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## PARARAUCARIA DELFUEYOI SP. NOV. FROM THE LATE JURASSIC CAÑADÓN CALCÁREO FORMATION, CHUBUT, ARGENTINA: INSIGHTS INTO THE EVOLUTION OF THE CHEIROLEPIDIACEAE

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The discovery of 16 cylindrical conifer seed cones at the Estancia Vilán locality in the Late Jurassic Cañadón Calcáreo Formation of Chubut Province, Patagonia, Argentina, provides anatomically preserved specimens, allowing for the description of a second species of *Pararaucaria* (Cheirolepidiaceae). The new species, *Pararaucaria delfueyoi*, is similar in general features to the type species, *Pararaucaria patagonica*, but has a specifically diagnostic combination of characters that include cone size, seed number, features of histology, and seed size. Specimens are cylindrical with a narrow axis that bears helically arranged bract/scale complexes. The bract and scale diverge from the axis at  $\sim 90^\circ$  and separate from each other almost immediately. The ovuliferous scale extends toward the margin of the cone and then arches over to enclose two inverted nonwinged seeds within a pocket of tissue. Although the specimens are abraded such that the distal regions of the ovuliferous scales are not preserved, this combination of morphological and histological characters allows for the assignment of *P. delfueyoi* to the Cheirolepidiaceae with confidence. The co-occurrence of this cone with an undescribed species of *Araucaria* extends the geographic and stratigraphic ranges of this association, which previously has been known only from the Middle Jurassic of Santa Cruz Province of Patagonia. This extends the knowledge of anatomical variation among seed cones of Cheirolepidiaceae and improves our understanding of homology relationships for conifer seed cone structures.

**Keywords:** Cheirolepidiaceae, conifers, Jurassic, *Pararaucaria*, Patagonia.

### Introduction

The genus *Pararaucaria* Wieland (1929, 1935) was erected for permineralized seed cones found in the historic Jurassic Cerro Cuadrado Petrified Forest in Santa Cruz Province, southern Argentina (Patagonia), where the specimens are frequently associated with *Araucaria mirabilis* (Spegazzini) Windhausen, another commonly permineralized conifer seed cone (Calder 1953; Stockey 1975, 1978; Falaschi et al. 2011). For many years these two species were the only well-known anatomically preserved conifer seed cones from South America. Subsequent descriptions and additional interpretations of the anatomy, morphology, and taxonomic affinities of *Pararaucaria patagonica* were provided by Calder (1953) and Stockey (1977), who each offered a more complete view of this taxon in the context of Mesozoic conifers.

As a result of those studies and other interpretations, *P. patagonica* has been systematically linked to several conifer families, including the Araucariaceae (Wieland 1929, 1935; Calder 1953), Cheirolepidiaceae (Wieland 1935; Archangel'sky 1968), Pinaceae (Stockey 1977; Smith and Stockey 2001, 2002), Taxodiaceae (=basal Cupressaceae; Calder 1953; Stockey 1977), and Voltziaceae (Miller 1999). However,

other authors have suggested either that *Pararaucaria* is a member of a distinct family of conifers (Stockey 1977; Taylor et al. 2009) or that it displays a structural organization that is intermediate between currently recognized families, based on features of the ovuliferous scale, putative seed wing, cone vascularization, and histology.

More recently, Escapa et al. (2012) have investigated both previously described and previously unstudied specimens of *P. patagonica*, resulting in the discovery of new characters and the reinterpretation of others. Most important among those discoveries are the presence of a flap of tissue covering the seed (or seeds), the absence of a seed wing, and a lobed ovuliferous scale distal margin. These new characters provide evidence for the systematic affinities of *P. patagonica* and have resulted in the recognition that this species represents the first anatomically preserved seed cone of the family Cheirolepidiaceae (Escapa et al. 2012). In the past, this extinct conifer family has been represented mostly by leafy shoots, pollen, compressed pollen and ovulate cone specimens, wood, and a single permineralized pollen cone (Watson 1977, 1988; Harris 1979; Alvin 1982; Clement-Westerhof and van Konijnenburg-van Cittert 1991; Axsmith and Jacobs 2005; Rothwell et al. 2006).

In this article, a new species of the genus *Pararaucaria* is described from geographically distant and slightly younger deposits in northern Patagonia than those that yielded *P. patagonica*. As with the type species of *Pararaucaria*, cones

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of the new species are anatomically preserved, allowing for confirmation of the diagnostic characters that define the genus, as well as providing evidence for structural and systematic diversity among these closely related plants. Together, these two species contribute a more robust suite of shared character states for cheirolepidiaceus seed cones and a more complete set of anatomical and morphological characters for interpreting familial relationships of Cheirolepidiaceae. The new species also contributes additional information for interpreting the homologies of conifer seed cone characters and for the structural transformations that define conifer evolution and familial relationships. In particular, the Cheirolepidiaceae now can be more confidently related to the evolution of crown group conifer families. This material also contributes to an increased understanding of plant associations and floristic assemblages in the Jurassic of Patagonia, where the *Araucaria-Pararaucaria* forests thrived, and also contributes to an improved understanding of the paleoecology of Jurassic forests within the South American region of Mesozoic Gondwana.

**Material and Methods**

*Geological Setting*

Cones were recovered from Estancia Vilán, a locality on the east side of the Chubut River within the middle valley, northwestern Chubut Province (fig. 1). In this area the fossiliferous horizon crops out as the uppermost part of a thick sequence of the Cañadón Calcáreo Formation. This unit is entirely terrestrial in origin, dominated by silicoclastic fluvial and lake deposits with several intercalated ash beds. In the study area, the Cañadón Calcáreo Formation unconformably overlies the volcanic and volcanoclastic sequence of the Lonco Trapial Formation. In addition to plant fossils, the Cañadón

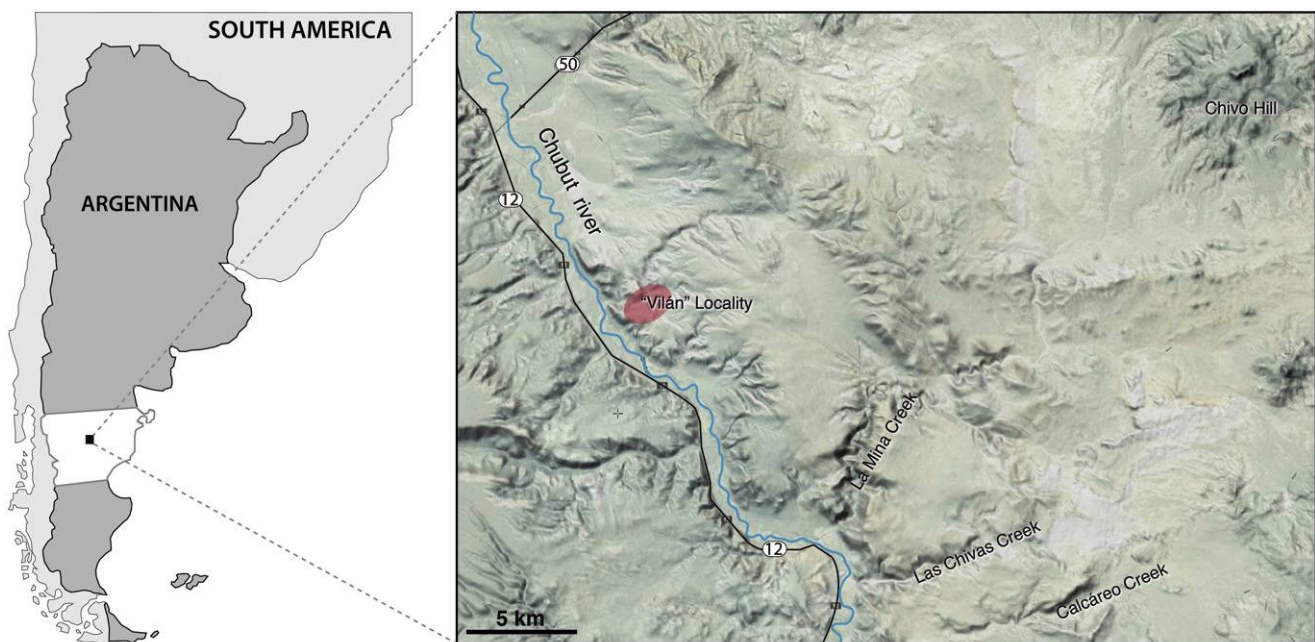
Calcáreo Formation preserves a vertebrate and invertebrate fauna, including dinosaurs (Carballido et al. 2011), fish (Lopez-Arbarello et al. 2008), and conchostracans (Volkheimer et al. 2009). In particular, the Estancia Vilán plant locality includes large numbers of *Araucaria* seed cones, seedlings, permineralized branches, and logs, as well as other anatomically preserved reproductive structures (Escapa 2009).

