Seed cone anatomy of Cheirolepidiaceae (Coniferales): Reinterpreting *Pararaucaria patagonica* Wieland[1]

Ignacio H. Escapa[2,5,6], Gar W. Rothwell[3,4], Ruth A. Stockey[3], and N. Rubén Cúneo[2]

[2]CONICET-Museo Paleontologico Egidio Feruglio, Av. Fontana 140, Trelew, Chubut 9100, Argentina; [3]Department of Botany and Plant Pathology, 2082 Cordley Hall, Oregon State University, Corvallis, Oregon 97331 USA; [4]Department of Environmental and Plant Biology, Ohio University, Athens, Ohio 45701 USA; and [5]Department of Biological Sciences, University of Alberta, Edmonton, Alberta AB T6G 2E9, Canada

• *Premise of the study:* Seed cone morphology and anatomy reflect some of the most important changes in the phylogeny and evolutionary biology of conifers. Reexamination of the enigmatic Jurassic seed cone *Pararaucaria patagonica* reveals previously unknown systematically informative characters that demonstrate affinities with the Cheirolepidiaceae. This paper documents, for the first time, internal anatomy for seed cones of this important extinct Mesozoic conifer family, which may represent the ghost lineage leading to modern Pinaceae.

• *Methods:* Morphology and anatomy of cones from the Jurassic La Matilde Formation in Patagonia are described from a combination of polished wafers and thin section preparations. New photographic techniques are employed to reveal histological details of thin sections in which organic cell wall remains are not preserved. Specific terminology for conifer seed cones is proposed to help clarify hypotheses of homology for the various structures of the cones.

• *Key results:* Specimens are demonstrated to have trilobed ovuliferous scale tips along with a seed enclosing pocket of ovuliferous scale tissue. Originally thought to represent a seed wing in *P. patagonica*, this pocket-forming tissue is comparable to the flap of tissue covering seeds of compressed cheirolepidiaceous cones and is probably the most diagnostic character for seed cones of the family.

• *Conclusions: Pararaucaria patagonica* is assigned to Cheirolepidiaceae, documenting anatomical features for seed cones of the family and providing evidence for the antiquity of pinoid conifers leading to the origin of Pinaceae. A list of key morphological and anatomical characters for seed cones of Cheirolepidiaceae is developed to facilitate assignment of a much broader range of fossil remains to the family. This confirms the presence of Cheirolepidiaceae in the Jurassic of the Southern Hemisphere, which was previously suspected from palynological records.

Key words: Cheirolepidiaceae; conifers; Jurassic; *Pararaucaria*; Patagonia; seed cones.

Throughout the evolutionary history of conifers phylogenetically informative changes have been disproportionally concentrated in the seed cone, the structure of which is usually diagnostic of generic and/or familial relationships (e.g., Florin, 1951; Miller, 1977; Page, 1990; Serbet et al., 2010; Rothwell et al., 2009). As illustrated by transformational series of modifications, the different "structural components" of the seed cone have been permanently altered, providing a suite of synapomorphies that help to explain the pattern of phylogeny for the group (Chamberlain, 1935; Florin, 1951; Serbet et al., 2010; Rothwell

et al., 2011). Fossil seed cones of *Pararaucaria patagonica* Wieland studied herein provide the first evidence for internal anatomy of the dominant extinct Mesozoic conifer family Cheirolepidiaceae, Takhtajan thus helping characterize an important ghost lineage of conifers and further clarifying the overall pattern of conifer phylogeny through time (Rothwell et al., 2009).

Pararaucaria patagonica was first described from anatomically preserved conifer seed cones of uncertain systematic affinities from the famous Jurassic Cerro Cuadrado petrified forest of Santa Cruz, Patagonia, Argentina. Following the initial description of this species by Wieland (1929, 1935), thorough descriptions were provided by Calder (1953) and Stockey (1977), and the cones have been discussed by additional authors (e.g., Archangelsky, 1968; Miller, 1977). However, there are several divergent interpretations of the affinities of *P. patagonica* that derive from different interpretations of cone structure, and systematic relationships of the species remain uncertain (Calder, 1953; Taylor et al., 2009). Over the years *P. patagonica* has been recognized as being similar to, or has been assigned to, several conifer families including Araucariaceae (Wieland, 1929, 1935; Calder, 1953), Cheirolepidiaceae (Wieland, 1935; Archangelsky, 1968), Pinaceae (Smith and Stockey, 2001, 2002), Taxodiaceae (= basal Cupressaceae; Calder 1953; Stockey, 1977), and Voltziaceae (Miller, 1999). Some authors have suggested that *Pararaucaria* cones represent a distinct family of conifers (e.g., Stockey, 1977; Taylor et al., 2009; Falaschi et al., 2011) or have a structure that is intermediate between

families, based on features of the ovuliferous scale, putative seed wing, cone vascularization, and histology.

Pararaucaria patagonica previously has been distinguished from seed cones of the Cheirolepidiaceae by an ovuliferous scale that is not dissected into lobes and by the absence of an adaxial flap of scale tissue enclosing the seed or seeds (e.g., Jung, 1968; Clement-Westerhof and van Konijnenburg-van Cittert, 1991; Del Fueyo et al., 2008). In addition, *P. patagonica* is described as having a seed wing, a structure that is absent from cheirolepidiaceous seed cones. Whereas *P. patagonica* typically has only one seed per cone-scale complex, cheirolepidiaceous seed cones frequently have two. However, in many cheirolepidiaceous cones only one seed matures while the other aborts (Clement-Westerhof and van Konijnenburg-van Cittert, 1991). Likewise, there is a small number of *P. patagonica* cones with two seeds per scale (Wieland, 1935; Calder, 1953; Stockey, 1977). Making close comparisons of *P. patagonica* to seed cones of the Cheirolepidiaceae has been difficult since *P. patagonica* is anatomically preserved and displays a largely disjunct set of characters as compared to all known specimens of the Cheirolepidiaceae, which are known from coalified compressions or impressions (e.g., Clement-Westerhof and van Konijnenburg-van Cittert, 1991).

