar = 2 mm. *B*, Same bract (b) as in fig. 2*A* at slightly more distal level, showing beginning of lateral separation (arrowhead) on right side. I_1 top, × 15. Scale bar = 2 mm. *C*, Oblique tangential section of cone showing bract (b) subtending ovuliferous scale (os) that surrounds single flattened seed (s). H bot, no. 15, × 15. Scale bar = 2 mm.

to be discovered in the Northern Hemisphere. Common characters of *P. carrii* and the type species *Pararaucaria patagonica* Wieland (1929, 1935) include cylindrical seed cones, woody cone axis with parenchyma and sclereids in the pith, helically arranged bract/scale complexes, bract and ovuliferous scale free to nearly the base, broad bract and ovuliferous scale, horseshoe-shaped vascular trace of ovuliferous scale and smaller bract trace separating shortly after departing from the axis stele, two triangular-shaped sclerenchyma bundles accompanying the ovuliferous scale trace, one seed per bract/scale complex, multilayered seed integument with a distinctive palisade adjacent to the epi-

dermis, and a pocket-forming tissue covering the seeds (Wieland 1935; Calder 1953; Stockey 1977; Escapa et al. 2012, 2013).

Escapa et al. (2012, 2013) recently described a species of *Pararaucaria* from the Late Jurassic Cañadón Calcáreo Formation, Chubut Province, Argentina, as *Pararaucaria delfueyoi* (Escapa et al. 2013). *Pararaucaria delfueyoi* is most easily distinguished from *P. patagonica* and *P. carrii* by the consistent occurrence of two seeds per bract/scale complex (table 1). Of the hundreds of specimens of *P. patagonica* that have been discovered, only one cone has been found with two seeds per scale (Wieland 1935; Stockey 1977), and in that cone two seeds were produced on only one side of the specimen (Wieland 1935). Only one seed per cone scale is known to be produced by *P. carrii*. *Pararaucaria patagonica* and *P. carrii* have a similar cone size, while cones of *P. delfueyoi* are much larger, at least twice the size of those of the other two species (Escapa et al. 2013; table 1). Seeds of *P. delfueyoi* are also consistently longer (up to 11 mm) than those of *P. patagonica* (6 mm) and *P. carrii* (5.3 mm; Escapa et al. 2013; table 1), but seeds of *P. carrii* are wider (6.5 mm) than those of the other two species (table 1). Seeds of *P. patagonica* are usually ~6.0 mm wide. In the double-seeded portion of the *P. patagonica* specimen illustrated by Stockey (1977, fig. 10) and Escapa et al. (2012, fig. 13), the seeds are narrower, ~3.3 mm wide (table 1). In the wholly two-seeded *P. delfueyoi*, the seeds are ~5 mm wide (table 1). Whereas the single seeds of *P. patagonica* are of about equal length and width, those of *P. delfueyoi* are at least twice as long as wide, and the seeds of *P. carrii* are slightly wider than long (table 1).

The distinctive I-beam appearance of integumentary palisade cells in *P. patagonica* is only rarely found in *P. carrii* and has not been seen in *P. delfueyoi*. At the present time we do not know whether this character is a structural difference among the species or whether it results from differential preservation. The calcium carbonate preservation of *P. carrii*, however, has allowed a better view of the tissue zones of the integument. In both *P. carrii* and *P. delfueyoi* there is a dome-shaped, cellular nucellar apex, with a nucellus that is seen to be attached to the integument from the chalaza to near the base of the solid nucellar apex.

The vascular system of the bract and ovuliferous scale and vascular tissue to the ovule of *Pararaucaria* are preserved in more detail in *P. carrii* than for the other specimens (table 1). In this species the horseshoe-shaped ovuliferous scale trace at first becomes flattened and has a vertical division producing a small seed bundle and large scale bundle near the seed chalaza. The larger scale bundle branches repeatedly distal to the seed to form several strands. Striated surfaces of ovuliferous scales in *P. patagonica* reported by Stockey (1977) apparently were weathered to the level of the ramifying scale traces. Interestingly, no resin canals have been found in *P. carrii* or the other two species of *Pararaucaria* (Escapa et al. 2012, 2013).