The Cañadón Calcáreo Formation has been the subject of controversy for many years with respect to its geological relationships and age in context of the Cañadón Asfalto Basin (Volkheimer et al. 2009 and citations therein). On the basis of its paleontological content (mostly charophytes and pollen/spores), the Cañadón Calcáreo Formation has been suggested to be Late Jurassic (Mussachio 1995; Zavattieri et al. 2010) to Early Cretaceous (Volkheimer et al. 2009) in age. However, two recent U-Pb radiometric dates indicate a more precise absolute age in the Late Jurassic, most probably near the Oxfordian/Kimmeridgian boundary (i.e.,  $157.5 \pm 0.05$  Ma; Cúneo et al. 2012).

*Fossil Preparation, Imaging, and Repository*

This study is based on a collection made over the past 10 yr at the Vilán locality. The specimens are permineralized within a silicate matrix. The original organic matter is no longer present in the cones, probably as a result of groundwater leaching. Seed cones typically show pre- and/or postdepositional abrasion; most are incomplete and crushed to varying degrees, but histological preservation is often quite good. The external appearance of the cones varies, depending on the degree of abrasion.

Specimens were sectioned following standard paleobotanical procedures (see Stockey 1977). Hillquist's (A/B) thin-section epoxy was used for mounting specimens on 2 × 3-in glass



**Fig. 1** Simplified map showing location of Vilán plant locality, Chubut Province, Argentina.

slides. Thin sections were cut and ground to  $\sim 40 \mu\text{m}$  thickness on a Hillquist thin-sectioning machine. They were then polished by hand on a glass plate using 600-grit carborundum. Coverslips were affixed with xylene-soluble Eukitt mounting medium (Kindler, Freiburg, Germany).

Images were captured using various techniques (Kerp and Bomfleur 2011). External cone surfaces and thick sections were photographed under reflected light using a Canon EOS t3 camera with a Canon EF-S 60-mm macro lens. Some thin sections were photographed using a Photophase (Phase One, Frederiksberg, Denmark) digital scanning camera mounted on a Leitz Aristophot bellows camera or with a Cannon PowerShot SX100 IS digital camera. Some thin sections were photographed using transmitted light with a Nikon SMZ1000 stereomicroscope or a Nikon DS-Fi1 camera mounted on a phototube and controlled with a Nikon DS-L2 camera control unit. In order to obtain greater depth of focus for high-magnification images, we used an image-stacking technique (Bercovici et al. 2009), in which a well-focused image is obtained from several images captured at slightly different focal planes. Helicon Focus software (<http://www.heliconsoft.com/heliconfocus.html>) was used, with the "Method B" (Depth Map) parameter, and the resulting image was carefully checked for the presence of artifacts. Several smaller, partially overlapping images were merged to create high-quality

images of critical features. This last technique was applied both manually and using the Adobe Photoshop CS5 Photomerge macro.

Terminology for seed cone structures in this article follows that of Escapa et al. (2012). Specimens and microscope slides are housed in the paleobotanical collection of the Museo Paleontológico Egidio Feruglio (Trelew, Chubut, República Argentina) under the designation MEF-Pb.

### Systematic Description

Order—*Coniferales*

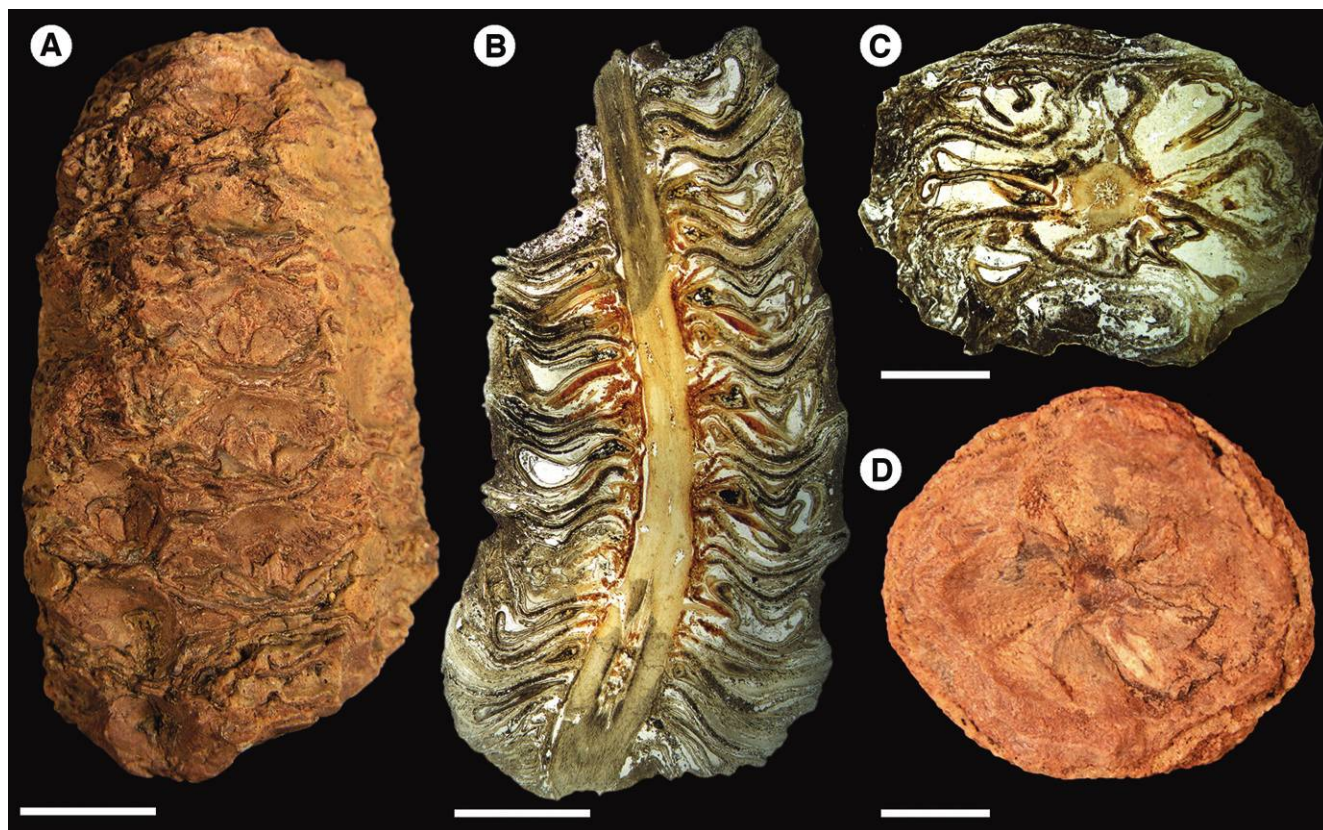
Family—*Cheirolepidaceae* Takhtajan

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

Type Species—*Pararaucaria patagonica* Wieland emend. Escapa, Rothwell, Stockey et Cúneo, 2012 (Figs. 2–7)

Species—*Pararaucaria delfueyoi* Escapa, Cúneo, Rothwell et Stockey, sp. nov.