During a comprehensive reexamination of Jurassic fossil plants from Patagonia, a large number of new specimens of *Pararaucaria patagonica* and a newly recognized species of the genus (which is being described elsewhere) have been assembled and prepared (Escapa, 2009). Together with previously described cones (Wieland, 1935; Stockey, 1977) and several specimens from La Plata Museum, Argentina, this new collection forms the basis for a thorough reevaluation and reinterpretation of *Pararaucaria*. Most significantly, the material includes some largely unweathered specimens of *P. patagonica* that display external features with dissected ovuliferous scales, while other cones preserve superb anatomical characters that together allow for a thorough characterization and reinterpretation of both ovuliferous scale morphology and the tissue that has previously been interpreted as a seed wing.

Although some earlier workers have suggested that *P. patagonica* may be related to the Cheirolepidiaceae (e.g., Wieland, 1935; Archangelsky, 1968), the newly recognized characters described here fully reconcile previously inferred differences between seed cones of the Cheirolepidiaceae and *P. patagonica*. These data provide the first evidence for anatomically preserved cheirolepidiaceous seed cones and new anatomical information about the ovuliferous scale and seed integument for emending the diagnosis of *P. patagonica*. They also corroborate presence of the family in pre-Cretaceous deposits of South America that previously have been based on dispersed pollen (i.e., *Classopollis* spp.; Quattrocchio et al., 2007 and citations therein).

MATERIALS AND METHODS

This study is based on three collections of anatomically preserved fossil seed cones that all conform to *Pararaucaria patagonica* Wieland. The specimens are from three stratigraphically contemporaneous localities of the La Matilde Formation (de Barrio et al., 2000) in Santa Cruz province of southern Patagonia (Wieland, 1935; Calder, 1953; Stockey, 1977) and are permineralized within a silicate matrix. The original organic matter is no longer present in the cones, probably due to leaching by ground water. Individual cones also have been subjected to varying degrees of postpreservational transport, and the outer cone surfaces have been abraded to varying degrees.

One group of cones, housed at the Field Museum of Natural History, Chicago, Illinois, USA (FMNH), was collected at Cerro Cuadrado (see Panza and Genini, 2001), and studied earlier by both Wieland (1935) and Stockey (1977). These specimens preserve excellent anatomical detail, but are weathered to a degree that external features of bract and scale tips are absent (i.e., plate 2: fig. 1, plate 2: figs. 3–6, 8–10, plate 4: fig. 1 of Wieland, 1935; figs. 1, 2 of Stockey, 1977). Specimens housed at the Facultad de Ciencias Naturales y Museo, La Plata, Argentina (LPPB) and the Museo Paleontológico Egidio Feruglio, Trelew, Argentina (MPEF) are from the Alma Gaucha and Puchulú localities. Cones from those sources do not preserve internal anatomy as completely as the Cerro Cuadrado specimens, but some are less abraded externally and thus reveal more of the external morphological features of the bracts and ovuliferous scale tips.

The area where the fossils occur occupies the central part of Santa Cruz Province in southern Patagonia, geologically known as the Deseado Massif. Massive volcanic events during the Jurassic formed the Chon-Aike volcanic province (Kay et al., 1989), a region that extends from the Atlantic Ocean through the Andes. These events deposited several square kilometers of mostly acidic lavas and pyroclastic rocks known as the Bahia Laura Group (Pankhurst et al., 1998; Guido, 2004) and represent the source for silica responsible for the plant permineralization process in the whole area.

The Bahía Laura Group overlies the early Jurassic Bajo Pobre Formation and unconformably underlies the early Cretaceous Baqueró Group (de Barrio et al., 2000). The Bahía Laura Group is in turn subdivided into the La Matilde Formation, which preserves *Pararaucaria patagonica* seed cones, and the Chon-Aike Formation. The volcaniclastic deposits of the La Matilde Formation are interbedded with rhyolitic to dacitic lavas and ignimbrites of the Chon-Aike Formation (Pankhurst et al., 1998; Panza and Genini, 2001; Guido, 2004). Even though this stratigraphic division is based on exposures at the eastern border of the Deseado Massif, the pertinent facies also can be recognized in central and western areas of Santa Cruz Province, where the localities bearing *Pararaucaria* seed cones are located. On the basis of fossil plant content and the regional geological context, the La Matilde Formation was previously considered to be Middle Jurassic (Callovian) in age (Stipanicic and Bonetti, 1970). More recently, based on radiometric dating, and in spite of some local diachronism, a 10 Myr span between 172 and 162 Myr (Bajocian-Callovian Stages) seems to be the most plausible time of accumulation for the entire volcanic complex of the Bahía Laura Group (Pankhurst et al., 2000).

External features of the cones were photographed, and selected specimens were wafered in either cross or longitudinal section. Wafers were attached to glass slides with epoxy, ground thin enough to transmit light, and cover slips were affixed with Eukitt (O. Kindler GmbH and Co., Freiburg, Germany). Other specimens were cut into a small number of thick sections and polished to reveal features on smooth surfaces. Images were captured using a Photophase (Phase One A/S, Frederiksberg, Denmark) digital scanning camera mounted on a Leitz Aristophot bellows camera and a Canon Power Shot SX100 IS digital camera. External cone surfaces and thick sections were photographed using reflected light. Some thin sections were photographed using transmitted light, while others were placed on a black background and photographed with reflected light to reveal histological details of cell walls from which organic matter has been lost.