The shape of the bract trace in transverse section as it diverges from the axis stele appears to be slightly different in the three *Pararaucaria* species (table 1). While bract traces in *P. patagonica* are circular in outline, those of *P. delfueyoi* appear subcircular in many cases, and in *P. carrii* traces are crescent shaped (table 1). The bract trace in *P. carrii* branches repeatedly, and these traces are accompanied by transfusion tissue. This detail is not known from the silicified specimens of the other two species. The ovuliferous scale trace divides repeatedly distal to the attachment of the seed in *P. patagonica* (Calder 1953) and *P. carrii*, but this feature has not been identified in *P. delfueyoi* (Escapa et al. 2013). The vascularized nucellus in *P. carrii* is also unknown from the other species (table 1).

The characteristic pair of triangular-shaped sclerenchyma strands that accompany the ovuliferous scale trace in *P. patagonica* (Calder 1953; Stockey 1977) are also present in *P. carrii* and *P. delfueyoi* (Escapa et al. 2013) and constitute one of the most easily recognizable anatomical characters of the genus. In *P. delfueyoi*, however, these strands are single and reniform near trace departure in the cortex, and they become dumbbell shaped farther out before they separate to form two triangular strands (Escapa et al. 2013; fig. 5*B*–5*D*). In addition, the sclerenchyma band is extremely thick in *P. delfueyoi* (Escapa et al. 2013), while in *P. carrii* the bands are much more delicate. Calder (1953) suggested that in *P. patagonica* these sclerenchyma strands may have been associated with the opening of the cone for seed dispersal.

In *P. patagonica* a specialized pad of ovuliferous scale tissue occurs at the chalazal end of the ovule (Escapa et al. 2012), and in *P. delfueyoi* there is a zone of radially aligned cells at the point of seed attachment (Escapa et al. 2013). This tissue is comparable to the closing tissue that forms in the same position in other living and fossil conifer seed cones and that is histologically comparable to the closing layer of an abscission zone (Escapa et al. 2013). In *P. carrii*, such tissue is absent, but a band of secondary tissue occurs within the pocket-forming tissue on the adaxial side of the ovule. It is uncertain whether this tissue was produced as a wound response. The discovery of more cones of this species may help to clarify the significance of this secondary tissue in *P. carrii*.

One of the more obvious histological differences between the cones of *P. delfueyoi* and *P. patagonica* and those of *P. carrii* is the histology of the seed-enclosing tissue (pocket-forming tissue of Escapa et al. 2012, 2013). In the two previously described species, the loosely arranged sinuous cells of the pocket-forming tissue have been a matter of debate. In *P. delfueyoi*, these cells are described as loosely organized elongated cells that follow a sinuous course (Escapa et al. 2013). In *P. patagonica*, Stockey (1977) compared their structure to seed wings in some taxa of Pinaceae (e.g., *Abies* or *Cedrus*). Calder (1953) referred to them as anastomosing stellate sclereids comparable to the "cellules étoilées" of *Abies nordmanniana* described by Radais (1894). Stockey (1977) compared them to the glandular hairlike trichomes similar to those found in *Cedrus* by Chowdhury (1961) and suggested that they might have functioned in cone closure after pollination by the production of resinous substances. This type of cell is seen both in the seed wings and on the upper ovuliferous scales of some Pinaceae (for discussion see Stockey 1977 and fig. 12 therein). By contrast, the pocket-forming tissue of *P. carrii* consists of more or less isodiameteric parenchyma cells in which numerous thick-walled sclereids are