*Specific diagnosis.* Cylindrical cones up to 8 cm long, 3–4 cm wide; slender axis with helically arranged bract/scale



**Fig. 2** *Pararaucaria delfueyoi* Escapa, Cúneo, Rothwell et Stockey, sp. nov. A, External view of seed cone showing arrangement of bract/scale complexes. MPEF-Pb 1957. Scale bar = 10 mm. B, Holotype; midlongitudinal section of cone showing central axis from which bract/scale complexes are diverging. MPEF-Pb 3627 V. Scale bar = 10 mm. C, Cross section of midregion showing overall cone features. MPEF-Pb 1957. Scale bar = 10 mm. D, Cross section of cone from broken surface. MPEF-Pb 3629 II. Scale bar = 10 mm.

complexes consisting of large ovuliferous scale subtended by broad, flattened bract. Bract and ovuliferous scale separate near base. Scale trace accompanied by sclerenchyma bundle with reniform shape basally, separating to form two triangular bundles before terminating near level of seed micropyle. Pocket-forming tissue of ovuliferous scale overarched and enclosing seeds, thinning toward base of scale and terminating near level of seed micropyle. Ovuliferous scales bearing two inverted seeds ~11 mm long, oriented parallel to long axis of scale, with elongated micropyle curving toward lateral margin of scale. Integuments multilayered, with one or two layers of palisade below epidermis, several layers of elongated sinuous cells internally. Nucellus with cellular apex.

*Etymology.* The specific epithet *delfueyoi* is in honor of Dr. Georgina Del Fueyo, for her numerous contributions to the understanding of living and fossil conifers of Gondwana.

*Specimens.* MPEF-Pb 1950–1952, 1955–1957, 1961, 1965, 3285, 3453–3455, 3627–3629, 5340–5342.

*Holotype hic designatus.* MPEF-Pb 3627; figures 2B, 5A, 5C, 5D, 6A, 6B.

*Type locality.* Estancia Vilán, Chubut Province, Patagonia, Argentina.

*Stratigraphy.* Cañadón Calcáreo Formation.

*Age.* Late Jurassic.

### Description

Seed cones are cylindrical, up to 8.0 cm long and 3.0–4.0 cm in diameter. Each cone consists of numerous helically arranged bract/scale complexes that diverge from the cone axis in what approaches a 3/8 phyllotaxis. At the cone base, the bract/scale complexes are reduced and modified, as compared to those in the remainder of the cone, and do not produce seeds; those at the apex have not been observed. Each bract/scale complex is composed of an ovuliferous scale and a subtending bract. As is typical for the genus *Pararaucaria*, the bract and ovuliferous scale separate from each other at or near their bases. Therefore, there is little or no fusion of these structures.

*Cone axis.* The cone axis is up to 3.5 mm in diameter with a small pith, up to 1.2 mm in diameter (fig. 2). The stellate outline of the pith in cross section is due to the outward divergence of traces toward the bract/scale complexes (fig. 3A, 3B). Such radial extensions of the pith have straight edges (fig. 3B–3D), are up to 200  $\mu\text{m}$  wide, and contain cells that are similar to those in the rest of the pith (fig. 3D, 3E). The best-preserved regions of the pith display isodiametric to slightly ovate thin-walled cells, 40–45  $\mu\text{m}$  in diameter, with irregular dark contents (fig. 3E). In transverse sections of the axis, it is also possible to identify scattered pith sclereids 80–100  $\mu\text{m}$  in diameter (fig. 3E).

Wood of the axis forms a complete cylinder (figs. 2C, 3A), with endarch maturation (fig. 3A–3D). The inner surface of the cylinder is dissected due to the diverging bract/scale traces (fig. 3A–3C). The diameter of the first 15 or 20 secondary xylem tracheids increases toward the outer margin of the wood (fig. 3C). Secondary tracheids toward the periphery of the zone are circular to slightly polygonal, with a mean diameter of 20  $\mu\text{m}$ , while the first-formed secondary xylem tracheids have diameters as small as 8–10  $\mu\text{m}$ . Wall-thickening

patterns of metaxylem appear to be helical, but on closer examination the presence of cross-linking bars reveals that most are scalariform (fig. 4A, 4C, 4D). Tracheids of the secondary xylem display uniseriate circular bordered pits on the radial walls (fig. 4A, 4B, 4E, 4F). Rays are typically uniseriate.

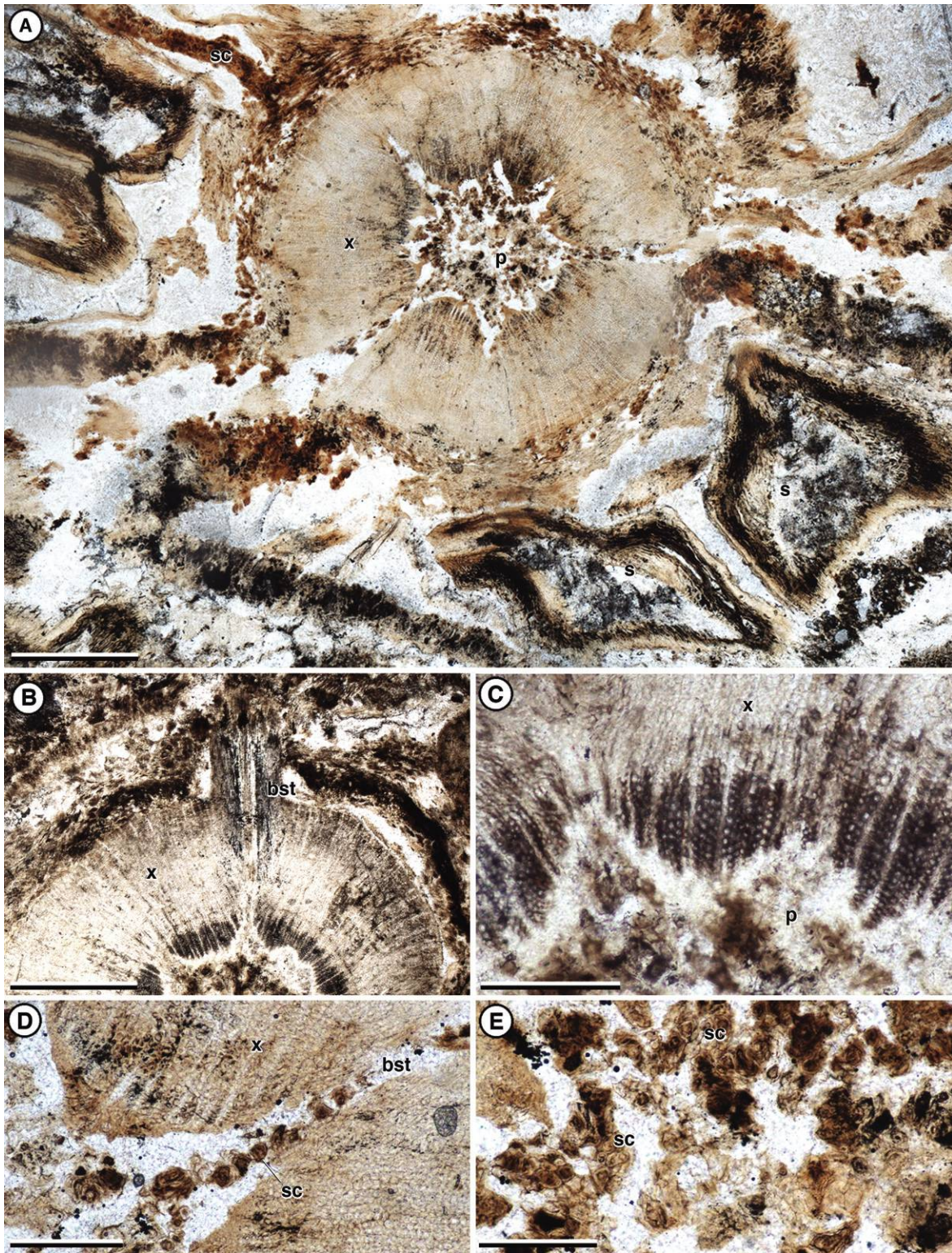
A zone of incompletely preserved tissue surrounds the vascular cylinder, and this area corresponds to the position of cambium and phloem (fig. 3A, 3B). However, numerous thick-walled sclereids are preserved within this zone, indicating that phloem sclereids were produced.