SYSTEMATICS

Order—Coniferales

Family—Cheirolepidiaceae Takhtajan

Genus—*Pararaucaria* Wieland

Emended generic diagnosis—Seed cones consisting of woody axes from which numerous bract/ovulifersous scale complexes diverge in helical phyllotaxis. Round bract trace diverging from cone axis separately from inverted U-shaped ovuliferous scale trace; prominent sclerenchyma strand or strands accompanying ovuliferous scale trace. Bract broad and thin, separating from ovuliferous scale near base and free distally. Ovuliferous scales with free distal lobes and adaxial pocket opening basally. Cones with either one or two inverted, unwinged seeds attached at chalaza within pocket of ovuliferous scale tissue.
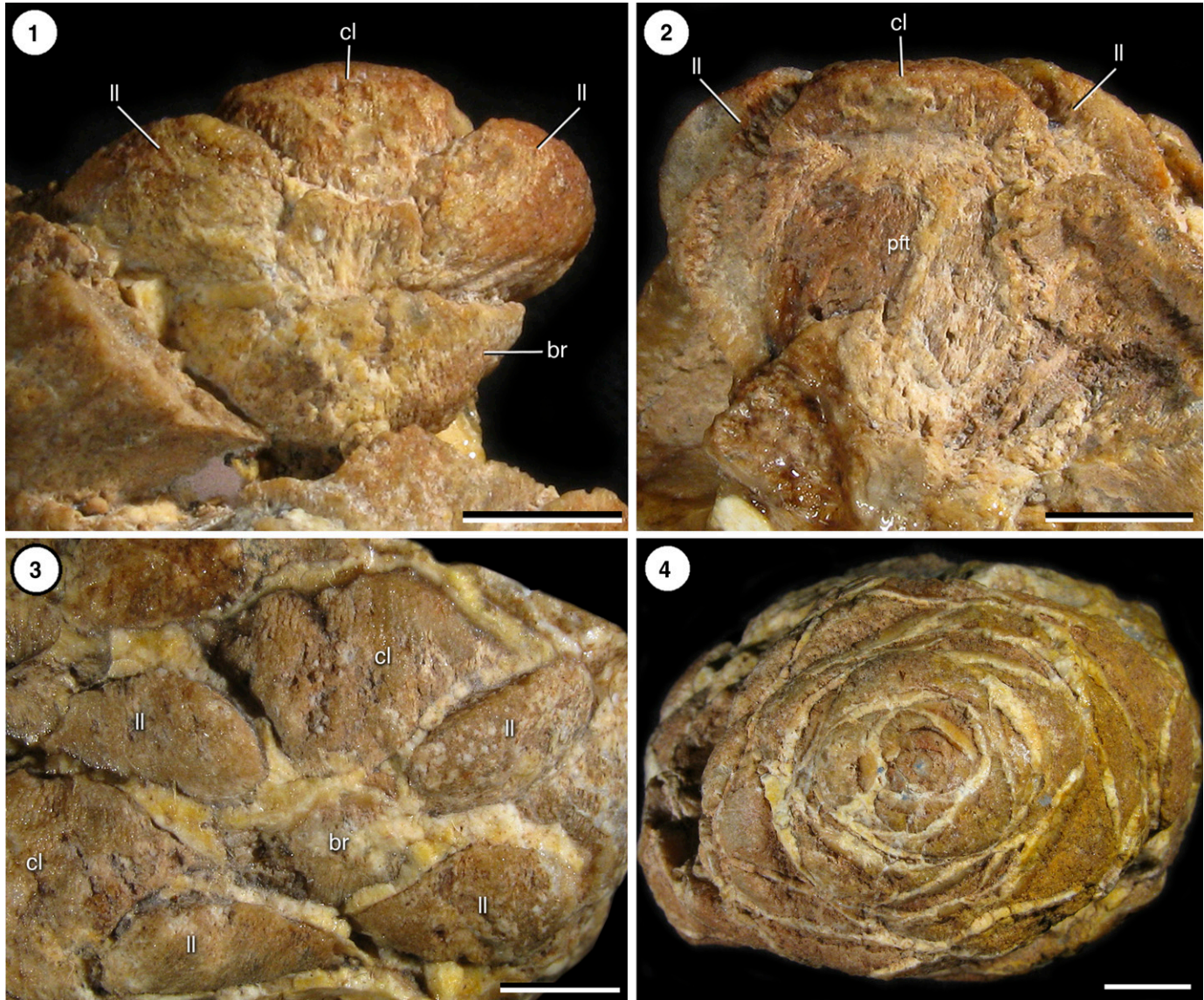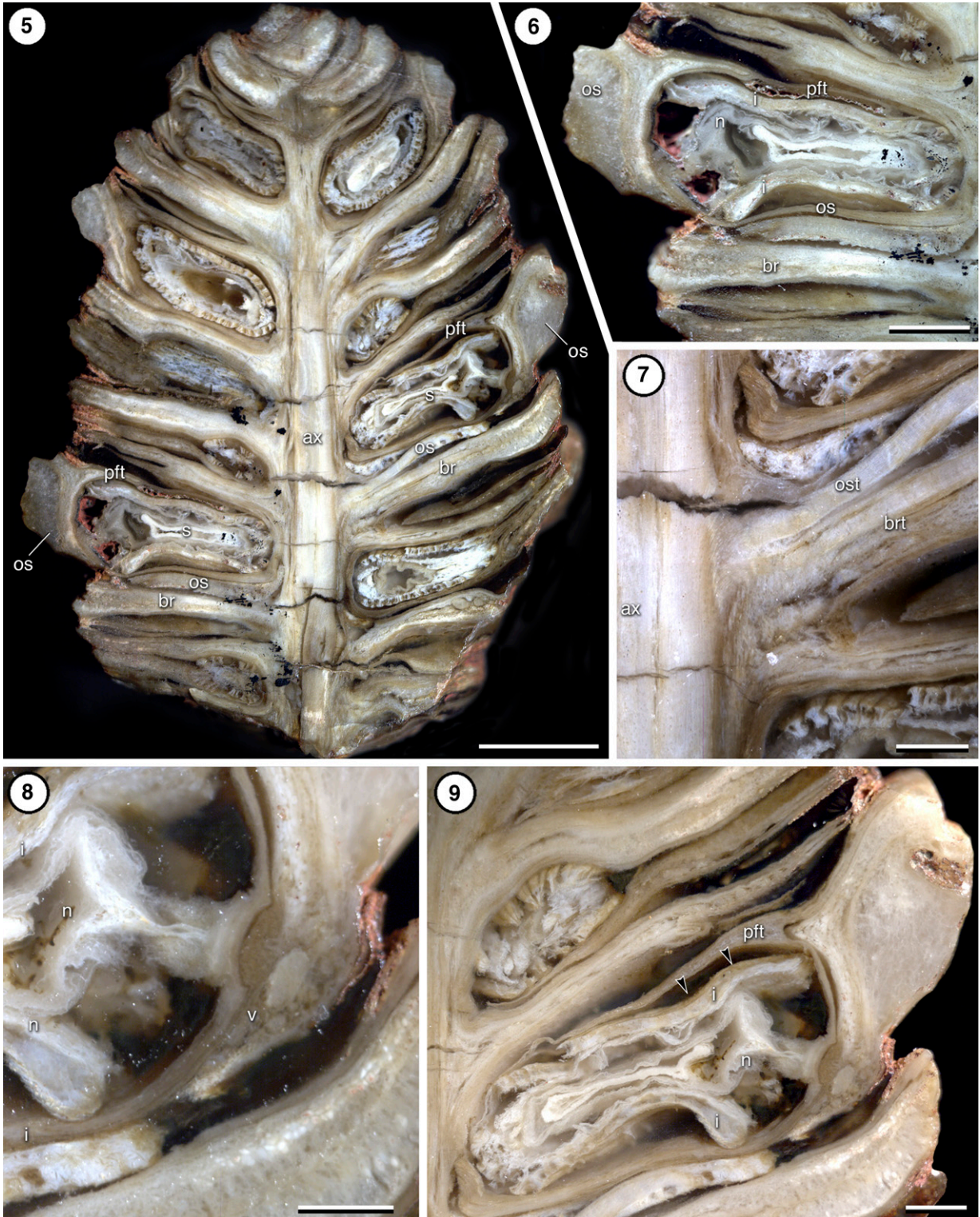
Figs. 1–4. *Pararaucaria patagonica* Wieland. **1.** Cone fragment showing cone-scale complex in front view, as seen from outside of cone, showing central and lateral lobes of ovuliferous scale and subtending bract. LPPB-122. Scale bar = 5 mm. **2.** Same cone-scale complex as in Fig. 1 from top view showing central and lateral ovuliferous scale lobes and pocket-forming tissue as seen from adaxial side of complex. LPPB-122. Scale bar = 5 mm. **3.** Surface view of cone fragment showing components of cone-scale complexes. Note vertical striations (cell files) on surface of ovuliferous scale lobes. LPPB-146a. Scale bar = 5 mm. **4.** Seed cone in apical view showing helically arranged cone-scale complexes. LPPB-146b. Scale bar =1 mm. br = bract, cl = central ovuliferous scale lobe, ll = lateral ovuliferous scale lobe, pft = pocket-forming tissue.