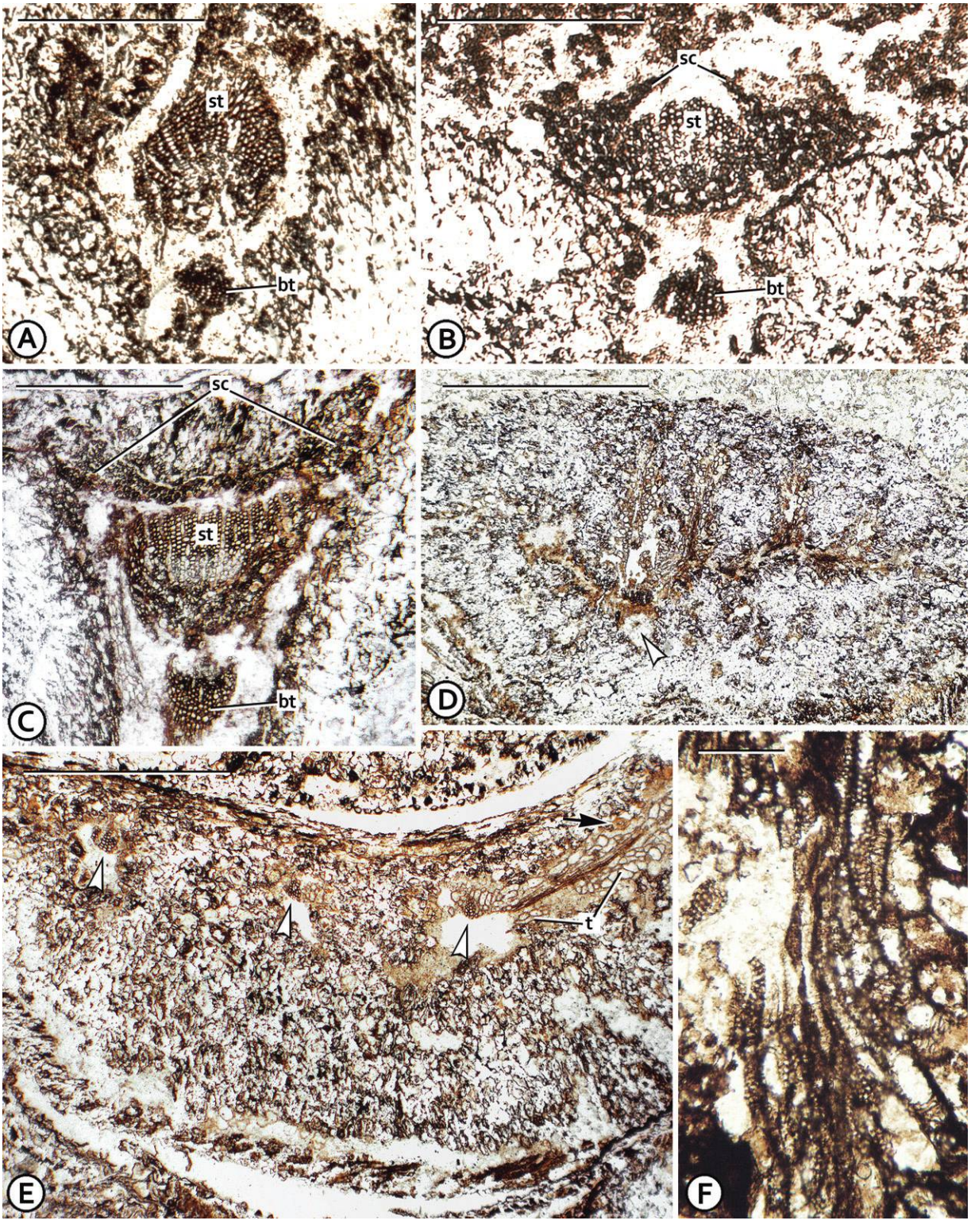

Fig. 4 *Pararaucaria carrii* Stockey et Rothwell sp. nov. Holotype (Oregon State University Paleobotanical Collections specimen P1). *A*, Oblique tangential section of cone showing diverging vascular tissue of bract/scale complex immediately distal to level of separation from stele, where bract trace (bt) is terete and ovuliferous scale trace (st) forms an inverted C, with convex side toward bract. H bottom (bot), no. 6, × 45. Scale bar = 1 mm. *B*, Level of diverging bract and scale traces slightly more distal than in *A*, with horseshoe-shaped scale trace and two separate triangular sclerenchyma bundles (sc) adaxial to traces. I_1 top, no. 21, × 50. Scale bar = 1 mm. *C*, Level of bract and scale traces similar to *B*. Note interconnected sclerenchyma bundles (sc) adaxial to traces. I_1 top, no. 25, × 40. Scale bar = 1 mm. *D*, Oblique tangential section of

embedded. The prominent multicellular bands of radially aligned cells that characterize the pocket-forming tissue of *P. carrii* are not found in either of the other *Pararaucaria* species (Escapa et al. 2012, 2013).