*Bract/scale complexes.* The abraded bract/scale complexes have a rhomboidal distal face (fig. 2A) up to 21–23 mm wide and 9–10 mm high in the midregion of the cone (fig. 5A, 5B). The distinction between ovuliferous scale and bract is not evident from external views (fig. 2A), probably due to the degree of abrasion that has occurred. In agreement with the type species, *P. patagonica*, bract/ovuliferous scale complexes diverge from the axis at  $\sim 90^\circ$  (fig. 2B). The bract is laterally expanded and up to 20 mm wide (fig. 5A, 5B). It is generally symmetrical in cross sections, with a depressed central region and two lateral regions that arch adaxially (fig. 5B). Bracts are 0.40–0.55 mm thick in the midregion and thin laterally. Bracts have a distinct abaxial and adaxial epidermis composed of cells with dark contents (fig. 5B). Internal to these layers is a dark central zone flanked by adaxial and abaxial areas of lighter color (fig. 5B, 5D). Because of incomplete preservation, additional details of the ground tissue cells cannot be characterized.

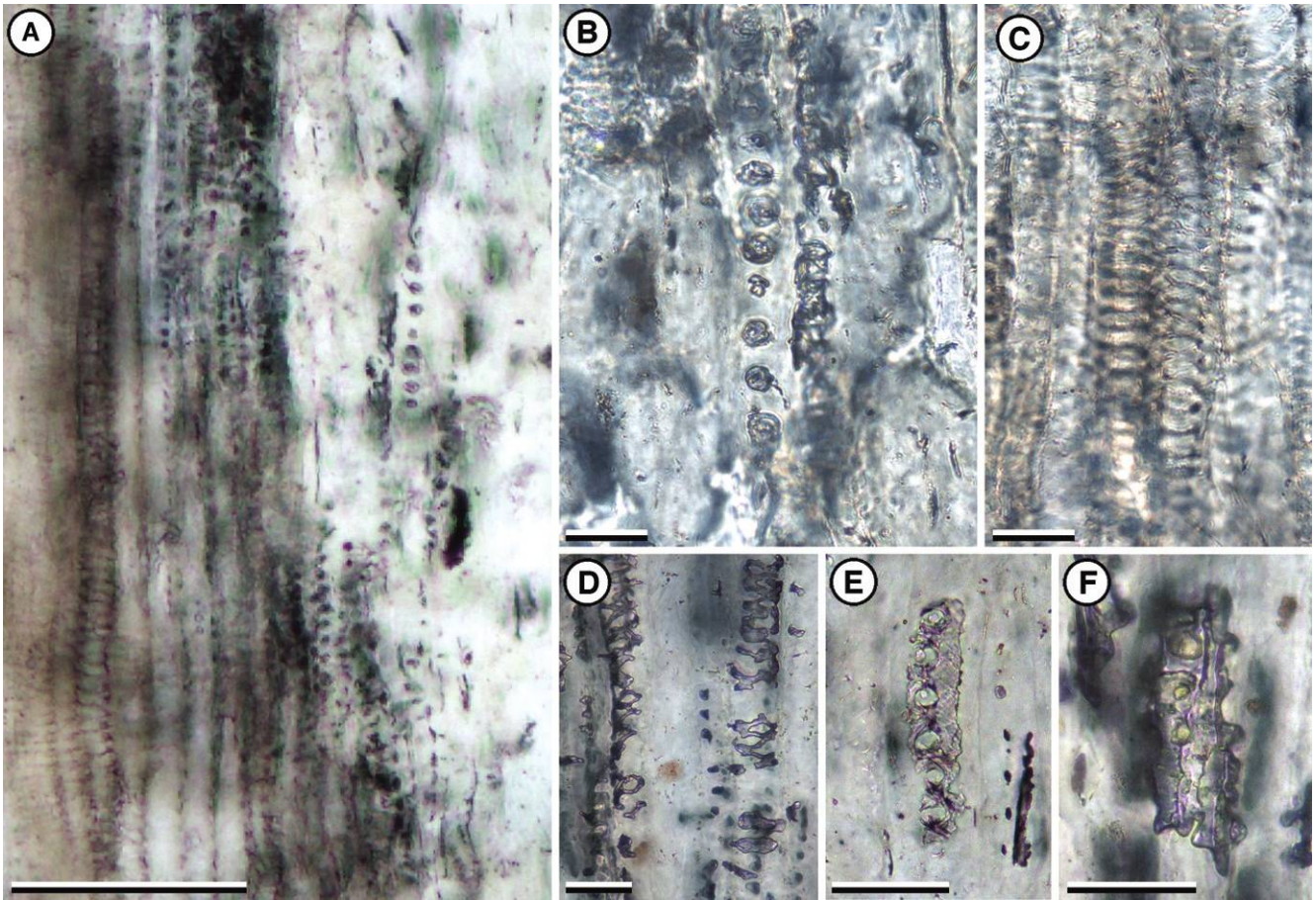
A vascular trace to the bract and scale forms a nearly complete cylinder with internal ground tissue (fig. 3B) but divides immediately upon diverging from the stele of the cone axis (fig. 5D). Ground tissue separating the bract and scale traces shows a high percentage of sclereids similar to those found in the pith (figs. 5B–5D, 6A). Somewhat distally, the scale trace is hemispherical with a convex adaxial side (figs. 5B, 5C, 6A) and up to 0.90–1.15 mm wide and 0.35–0.50 mm high. The bract trace is smaller, circular to subcircular in outline (figs. 5B–5D, 6A), and up to 0.2 mm in diameter. The distance between the bract and scale traces characteristically increases distally, ranging from 0.1 to 1.0 mm (fig. 5B–5D). At the level of the seed chalaza, the traces diminish in size and are hard to identify (fig. 5A).

As is also characteristic of *P. patagonica* (Calder 1953; Stockey 1977), the scale trace is accompanied by distinctive sclerenchyma. From its origin in the cortex of the cone axis, the sclerenchyma forms a bundle that is reniform in cross sections (fig. 5D), but in some more distal sections, the sclerenchyma divides (figs. 5C, 6A) into two closely spaced bundles that are triangular in outline (fig. 5B) like those of *P. patagonica*. The sclerenchyma extends the length of the scale but disappears close to the chalazal end of the seeds (fig. 5A). These sclerenchyma bundles are composed of elongated, thick-walled cells that are circular in cross section (fig. 6A), 20–40  $\mu\text{m}$  in diameter, and of variable length (up to 300  $\mu\text{m}$ ).