Species—*Pararaucaria patagonica* Wieland

Emended specific diagnosis—Cylindrical, conical, or ovoid cones 2.3–5.1 cm long, 1.3–3.0 cm wide; slender axis with helically arranged bract/scale complexes consisting of large ovuliferous scale with three distal lobes subtended by broad flattened woody bract. Scale trace flanked by two triangular sclerenchyma bundles within cone axis and basal region of ovuliferous scale. Spongy adaxial tissue toward apex of central scale lobe extending basally, overarching and forming seed enclosing pocket. Overarching adaxial pocket-forming tissue thinning toward base of scale and terminating near level of seed micropyle. Most cones with one seed per scale, others cones with two seeds per scale; single seed heart-shaped ca. 6 mm long oriented obliquely to long axis of scale, paired seeds narrower, oriented parallel to long axis of scale. Outer integumentary zone of one or two palisade layers and interdigitating, radially elongate cells forming distinct I-beam shape in cross sections.

Discussion of terminology employed—From the extensive work of Rudolph Florin (1938–1945, 1951, 1963), a general consensus has developed in which ovulate conifer cones are regarded as typically compound (i.e., composed of two branching orders), and as derived from the basic morphology of Paleozoic Cordaitales. However, recent contributions show that the original transformational series suggested by Florin, although highly useful as a starting point, may not explain the whole spectrum of seed cone structure that characterizes both extant and fossil conifers

Figs. 5–9. *Pararaucaria patagonica* Wieland. FMNH-P13978. **5.** Midlongitudinal section of cone showing bracts and ovuliferous scale complexes with attached inverted seeds. Scale bar = 5 mm. **6.** Longitudinal section of cone-scale complex showing bract subtending ovuliferous scale with one attached seed. Note pocket-forming tissue of ovuliferous scale on adaxial side of seed. Scale bar = 2 mm. **7.** Radial section of cone showing vascular tissue of bract and scale at the level of divergence from cone axis. Scale bar = 1 mm. **8.** Longitudinal section of seed at level of attachment to ovuliferous scale. Note vascular bundle of scale, nucellus, and base of integument, which has separated from chalaza in this specimen. Scale bar = 1 mm. **9.** Longitudinal section of ovuliferous scale complex showing pocket-forming tissue of ovuliferous scale extending toward micropylar end of seed. Note how pocket-forming tissue thins and terminates toward seed apex. Arrowheads indicate outer surface of seed integument. Scale bar = 1 mm. ax = cone axis, br = bract, brt = bract trace, i = integument, n = nucellus, os = ovuliferous scale, ost = ovuliferous scale trace, pft = pocket-forming tissues, v = vascular bundle.