The realization that *Pararaucaria* seed cones represent the family Cheirolepidiaceae is based on numerous similarities between the anatomically preserved species of the genus and the compressed species of cheirolepidiaceous seed cones (Escapa et al. 2012, 2013). These include the shared morphological characters of *P. carrii*, *P. patagonica*, and *P. delfueyoi* detailed above, particularly, the presence of external lobes of the ovuliferous scale, the presence of a pocket of ovuliferous scale tissue covering the seed or seeds, and, in the case of *P. delfueyoi*, pollen of the *Classopollis* type at the nucellar apex in the seed micropyle (Escapa et al. 2012, 2013). Since cones of *P. carrii*, like those of most other *Pararaucaria* specimens, have been abraded, the exact configuration of the scale apex in both *P. carrii* and *P. delfueyoi* has yet to be determined.

Homologies of Seed Cone Structures and Conifer Phylogeny

Questions about gnetophyte relationships to conifers notwithstanding (Mathews 2009), systematic relationships among living conifers have become highly resolved through analysis of nucleotide sequences (Quinn et al. 2002; Rydin et al. 2002; Rai et al. 2008; Parks et al. 2009), plant structure (Hart 1987; Gernandt et al. 2011), and rare genetic markers (Raubeson and Jansen 1992), but relationships among living species do not always accurately reflect the overall pattern of phylogeny for an ancient clade in which a great deal of extinction has occurred (Rothwell and Nixon 2006; Mathews 2009). Therefore, resolving the overall pattern of phylogeny for conifers relies heavily on structural features of seed cones from a combination of fossil and living species (Pilger 1926; Florin 1951; Miller 1988, 1999; Smith and Stockey 2001, 2002; Gernandt et al. 2011; Rothwell et al. 2005, 2009, 2011; Serbet et al. 2010; Escapa et al. 2012). Likewise, phylogenetic analyses of such cones are heavily impacted by homology hypotheses for the various cone structures.

In his classic paradigm-establishing hypothesis for seed cones of modern conifers, Florin (1951) employed a transformational series of morphologies to convincingly document that the ovuliferous scale of Pinaceae is homologous to the axillary ovuliferous (secondary) shoot of cordaites and Paleozoic fossil conifers (Florin 1938–1945, 1951; Stockey 1981; Stewart and Rothwell 1993; Taylor et al. 2009). More recently, an additional and alternative transformational series for ovuliferous scale evolution of Cupressaceae from Voltziales has been proposed (Rothwell et al. 2011). As with the earlier, more general hypothesis of Florin (1951), the recent hypothesis relies heavily on homology assessments for bract/scale complexes, thereby confirming that seed cones of Cupressaceae are also derived from a compound shoot system (Rothwell et al. 2011).

As in the other conifer families, accurate resolution of systematic relationships for Cheirolepidiaceae relies heavily on accurate homology assessments for seed cone structures and, more specifically, for tissues located on the adaxial side of the seed in *Pararaucaria*. That tissue is an integral component of the ovuliferous scale complex in *P. patagonica* (Wieland 1935; Escapa et al. 2012, 2013) that traditionally has been regarded as a seed wing, homologous to that of the Pinaceae (Calder 1953; Stockey 1977). However, a recent reinterpretation of that tissue (Escapa et al. 2012) has revealed that it is not a seed wing. Rather, the pocket-forming tissue of *Pararaucaria* is homologous to the flap of tissue covering the ovule in compressed species of Cheirolepidiaceae (Archangelsky 1968; Clement-Westerhof and van Konijnenburg-van Cittert 1991; Kvaček 2000; Del Fueyo et al. 2008).