Morphology of the ovuliferous scale has been reconstructed by comparing serial sections in longitudinal and transverse views. In midlongitudinal sections, the ovuliferous scale appears to extend from the level of attachment at the cone axis to the margin of the cone, bend distally over the seeds, and ex-



**Fig. 3** *Pararaucaria delfueyoi* Escapa, Cúneo, Rothwell et Stockey, sp. nov. **A**, Cross section of seed cone showing central axis and pairs of seeds attached to two bract/scale complexes. MPEF-Pb 3629 IV. Scale bar = 1 mm. **B**, Cross section of seed cone showing vascular tissue of bract/scale complex at level of divergence from central axis. Note ground tissue at center of diverging bract/scale trace. MPEF-Pb 5341 B III. Scale bar = 1 mm. **C**, Cross section of central axis showing pith and tracheids of stele and wood. Note radial extension of pith that helps define positions of



**Fig. 4** *Pararaucaria delfueyoii* Escapa, Cúneo, Rothwell et Stockey, sp. nov.; all sections from MPEF-Pb 5341 A IV. **A**, Longitudinal section of central axis showing wood in radial section. Note metaxylem with scalariform thickenings at left and secondary xylem tracheids with uniseriate circular bordered pits at right. Scale bar = 0.1 mm. **B**, Detail of secondary xylem tracheids with bordered pits. Scale bar = 0.02 mm. **C**, Detail of wall-thickening patterns on metaxylem tracheids. Scale bar = 0.02 mm. **D**, Detail of incompletely preserved metaxylem tracheid wall thickenings. Scale bar = 0.02 mm. **E, F**, Detail of pits on the radial walls of secondary xylem tracheids. Scale bar = 0.02 mm.

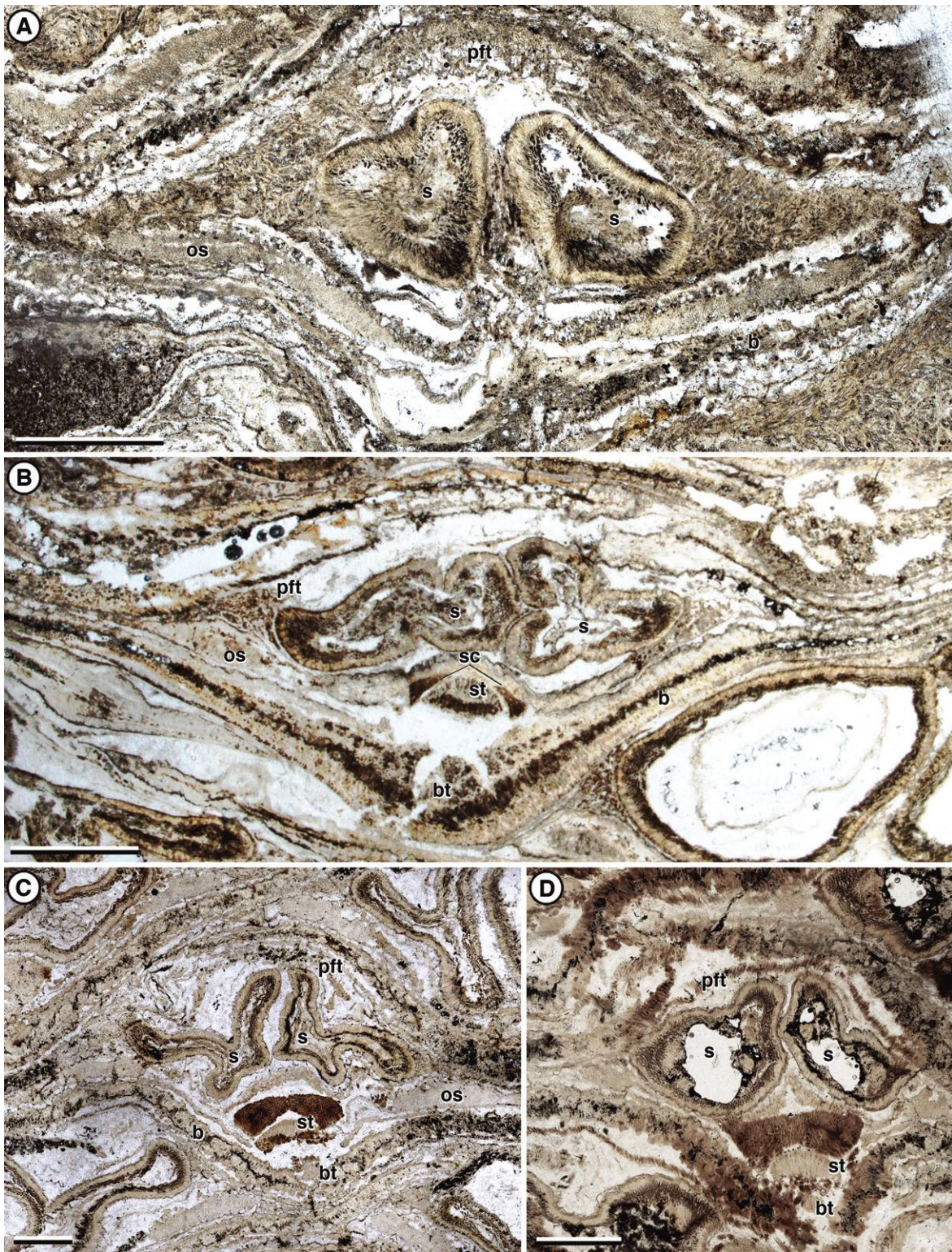
tend back toward the cone axis (figs. 2B, 7A). It then thins (cf. fig. 5A, 5B) and terminates at about the level of the seed micropyle (figs. 2B, 7A). In cross sections near the distal end of the ovuliferous scale, the tissues are rather thin between the seeds and the bract of each bract/scale complex (fig. 5A). At this level, the scale tissue thickens at the margins of the seeds, where it overarches and encloses the seeds and thins laterally (fig. 5A). In a series of cross sections of the ovuliferous scale (i.e., cone tangential sections) progressing toward the cone axis (fig. 7A–7D), the pocket-forming tissue adaxial to the seeds becomes successively thinner. Together, these longitudinal and cross sections of the ovuliferous scale reveal a pocket like that of *P. patagonica*, which is open on the side adjacent to the cone axis but encloses the seeds (figs. 5A, 7A).

Ground tissues of the ovuliferous scale are incompletely preserved and difficult to characterize in most specimens.

However, the histology of these cells differs markedly between cells abaxial to the seeds and those that make up the pocket-forming tissue (figs. 5A, 6B). Cells in both regions lack obvious contents. Abaxial to the seeds are thin-walled parenchyma cells, polygonal in transverse section (fig. 6B), 30–40  $\mu\text{m}$  in diameter and  $\sim 50 \mu\text{m}$  long. However, the pocket-forming tissue lateral and adaxial to the seeds consists of loosely organized elongated cells that follow a sinuous course (fig. 6B). Such cells are extremely similar to those in the same position as in *P. patagonica* that Stockey (1977) compared to anastomosing rows of glandular hairs.

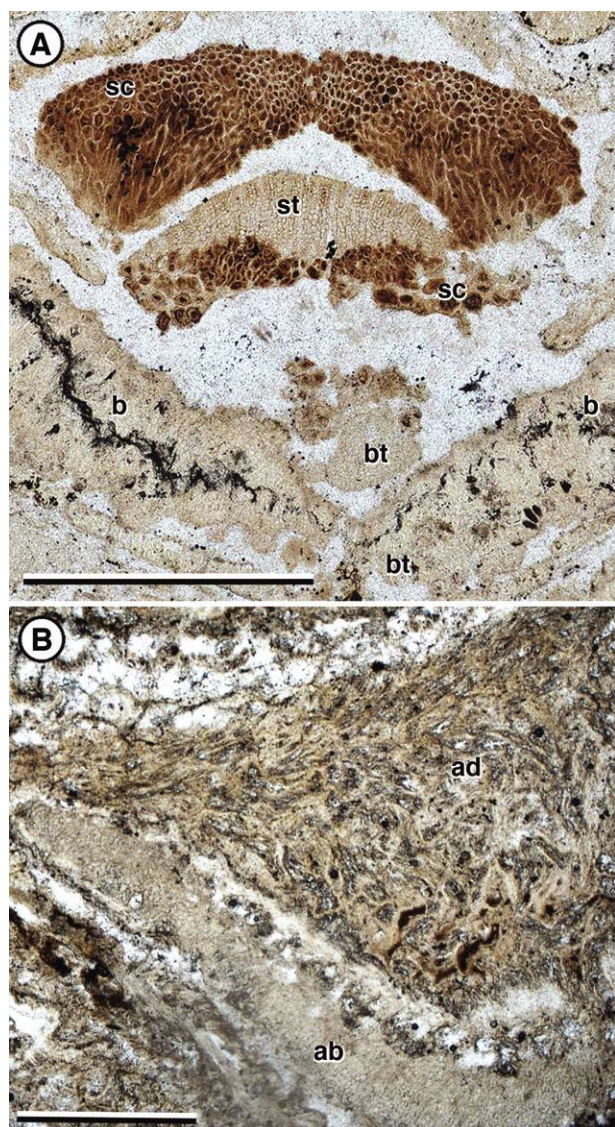
**Seeds.** Two seeds are produced on each ovuliferous scale (figs. 3A, 5A–5D) and are enclosed by scale tissue (i.e., pocket-forming tissue) that arches over and covers both of them (figs. 5A, 7A). Seeds are up to 11 mm long and 5 mm wide and in cross sections commonly appear to be collapsed