(see discussions in Hernandez-Castillo et al., 2001; Tomlinson and Takaso, 2002; Farjon and Ortiz Garcia, 2003; Escapa et al., 2008; Serbet et al., 2010; Rothwell et al., 2011), and does not adequately convey the parallel evolutionary radiations in cone structure that most certainly have led to the various cone morphologies that are considered to have evolved from Voltziales.

Specific terminology used to describe different seed cone parts derives from specific hypotheses of homology for cones of each family, and these need to be clarified to avoid misinterpretations. In this regard, the following is a list of concepts and hypothesized homology relationships employed in the current study:

Bract—The bract is the leaf homologue born at each node on a seed cone axis, in the axil of which either a dwarf shoot or an ovuliferous scale is borne.

Ovuliferous scale—The term "ovuliferous scale" (or simply "scale") frequently has been used for two different types of structures that are not fully homologous. In Paleozoic conifers and coniferophytes (e.g., *Cordaianthus* Grand-Eury, *Barthelia* Rothwell et Mapes, *Otovicia* Kerp, Poort, Swinkels et Verwer, *Thucydia,* Hernandez-Castillo, Rothwell et Mapes.), the term scale is used for every leaf homologue born on the secondary axis (or "dwarf shoot") of compound cones. Such scales can either be vegetative scales or ovule-bearing sporophylls. By contrast, several species of Permian Voltziaceae, as well as more recent conifers of the Mesozoic, Tertiary, and Recent bear ovuliferous complexes with highly variable, and presumably, extensively modified morphologies. It is generally accepted the structure in the axil of the bract (or adnate to the bract) and termed "ovuliferous scale" (or merely "scale") is homologous to the dwarf shoot of the Paleozoic taxa.

Bract/scale complex—The term "bract/scale complex" (= cone-scale complex of some authors) refers to the lateral, ovule-bearing structures emerging from the cone axis at a single node. This typically includes a bract and an axillary seed-bearing structure (or ovuliferous scale) that is interpreted as being derived from the fertile axillary dwarf shoot like those of cordaitaleans or walchian conifers. These may be free from each other, partially fused, or completely fused to each other. The term "cone scale" has been variously used by authors to refer to the cone-scale complex, while others loosely use "cone scale" to refer to only the ovuliferous scale.

Epimatium—The term "epimatium" is commonly used for the enlargement subtending each seed in living species of Podocarpaceae and is considered to be homologous to the ovuliferous scale of other conifers (de Laubenfels, 1988). In the past, "epimatium" also has been employed for the flap of tissue that covers the ovules in some species of Cheirolepidiaceae (e.g., Clement-Westerhof and van Konijnenburg-van Cittert, 1991; Del Fueyo et al., 2008), which represents only part of the ovuliferous scale and therefore is not homologous to the epimatium of podocarps. Therefore, in this paper, we use the more neutral and descriptive terminology "pocket-forming tissue" for the flap of tissue or pocket that encloses the seed or seeds on the adaxial side of the ovuliferous scale.

RESULTS

General focus and features—Most facets of cone morphology and anatomy of *Pararaucaria patagonica* have been thoroughly described and evaluated by Wieland (1929, 1935),

Calder (1953), and Stockey (1977), so the description that follows focuses primarily on those characters that either have not previously been observed or are being reinterpreted in the present study. The most important of these is the occurrence of free distal lobes of the ovuliferous scales (Figs. 1–3), adaxial scale tissue enclosing one or two seeds (i.e., "pocket-forming tissue"; Figs. 5, 6, 9, 10, 12–14) that previously has been interpreted as a seed wing, and histology of the wingless seed integument (Figs. 11, 13, 14).

Pararaucaria patagonica cones show helical arrangement of the cone-scale complexes from both external (Fig. 4) and internal (Figs. 5, 10) views. Complexes consist of a flattened bract that subtends an ovuliferous scale bearing either one (Fig. 14) or two (Fig. 13) inverted seeds (Figs. 5, 6, 10, 12). Bracts almost always show a smoothly rounded apex (Fig. 4), but that configuration is the result of abrasion. Internally, the cone has a central axis with a broad zone of secondary xylem (Fig. 5). Bract and scale traces appear to diverge together (Fig. 5), forming a ring of tissue in tangential sections (Fig. 10, at center), but close examination reveals that this configuration consists of a round bract trace that is separated from an inverted U-shaped scale trace by a few parenchyma and sclerenchyma cells (Calder, 1953; Stockey, 1977). Therefore, the bract and scale traces are separate from their origin at the axis stele. A distinctive pair of triangular sclerenchyma strands accompanies the scale trace through the cortex of the axis and basal region of the ovuliferous scale (Figs. 13, 14).

Bract/scale complexes—Whereas previously described specimens of *P. patagonica* all have been eroded to a degree that the ovuliferous scales appear to consist of a single unit (e.g., plate 2, fig. 1 of Wieland, 1935), a small number of cones and cone fragments from the Alma Gaucha locality that are less eroded reveal that each scale is divided at the apex into three free distal lobes (Figs. 1–3). There are two lateral lobes that lie somewhat abaxial to the plane of a broad central lobe (Fig. 1). The bract extends up to about the level of scale dissection in the mid region of the cone (Figs. 2, 3), but the exact level is difficult to determine because bract tips are all eroded to varying degrees (Figs. 1, 3). Toward the apex of the cone only the abaxial surfaces of ovuliferous scale tips are exposed (Fig. 4). External views of the bracts and ovuliferous scales show longitudinal striations (Figs. 1–3) that are formed by cellular patterns at the surface of the organs.

Lobed ovuliferous scale tips—Individual ovuliferous scales measured from external surfaces of cones are up to 17 mm wide, and the free lobes are up to 6 mm long. Lateral lobes usually appear rounded at the apex and ca. 0.5 mm thick, but a small number of lateral lobes seen in surface view show that they continued to thin toward a pointed apex (Fig. 15). The central lobe is wider and thicker than the lateral lobes, up to 11 mm wide, and usually has a gently rounded apex (Fig. 5 at right, 12, 15) up to 1.5 mm thick.