This reinterpretation also suggests that the ovuliferous scale of *Pararaucaria* may show structural similarities to Podocarpaceae and possibly Araucariaceae, like those that have been recognized for compressed seed cones of Cheirolepidiaceae for many years (Hirmer 1936; Clement-Westerhof and van Konijnenburg-van Cittert 1991). The flap of tissue in compressed cheirolepidiaceous seed cone species often has been termed an epimatium, like that of the Podocarpaceae (Clement-Westerhof and van Konijnenburg-van Cittert 1991; Del Fueyo et al. 2008), which reflects one homology hypothesis for the ovuliferous scale of seed cones of the Cheirolepidiaceae. However, the epimatium of Podocarpaceae is considered to be homologous to the entire ovuliferous scale, while that of Cheirolepidiaceae represents only that portion of the ovuliferous scale that extends over the adaxial surface of the seed (Escapa et al. 2012). Therefore, in *P. patagonica* (Escapa et al. 2012), *P. delfueyoi* (Escapa et al. 2013), and *P. carrii*, the more neutral and descriptive terminology "pocket-forming tissue" has been used for the flap of tissue that encloses the seed or seeds on the adaxial side of the ovuliferous scale in the Cheirolepidiaceae, as it has a distinct tissue component not seen in the rest of the ovuliferous scale (table 1).

In *P. carrii*, this pocket-forming tissue is distinctly different from the parenchyma/glandular trichomes (Stockey 1977) or branching sclereids (Calder 1953), with air spaces that characterize the other two *Pararaucaria* species. In *P. carrii*, the pocket-forming tissue is similar in its tissue composition of mixed parenchyma and sclereids to the rest of the ovuliferous scale, cortex, and bract, thus making it more similar to a podocarp epimatium in that respect. However, we do not know the full extent of the ovuliferous scale tissue in *P. carrii*, and as such, speculation about homologies for this structure will have to

ovuliferous scale distal to seed showing vascular bundle dividing repeatedly in horizontal plane and vertically to produce terete seed trace (at white arrowhead). I_1 top, no. 4, × 25. Scale bar = 2 mm. *E*, Oblique longitudinal section of bract showing histology and several branching bundles (at white arrowheads) with accompanying transfusion tissue (t) adjacent to bundles distally. I_1 top, no. 7, × 50. Scale bar = 1 mm. *F*, Enlargement of transfusion tissue showing alternate, multiseriate, circular bordered pits on conducting cells. I_1 top, no. 20, × 200. Scale bar = 100 μm.