primary bundles. MPEF-Pb 5341 B III. Scale bar = 0.5 mm. **D**, Cross section of central axis showing sclereids of pith and in pith ray. MPEF-PB 3629 III. Scale bar = 0.5 mm. **E**, Detail of pith showing sclereids and incompletely preserved pith parenchyma. MPEF-Pb 3629 IV. Scale bar = 0.2 mm. bst = bract/scale complex vascular trace; p = pith; s = seed; sc = sclereids; x = xylem.



**Fig. 5** *Pararaucaria delfueyoi* Escapa, Cúneo, Rothwell et Stockey, sp. nov. *A*, Longitudinal section of holotype showing the bract/scale complex in cross section near level of seed attachment. Note pocket-forming tissue completely overarching and enclosing two seeds. MPEF-Pb 3627 II. Scale bar = 2 mm. *B*, More proximal view of bract/scale complex from *A* showing thinner incompletely preserved pocket-forming tissue. Note bract and scale traces and two triangular sclerenchyma bundles accompanying scale trace. MPEF-Pb 5342 II. Scale bar = 2 mm. *C*, More proximal view of bract/scale complex than shown in *B* showing thin pocket-forming tissue overarching two collapsed seeds and partially fused sclerenchyma bundles accompanying scale trace (holotype). MPEF-Pb 3627 IV. Scale bar = 1 mm. *D*, Cross section of bract/scale complex of





**Fig. 6** *Pararaucaria delfueyoi* Escapa, Cúneo, Rothwell et Stockey, sp. nov. *A*, Details of bract/scale complex in cross section showing sclereids and poorly preserved parenchyma separating bract and scale traces and sclereids adaxial to scale trace of bundle before division into two strands (holotype). MPEF-Pb 3627 III. Scale bar = 1 mm. *B*, Details of ovuliferous scale histology in holotype showing differences between cells in abaxial region and those in adaxial region (including pocket-forming tissue). MPEF-Pb 3627 II. Scale bar = 1 mm. ab = abaxial tissue of ovuliferous scale; ad = adaxial tissue of the ovuliferous scale; b = bract; bt = bract trace; sc = sclereids; st = ovuliferous scale trace.

with a sinuous outer margin (fig. 5*B*, 5*C*). Longitudinal sections of the seeds reveal that they are inverted, with the micropyle (fig. 7*E*) directed toward the cone axis (fig. 7*A*), and

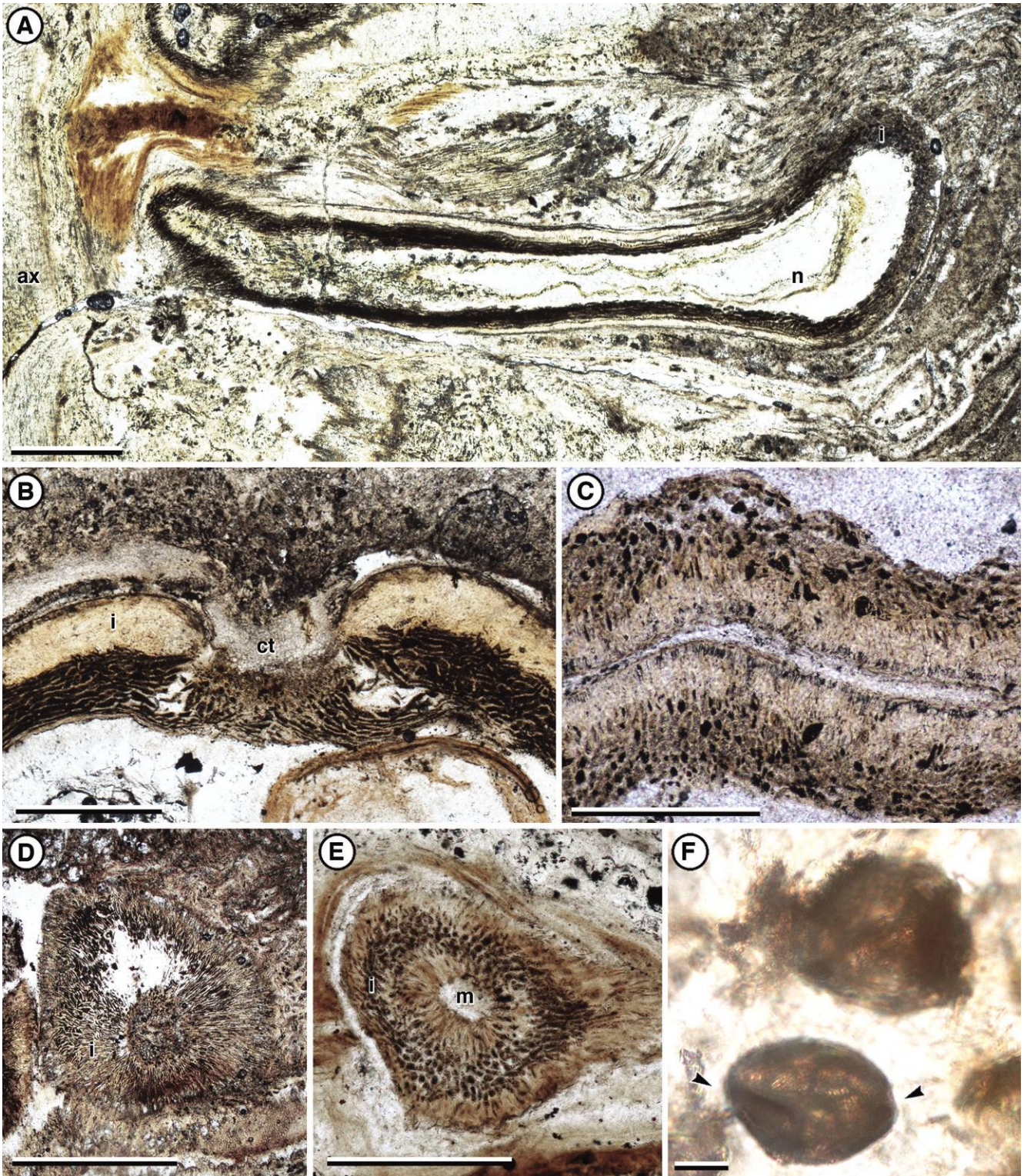
that they are attached at the chalaza (fig. 7*D*) to the inner surface of the distalmost tissue of the scale (fig. 7*B*). As seen in radial sections of the cone (fig. 2*B*), longitudinal sections that extend through the midregion for most of the length of the seeds never show the micropyle in longitudinal section (fig. 7*A*). Rather, those views usually show a micropyle in what approaches a cross section (fig. 7*C*). This suggests that the micropylar canal curves to the side as it extends from the seed body, such that the micropyles of adjacent seeds on each ovuliferous scale are oriented away from each other and toward the lateral margin of the ovuliferous scale. In cross sections the micropyle is round or oval in shape (fig. 7*E*). There is a zone of radially aligned cells at the point of seed attachment (fig. 7*B*) that is comparable to the closing tissue that commonly forms in the same position as in other living and fossil conifer seed cones and that is histologically comparable to the closing layer of an abscission zone.