Tissue of the distal lobe appears aerenchymatous (Figs. 10, 12–14). Stockey (1977) has described histology on the abaxial side of the scale near the seed chalaza (originally interpreted as a seed wing) as consisting of anastomosing rows of glandular hairs with patches of thin-walled cells and many intercellular spaces. Abaxial to this tissue in longitudinal sections is a dense tissue that occurs in a line beneath the seed and distal to the seed enclosing pocket and that extends vertically and outward into the distal lobe (Figs. 10, 12). High magnification views of
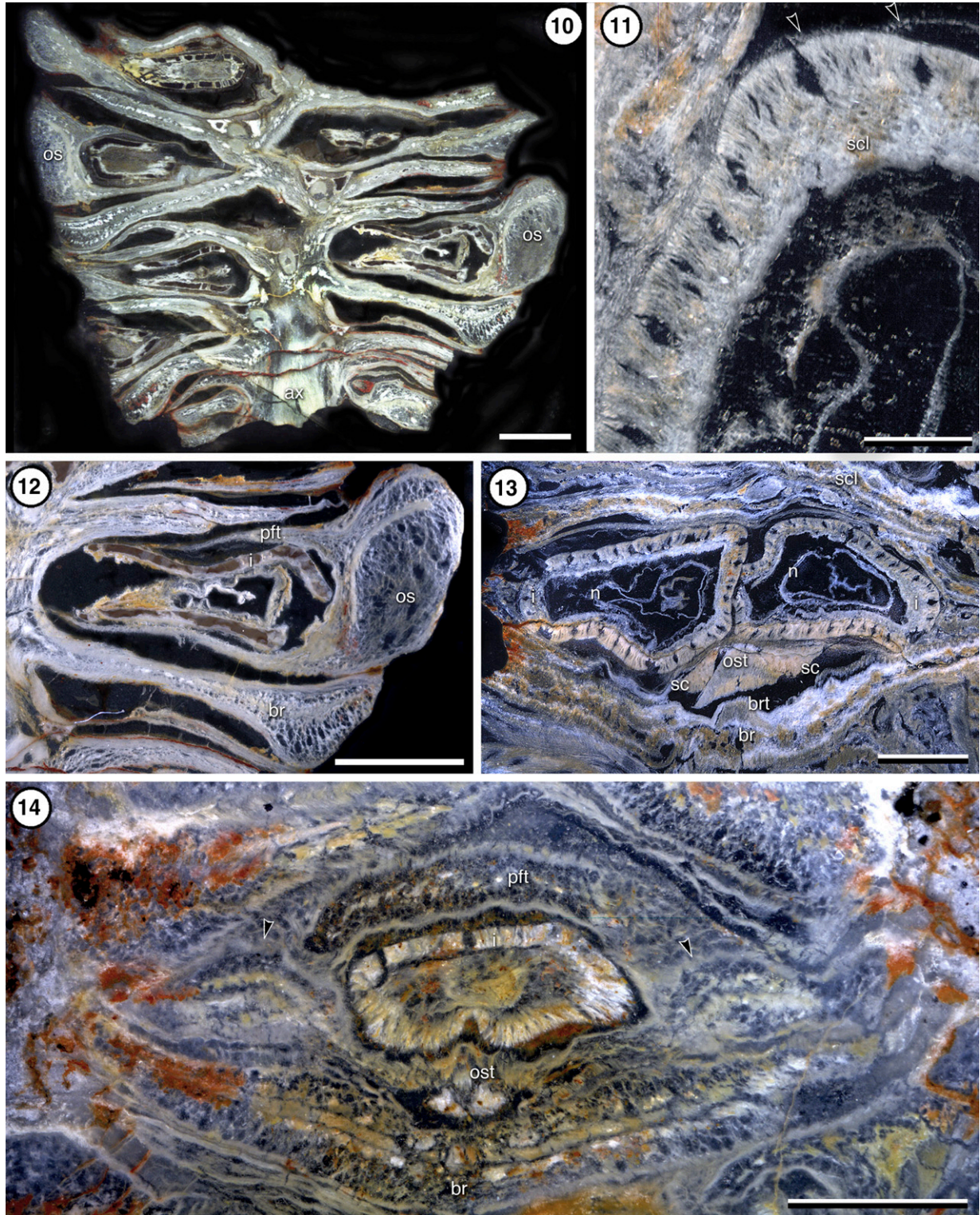
Figs. 10–14. *Pararaucaria patagonica* Wieland. **10.** Tangential section of cone fragment showing helical arrangement of cone-scale complexes. FMNH-P13954#1. Scale bar = 3 mm. **11.** Cross section of seed integument showing interior cuticle sclerotesta, outer layer of distinctive cells, and external seed cuticle (at arrowheads). FMNH-P13979 Side #1. Scale bar = 0.5 mm. **12.** Enlargement of ovuliferous scale complex with subtending bract from right side of Fig 10, showing histology of tissues. FMNH-P13979 Side #1. Scale bar = 3 mm. **13.** Tangential section of cone showing cone-scale complex with two seeds in cross section. Arrowheads indicate position of pocket-forming tissue. FMNH-P13979 Side#2. Scale bar = 2 mm. **14.** Cross section of cone-scale complex with one seed at more distal level than complex in Fig. 13. Note thickness of pocket-forming tissue at this level and histological details of tissues. Arrowheads indicate positions of fusion between lateral and central scale lobes. MPEF-Pb 5261#1. Scale bar = 3 mm. ax = cone axis, br = bract, brt = bract trace, n = nucellus, os = ovuliferous scale, ost = ovuliferous scale trace, pft = pocket-forming tissues, sc = sclerenchyma bundles, scl = sclerotesta.

this tissue reveal that it consists of small, densely packed parenchyma cells in which there are tracheids with scalariform or uniseriate pitted walls.