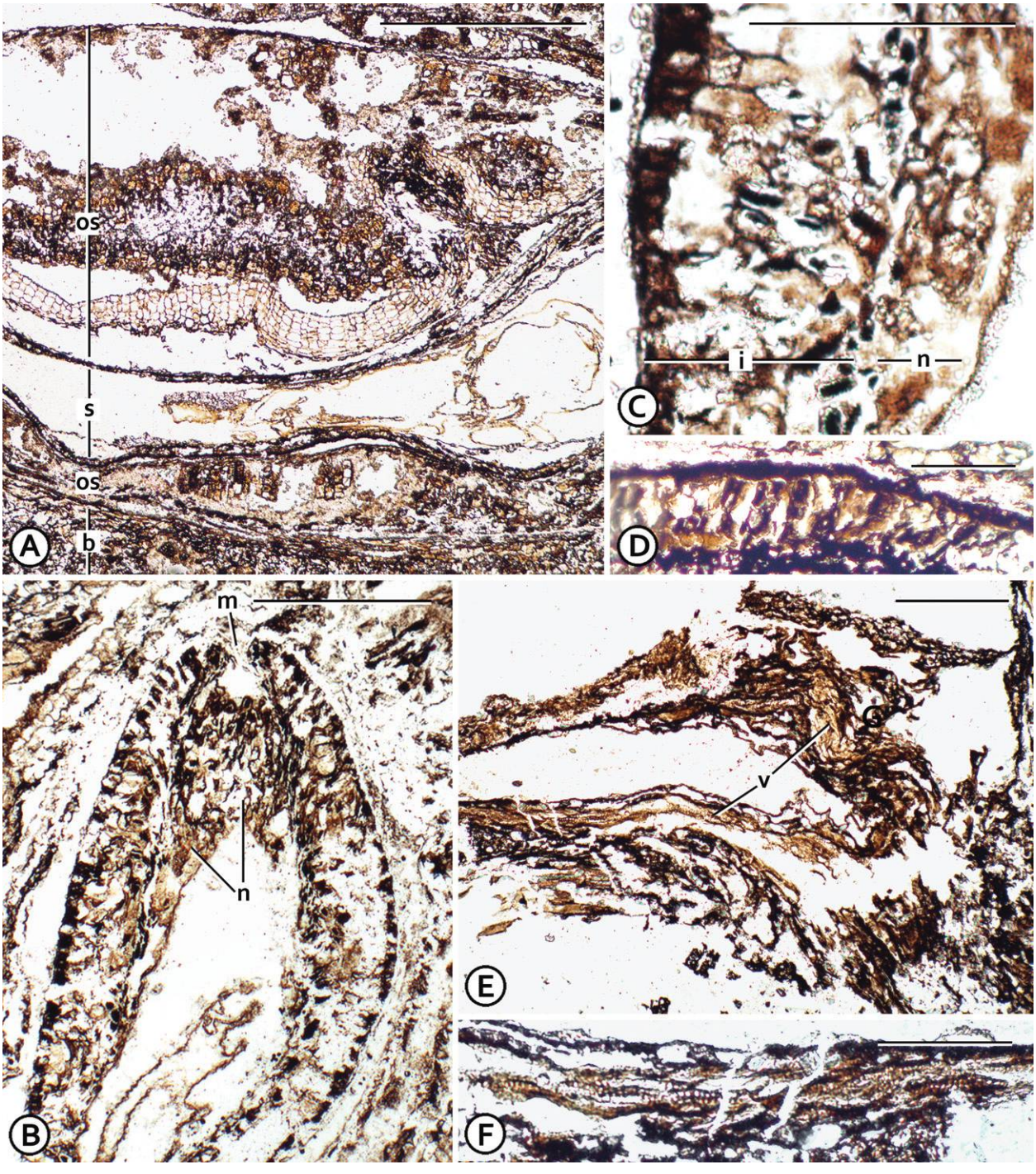

Fig. 5 *Pararaucaria carrii* Stockey et Rothwell sp. nov. Holotype (Oregon State University Paleobotanical Collections specimen P1). *A*, Enlargement of central region of bract/scale complex in longitudinal section showing relationships and histological features of bract (b), ovuliferous scale (os), seed (s), and overarching ovule enclosing tissue of ovuliferous scale (os, toward top). Note both isodiametric randomly arranged cells of primary tissue and radially aligned cells of secondary tissue. H bottom (bot), no. 22, × 35. Scale bar = 1 mm. *B*, Longitudinal section in apical region of seed viewed in minor plane of symmetry, showing integument with micropyle (m) and nucellus (n) that is attached to integument below apical mound of tissue. H bot, no. 32, × 60. Scale bar = 0.5 mm. *C*, Cross section showing histology of seed integument (i) and attached nucellus (n). H bot, no. 25, × 228. Scale bar = 200 μm. *D*, Cross section of outer zone of integument showing palisade layer below epidermis (dark line toward top). Note shrunken palisade cells that approach an I-beam shape. H bot, no. 36, × 180. Scale bar = 100 μm. *E*, Nucellar tissue (torn away from integument at sides) at chalaza of seed showing tracheids of vascular tissue (v). I_1 top, no. 25, × 96. Scale bar = 100 μm. *F*, Enlargement of vascular tissue toward bottom of *E*, showing scalariform wall thickenings of tracheids. I_1 top, no. 25, × 228. Scale bar = 100 μm.

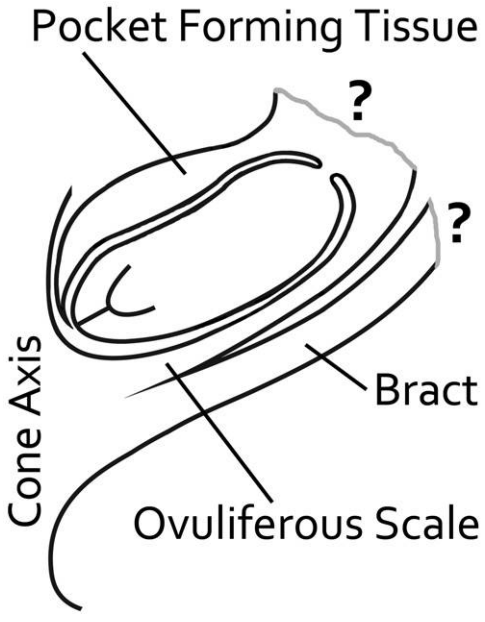

Fig. 6 *Pararaucaria carrii* Stockey et Rothwell sp. nov. Diagram of bract/ovuliferous scale complex as viewed in radial section of cone. Gray lines with accompanying question mark represent preserved extent of eroded bract and ovuliferous scale tips, the distal structure of which remains unknown. Note orientation and attachment of seed from cartoon of micropyle and nucellar apex and relationship of pocket-forming tissue to lower part of the ovuliferous scale.