The integument is multilayered, consisting of an outer epidermis of dark cells (fig. 7*B*, 7*C*) that often are difficult to distinguish from one another. Within the epidermis are one or two layers of transversely elongated palisade cells 100–120  $\mu\text{m}$  long that often are characterized by black contents in at least part of the lumen (fig. 7*B*, 7*C*). To the inside of the palisade is a zone of incompletely preserved, randomly oriented cells up 40  $\mu\text{m}$  in diameter that often have dark contents and that follow a sinuous course (fig. 7*B*–7*E*).

Interior to the integument is a nucellus and megaspore membrane that surrounds a large hollow central region (fig. 7*A*) that is interpreted to represent the megagametophyte in the precellular stage of development. No cellular megagametophytes or embryos like those of *P. patagonica* have been identified in seeds of *P. delfueyoi*. The nucellus extends from the chalaza to the micropylar region of the seeds as a narrow zone of incompletely preserved cells that are adjacent to the inner margin of the integument (fig. 7*A*). As with seeds of *P. patagonica*, an outer nucellar cuticle is absent below the micropylar region, and the nucellus appears to have been torn away from the integument (fig. 7*A*). Although the preservation is incomplete, currently available evidence indicates that the apex of the nucellus consists of a solid dome of parenchyma (fig. 7*A*, at left).

Within the micropylar region of one seed there are two subspheroidal bodies that may represent pollen grains (fig. 7*F*). The better preserved of these bodies has a maximum diameter of  $\sim 30 \mu\text{m}$  (fig. 7*F*, at bottom). It has a radial furrow parallel to the long axis of the oval that is located closer to one end than to the other (fig. 7*F*, at arrowheads). In the ground thin-section preparation of this cone, more detailed information about this body, such as a potential cryptospore, haptopypic mark, or internal striations, is not evident. However, information that is preserved is all consistent with these objects being pollen grains that have a rimula that separates a distal cap from the remainder of the pollen grain (fig. 7*F*, at arrowheads). These features allow this pollen to be inter-

holotype somewhat distal to the divergence from the cone axis showing extremely thin pocket-forming tissue and completely fused sclerenchyma bundles. MPEF-Pb 3627 III. Scale bar = 1 mm. b = bract; bt = bract trace; os = ovuliferous scale; st = ovuliferous scale trace; pft = pocket-forming tissue; s = seed; sc = sclereids.



**Fig. 7** *Pararaucaria delfueyoi* Escapa, Cúneo, Rothwell et Stockey, sp. nov. *A*, Longitudinal section of bract/scale complex showing inverted seed with micropylar end toward left. Note separation of nucellus from integument and central region that probably represents free nuclear stage of megagametophyte. MPEF-Pb 5341 IV. Scale bar = 1 mm. *B*, Detail of seed attachment showing closing tissue in attachment region and histology of integument. MPEF-Pb 3454 III. Scale bar = 1 mm. *C*, Detail of integument histology shown for two adjacent seeds. MPEF-Pb 5342 II. Scale bar = 0.5 mm. *D*, Cross section of seed near chalaza (holotype). MPEF-Pb 3627 II. Scale bar = 2 mm. *E*, Cross section of seed in micropylar region. MPEF-Pb 5341 IV. Scale bar = 0.02 mm. *F*, Putative *Classopolis* pollen in apical region of seed. Arrowheads indicate position of apparent cingulum. MPEF-Pb 5340 VI. Scale bar = 0.02 mm. ax = cone axis; ct = closing tissue; i = integuments; m = micropyle; n = nucellus.

puted as conforming to the sporae dispersae genus *Classopollis* Pflug (Traverse 1988), which is commonly found in compressed cheirolepidiaceous seed cones and is the defining structure of the conifer family Cheirolepidiaceae.

**Discussion**



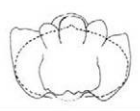
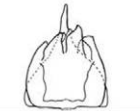
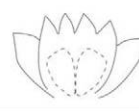

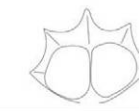
These new seed cones from the Cañadón Calcáreo Formation are assigned to the genus *Pararaucaria* of the Cheirolepidiaceae on the basis of numerous diagnostic morphological and anatomical characters, including (1) cylindrical seed cones with (2) helically arranged bract/scale complexes, (3) bract and ovuliferous scale almost entirely free from each other, (4) vascular traces of bract and ovuliferous scale that are independent for nearly their entire length, (5) bract broader than the ovuliferous scale, and (6) presence of a pocket-forming tissue partially covering the seeds. Diagnostic anatomical features that the new cones share with *Pararaucaria patagonica* include sclerenchyma bundles that accompany the ovuliferous scale trace (separating and becoming triangular distally), multilayered integument with a distinctive palisade adjacent to the epidermis, woody cone axis with a stellate pith that includes both parenchyma and sclereids, and loosely arranged sinuous cells of the pocket-forming tissue. All these features confirm a close relationship between *P. patagonica* and *Pararaucaria delfueyoi* and support assignment of *Pararaucaria* to the Cheirolepidiaceae (Escapa et al. 2012).

*Pararaucaria delfueyoi* is most easily distinguished from *P. patagonica* by the number of seeds per bract/scale complex (fig. 8) and the general dimensions of the seed cone. Seeds of *P. delfueyoi* also are consistently longer (i.e., up to 11 mm) than those of *P. patagonica* (i.e., 6 mm). There are additional subtle anatomical differences, such as the distinctive “I-beam” appearance of integumentary palisade cells in *P. patagonica* that are not present in *P. delfueyoi*. At present we do not

know whether those features represent structural differences or whether they result from differential preservation, as both species show palisade cells within this region of the integument. The specimens of *P. delfueyoi* are derived from the Late Jurassic of Chubut Province, and those of *P. patagonica* are from the Middle Jurassic of Santa Cruz Province.

Most specimens of *P. patagonica* have only one seed per bract/scale complex (rarely there are two; Wieland 1935; Stockey 1977), but all examined specimens of *P. delfueyoi* consistently show two (see fig. 8). Wieland (1935) interpreted the infrequent occurrence of two-seeded ovuliferous scales in *P. patagonica* to indicate the ancestral condition for the species. More recently, the variable number of seeds per bract/scale complex in *Hirmeriella muensterii* cones has been suggested (Clement-Westerhof and van Konijnenburg-van Cittert 1991) to relate to differential developmental pathways. Whereas the seed cones of Cheirolepidiaceae appear to have two sites of seed initiation on each ovuliferous scale, only one seed matures in some instances, while both mature in others (Clement-Westerhof and van Konijnenburg-van Cittert 1991; Escapa et al. 2012). The consistent presence of two seeds in *P. delfueyoi*, while only one is present in nearly all examined specimens of *P. patagonica*, represents a specifically diagnostic developmental character for distinguishing these two species.