Pocket-forming tissue—In longitudinal sections, tissue at the adaxial side of the central scale apex extends basally, thinning toward the level of the seed micropyle, forming a seed-enclosing pocket (Figs. 5, 6, 10, 12) that is open only at the side facing the cone axis (Fig. 15). Cross sections of the ovuliferous scale somewhat proximal the level of seed attachment (i.e., relatively distal level of the ovuliferous scale), reveal that this adaxially positioned, pocket-forming tissue is mostly parenchymatous (as described by Stockey, 1977) and thicker than the ovuliferous scale tissue abaxial to the seed at this level (Fig. 14). Adjacent to the epidermises, however, the material making up this structure is distinctly denser, and cell structure is difficult to identify (Figs. 6, 9, at "pft"). At this level, the tissue is continuous with the lateral margins of the ovuliferous scale (Fig. 14), forming a pocket in which the seed or seeds are borne. At successively more proximal levels of the ovuliferous scale, the pocket-forming tissue thins progressively (Figs. 5, 9, 10, 12) and separates from one or both sides of the lateral scale tissue, indicating that the pocket containing either one (Fig. 14) or two (Fig. 13) seeds is open on the side facing the cone axis and also laterally for a short distance.

Nature of seed integument and associated tissue—In single-seeded cones of *P. patagonica*, the seed is roughly cordate with an elongated micropyle (see Stockey, 1977) and somewhat flattened parallel to the ovuliferous scale in cross sections (Figs. 10 at top, 14). Each seed is inverted and oriented with the elongated and curved micropyle rotated somewhat tangentially with respect to the long axis of the ovuliferous scale (Fig. 15) (Stockey, 1977). Paired seeds are narrower than single seeds (cf., Figs. 13, 14) and oriented parallel to the long axis of the ovuliferous scale. Otherwise, they are extremely similar to single seeds.

Individual seeds consist of a multilayered integument that surrounds a nucellus that appears to be attached only at the chalaza (Figs. 5, 6, 8, 9, 10–13), but the outer surface of the nucellus is irregular and lacks a cuticle for most of its length. This suggests that nucellus and integument were originally adnate below the nucellar apex and that the separation is taphonomic in origin. Some of the best-preserved specimens also have polycotyledonary embryos within the megaspore membrane (see Stockey, 1977 for details). The integument consists of an endotesta of delicate cells that often are incompletely preserved or absent (Fig. 11). To the outside of the endotesta are several layers of small, apparently thick-walled isodiametric sclereids (Fig. 11 at "scl"). The most distinctive feature of the *P. patagonica* seed integument is an outer zone of cell layers that often look superficially like a line of "I-beams" (Figs. 11, 13, 14). Upon closer inspection, this zone consists of one or two palisade layers of small, thick-walled cells toward the outside, and one or two layers of radially elongated and interdigitated cells (Fig. 11) (see Stockey, 1977 for a detailed description). The distinctive "I-beam" appearance of the outer integument of *P. patagonica* (Figs. 5, 11, 13, 14) may be the result of tissue shrinkage. There appears to be an indistinct, incompletely preserved epidermis with a delicate cuticle to the outside of the palisade (Fig. 11, at arrowheads) revealing that this cell layer represents the surface of the seed integument.

As described and interpreted by previous authors, the seeds of *P. patagonica* were considered to have a wing of tissue that attaches to the ovuliferous scale laterally and extends over the adaxial side of the integument (e.g., Stockey, 1977). However, careful reexamination of all available specimens reveals no cones where real cellular continuity can be demonstrated between the seed and putative seed wing tissue (e.g., Figs. 5, 6, 9, 10, 12–14). Also, in cones with two seeds per ovuliferous scale, the putative wing tissue is continuous over the adaxial surface of both seeds, such that the putative wing would have to connect the seeds into a single dispersal unit (Fig. 13). In a few of the most completely preserved specimens, there is a cuticle between the putative wing tissue and the outer surface of what previously has been interpreted as seed sclerotesta (Fig. 11, at arrowheads), documenting that the two are not part of a continuous tissue. This reveals that the outermost layer of the integument is the epidermis adjacent to the uniseriate or biseriate layer of cells. The only place that the seed is attached is at the chalaza where it extends from a specialized pad of ovuliferous scale tissue (Fig. 8, at arrowhead).

DISCUSSION

Structure and familial relationships of **P. patagonica**—Reexamination of anatomically preserved Jurassic seed cones assignable to *Pararaucaria patagonica* confirms most of the morphological and anatomical features detailed by earlier researchers (Wieland, 1935; Calder, 1953; Stockey, 1977) and further provides for the characterization of some previously unknown systematically diagnostic characters (e.g., distal ovuliferous scale lobes) and for the reinterpretation of others (e.g., seed wings). Cones are constructed of numerous helically arranged bract/scale complexes that consist of a broad bract and an axillary ovuliferous scale, which are separate from each other for most of their length. The ovuliferous scale expands laterally from the level of attachment and divides distally to form three separate apical lobes. There are two lateral lobes that lie somewhat abaxial to the plane of a broad central lobe. Proximal to the level where the distal lobes diverge from each other and below the central lobe, adaxial scale tissue separates basally to form a pocket that is open toward the cone axis. This pocket contains either one or two inverted seeds that are attached at the chalaza. Almost all of the cones are characterized by one broad seed per ovuliferous scale, but a small percentage of cones are characterized by two somewhat narrower seeds per scale in at least part of the cone (Wieland, 1935; Stockey, 1977). The two varieties of seed cones are otherwise identical in all morphological and anatomical characters and all fall within the same range of size and shape.

Internally, cones of *P. patagonica* are easily recognized by a combination of diagnostic anatomical and histological characters, thus allowing for the identification of such cones even when the outer surface features are absent. Bract and scale traces diverge from the woody cone axis separately (Fig. 7), with the round bract trace originating adjacent to the inverted U-shaped scale trace. A prominent sclerenchyma bundle occurs immediately adaxial to the bract trace, dividing to form two triangular bundles that accompany the ovuliferous scale trace in the cortex of the cone axis and the proximal region of the scale (Figs. 13, 14).