await further discoveries of more complete, unweathered cones.

Summary and Conclusions

The discovery of a third species of the anatomically preserved seed cone *Pararaucaria* in the Callovian Trowbridge Formation of eastern Oregon State establishes the second Middle Jurassic species of the genus and extends the range of the *Araucaria/Pararaucaria* forest associations to the Jurassic of the Northern Hemisphere. The new species shares a larger number of characters with the other Middle Jurassic species, *P. patagonica*, than it does with the Late Jurassic *P. delfueyoi*, but it is easily distinguished from the former by seed size and shape, by features of sclerenchyma bundles that accompany the scale trace, by histological features of the pocket-forming tissues, and by the presence of radially aligned cortical tissue within the pocket-forming tissue (table 1). *Pararaucaria carrii* demonstrates for the first time within the genus *Pararaucaria* that the bract trace can branch to form several bundles with accompanying transfusion tracheids and that the seed is vascularized by a cup-shaped sheath of tracheids within the base of the nucellus.

Reinterpretation of *Pararaucaria* as having lobed ovuliferous scales, unwinged seeds, and seeds that occur within a pocket of ovuliferous scale tissue places the genus securely within the extinct conifer family Cheirolepidiaceae. That reinterpretation also calls into question previously suspected relationships of the Cheirolepidiaceae to the Pinaceae (Rothwell et al. 2009) and other extinct representatives of the non-"Cupressophyta" clade (sensu Rai et al. 2008) of crown group conifers. Based on previous interpretations (Calder 1953; Stockey 1977), *Pararaucaria* appeared to share several important characters of the vascular tissues, ovuliferous scale, and seeds with Pinaceae (i.e., horseshoe-shaped scale trace and smaller bract trace, unlobed ovuliferous scale apex, seeds borne superficially on the adaxial surface of the ovuliferous scale, and seed wing constructed of ovuliferous scale tissue). However, as a result of the new interpretation of seed and scale characters, possible similarities to the bract/scale complex of Podocarpaceae and Araucariaceae have become more apparent, particularly within a developmental context (see Chamberlain 1935; Hirmer 1936). These new data emphasize the importance of developing accurate homology hypotheses for conifer seed cone structures and the central role of stem group conifers for ultimately resolving the overall pattern of conifer phylogeny.

Table 1

Morphological Comparison of *Pararaucaria* Seed Cone Species

Taxon	*Pararaucaria patagonica*	*Pararaucaria delfueyoi*	*Pararaucaria carrii*
Age	Middle Jurassic	Late Jurassic	Middle Jurassic
Distribution	Santa Cruz, Argentina	Chubut, Argentina	Oregon
Length (cm)	2.3–5.1	8	At least 2.8
Width (cm)	1.3–3.0	3.0–4.0	At least 1.3
No. seeds/scale	1 (2)	2	1
Seed length (mm)	6.0	11.0	5.3
Seed width (mm)	6.0 (single seed), 3.3 (double seeds)	5.0 (double seeds)	6.5
Bract trace at origin, x.s.	Circular	Circular or subcircular	Crescent shaped
Branching of bract trace	?	?	Repeatedly
Bract transfusion tissue	?	?	Present
Branching of scale trace	Distally producing several strands	?	Vertically (seed bundle), distally producing several strands
Pocket-forming tissue	Parenchyma and anastomosing, branched cells	Parenchyma and anastomosing, branched cells	Parenchyma and numerous sclereids
Radially aligned cells	At seed attachment?	At seed attachment	Within pocket-forming tissue
Seed vascularization	?	?	Cup shaped, at base of nucellus

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