Escapa et al. (2012) demonstrated that *P. patagonica* is assignable to the Cheirolepidiaceae on the basis of the presence of distal lobes of the ovuliferous scales and enclosure of the seeds by pocket-forming tissues of the ovuliferous scale. Because of the considerable abrasion of all cones assignable to *P. delfueyoi*, the former diagnostic character is not available for the new species. Nevertheless, specimens of *P. delfueyoi* can be assigned to both the genus *Pararaucaria* and the family Cheirolepidiaceae with confidence because of a diagnostic suite of internal characters that are comparable to *P. patagonica*. Perhaps the most diagnostic of these characters is the pocket-forming tissue that overarches and encloses the seeds (Escapa

	<i>Pararaucaria delfueyoi</i>	<i>Pararaucaria patagonica</i>	<i>Hirmeriella muensterii</i>	<i>Kachaikostrobus acuminatus</i>	<i>Tomaxellia biforme</i>	<i>Alvinia bohémica</i>	<i>Pseudohirmeriella delawarensis</i>
							
Age and distribution	Jurassic, South America	Jurassic, South America	Jurassic, Europe	Cretaceous, South America	Cretaceous, South America	Cretaceous, Europe	Triassic, North America
PFT	Present	Present	Present	Present	Present	Present	Absent
OS adaxial lobes	(?)	1 central (undiv.) 2 lateral	1 central (div.) 2 lateral	1 central (div.) 2 lateral	1 central (div.) 2 (?)lateral	1 central (undiv.) 2 lateral*	1 central (div.) (?)
OS abaxial	(?)	Absent	Present (1)	Present (3)	Absent (?)	Absent	Absent
Bract	Present	Present	Present	Present	Present	Present	Absent
Bract/scale fusion	Present, at the base only	Present, at the base only	Present, at the base only	Present, at the base only	Absent, or fused at the base only	Present, at the base only	Absent
Ovules per OS	2	1 or 2	1 or 2	? (1-2)	2	1 or 2	2

**Fig. 8** Comparison of morphological features of selected cheirolepidiaceous seed cones (modified from Escapa et al. 2012). *Hirmeriella muensterii*, modified from Clement-Westerhof and van Konijnenburg-van Cittert (1991); *Kachaikostrobus acuminata*, taken from Del Fueyo et al. (2008); *Tomaxellia biforme*, line drawings based on original description and illustrated specimens (Archangelsky 1968, pl. 1, figs. 4, 5); *Alvinia bohémica*, from Kvaček (2000); *Pseudohirmeriella delawarensis*, modified from Axsmith et al. (2004). An asterisk indicates that Kvaček (2000) considered the two lateral lobes of *Alvinia bohémica* to be abaxial. However, they are comparable to the lateral adaxial lobes of the other species. div. = divided; PFT = pocket-forming tissue; OS = ovuliferous scale; undiv. = undivided.

et al. 2012). Additional characters that unite these species include the bract and scale separating near the cone axis, the bract being broader than the ovuliferous scale, the bract and scale trace diverging from the stele of the axis as a cylinder and immediately separating into separate bundles, the sclerenchyma bundle(s) that accompany the ovuliferous scale trace, and the characteristic histological features of the seed integument. Structural diversity and generic comparisons of *P. patagonica* to other cheirolepidaceous seed cones recently have been detailed by Escapa et al. (2012). We have added the features of *P. delfueyoi* to this comparison to further emphasize the familial and generic relationships of this new species (fig. 8).

Our understanding of the preservational and taphonomic histories for *Pararaucaria* cones from the two different sources remains incomplete. Nevertheless, it is clear that those differences have led to the preservation of some features in each species that also can be expected to have occurred in the other. For example, the less abraded ovuliferous scale apexes in some specimens have allowed for identification of separate apical lobes in *P. patagonica* that probably also occur in unabraded cones of *P. delfueyoi*. *Pararaucaria patagonica* seeds contain polycotyledonary embryos that are not known for *P. delfueyoi*, but the latter species has better preservation of some histological details. These features include the changes in the bract/scale vascularization from the base to more distal levels (figs. 5A–5D, 6A), the closing tissue at the point of attachment for the seeds (fig. 7B), and a cellular apical region of the nucellus (fig. 7A). The absence from *P. delfueyoi* of the characteristic I-beam shape of integumentary cells that characterize *P. patagonica* also may reflect differential preservation for cones, as both species have palisade cells in this region of the integument. The presence of a putative *Classopollis*-type pollen grain within the micropylar region of a *P. delfueyoi* seed is also a relevant character linking these cones to the Cheirolepidaceae.

Two clearly differentiated histological regions are preserved in different areas of the ovuliferous scales of both *P. patagonica* and *P. delfueyoi*. Most clear, in both species, is the difference between cells at the base of the ovuliferous scale (fig. 6B, at bottom) and those that form the pocket-forming tissue lateral to (fig. 6B, at top) and overarched (fig. 5A, at top) the seeds. Histological variations also are evident between the central and lateral regions of the ovuliferous scale tissue of *P. patagonica* as seen in cross sections at the midlevel (i.e., fig. 14 of Escapa et al. 2012). Those differences define different histological regions that are immediately proximal to the central lobe and the more abaxially disposed lateral ovuliferous scale lobes of that species. This suggests that the presence of lobed ovuliferous scales can be determined from anatomical features, even if specimens become highly abraded. The ovuliferous scale lobes of compressed cheirolepidaceous seed cones (e.g., *Alvinia bohemica*, *Hirmeriella munsteri*, *Kachaikostrobus acuminatus*) also show differences in position, with some being more abaxial and others being more adaxial (Jung 1968; Alvin 1982; Clement-Westerhof and van Konijnenburg-van Cittert 1991; Kvaček 2000; Del Fueyo et al. 2008), suggesting an additional homology between anatomically preserved and compressed cone ovuliferous scale.

An overview of conifer diversity reveals transformational series of seed cone structure that have been used to infer both the origin of crown group morphologies and the overall pattern of conifer evolution through time (Florin 1938–1945, 1951; Vázquez-Lobo et al. 2007; Rothwell et al. 2009, 2011; Serbet et al. 2010). However, there are large morphological gaps between different conifer clades, and these gaps leave in doubt both the homologies and the pattern of evolution for many structures. Recent improvements to the understanding of *Pararaucaria* (Escapa et al. 2012; this article) provide a more accurate picture of the homologies of some cone structures and therefore for the phylogenetic relevance of the Cheirolepidaceae. For example, the ovuliferous scale tissue that overarches and encloses seeds in Cheirolepidaceae, which we refer to as pocket-forming tissue, has potential homologies to the seed wing of Pinaceae and/or to the epimatium of Podocarpaceae and possibly also to seed-enclosing tissue of the genus *Araucaria* (Araucariaceae).

In Pinaceae, seed cones have a large number of helically arranged bract/scale complexes that are separate structures from near their bases, and the ovuliferous scale is characteristically much larger than the bract (but see *Eathiestrobus* Rothwell, Mapes, Stockey et Hilton 2012), with the seed wing being widely regarded as modified scale tissue (Miller 1988). By contrast, in Podocarpaceae seed cones typically have a small number of bract/scale complexes (but see *Saxegothaea* for larger numbers of cone parts; Farjon 2010), which are separate structures from near their base to their tips, and in almost all the genera, the ovuliferous scale overarches and partly encloses the seed to form an epimatium. Seed cones of *Araucaria* (Araucariaceae) show a third novel suite of characters that include a large number of helically arranged bract/scale complexes, where the bract and scale are fused throughout most or all of their length and the seed may be largely enclosed in scale tissue (i.e., *Araucaria* spp.; Hirmer 1936).

Has the pocket-forming tissue of Cheirolepidaceae been transformed through time to produce the seed wing of Pinaceae, and/or the epimatium of Podocarpaceae, and/or the seed-enclosing scale tissue of *Araucaria*? At present we do not know to which, if any, of these characteristic seed cone structures in Pinaceae, Podocarpaceae, and Araucariaceae the pocket-forming tissue of Cheirolepidaceae may be homologous. In part, this is because the morphological gaps between species of these families are too large to confidently assess homologies of the seed-enclosing tissues. Although much work remains before these questions can be confidently answered, the fossil record has great potential for providing the required information. Several empirical and theoretical studies have convincingly demonstrated the crucial role of fossils in phylogenetic reconstruction (Gauthier et al. 1988; Donoghue et al. 1989; Escapa and Pol 2011). In this regard, continued descriptions, documentation, and additions to the conifer fossil record are crucial for providing new structural intermediates that demonstrate the order in which various anatomical and morphological transformations have occurred in each lineage and thereby for establishing the overall pattern of conifer evolution.

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