The inverted seed or seeds are unwinged and attached at the chalaza to a specialized pad of tissue (Stockey, 1977), with single seeds being roughly cordate and oriented somewhat obliquely to the long axis of the ovuliferous scale. Paired seeds
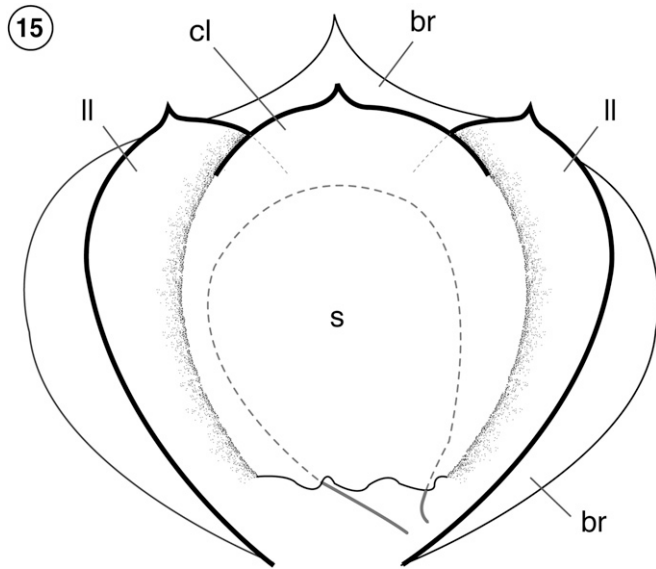
Fig. 15.   Diagrammatic view of bract-scale complex of *Pararaucaria patagonica* as seen from adaxial side. Note three distal lobes of ovuliferous scale and orientation of single inverted seed with elongated and curved micropylar region within pocket of ovuliferous scale tissue. br = bract, cl = central ovuliferous scale lobe, ll = lateral ovuliferous scale lobe, s = seed.

are somewhat narrower and lie parallel to both each other and to the long axis of the ovuliferous scale. All are roughly oval in cross sections. The outer zone of the integument is characterized by one or two layers of radially elongated cells, often with an "I beam" appearance in cross section, that are also probably diagnostic of the species. The preservation of a cuticle on this layer of some specimens confirms that this distinct layer of cells forms the outer margin of the seed.

The most important new information about the systematic relationships of *P. patagonica* is derived from character combinations that are revealed by comparing the relatively unabraded cones, which provide evidence that ovuliferous scales divide distally to produce free lobes, to specimens with the most complete histological preservation, which provide evidence that seeds are unwinged and located within a pocket of adaxial ovuliferous scale tissue that is open toward the cone axis. Together, these characters allow for the recognition that *P. patagonica* shares diagnostic features with seed cones of the Cheirolepidiaceae, an extinct conifer family that previously has been represented primarily by *Classopollis* pollen, compressed specimens, wood, and a single permineralized pollen cone (e.g., Wieland, 1935; Jung, 1968; Watson, 1988; Harris, 1979; Alvin, 1982; Clement-Westerhof and van Konijnenburg-van Cittert, 1991; Axsmith and Jacobs, 2005; Rothwell et al., 2007; Taylor et al., 2009).

In agreement with *P. patagonica*, compressed cheirolepidiaceous seed cones are relatively large structures with numerous helically arranged bracts and ovuliferous scales that separate from each other near their base and are free for most of their length. Such cones have a diagnostic suite of characters (Table 1) including (1) unwinged seeds that are located within a pocket or under a flap of ovuliferous scale tissue on the adaxial surface of the scale, (2) dissected ovuliferous scales with three main lobes (more highly divided in some species), and (3) either one or two inverted seeds per ovuliferous scale that are normally placed proximal to the central lobe (Table 1). Such cones specimens often are preserved with *Classopollis* pollen preserved within

the cuticular envelopes of the cone structures and seeds (e.g., Archangelsky, 1968; Harris, 1979; Krassilov, 1982; Kvaček, 2000).

The well-preserved anatomy of *Pararaucaria patagonica* now reveals that the seeds are located within an adaxial pocket of ovuliferous scale tissue that is open toward the cone axis. This character is highly distinctive and extremely similar to the seed-covering tissue of compressed specimens, which has been interpreted by most authors as a flap that is attached to the adaxial surface of the scale proximal to the division of the free distal lobes. As described by several authors, the flap of tissue extends toward the base of the scale and is open at the sides (see Clement-Westerhof and van Konijnenburg-van Cittert, 1991). However, Hörhammer (1933), Hirmer and Hörhammer (1934), and Krassilov (1982) all described the ovules as being surrounded by internal cuticles, which is consistent with the ovuliferous scales of those cones also producing a seed-bearing pocket like that of *P. patagonica*.

Structural diversity of cheirolepidiaceous seed cones— Previously described cheirolepidiaceous seed cones are all preserved as coalified compressions or impressions (Taylor et al., 2009), many with excellently preserved cuticles (e.g., Clement-Westerhof and van Konijnenburg-van Cittert, 1991; Kvaček, 2000). Nevertheless, the new morphological and anatomical features here described and/or reinterpreted for *P. patagonica* allow for detailed comparisons of the relevant structures to the compressed species. In particular, the presence of scale tissue that covers the seed almost up to the level of the micropyle, but without enclosing it completely, seems to be diagnostic in nearly all seed cones thus far attributed to the Cheirolepidiaceae (but see *Pseudohirmerella delawarensis*; Table 1). All known species also have ovuliferous scales that are dissected, apically forming, free distal lobes, and all of the distal lobes are dorsiventrally flattened.

Cone size and shape, the number of cone-scale complexes, the size and shape of cone-scale complexes, and the number of free ovuliferous scale lobes varies among different genera and species of Cheirolepidiaceae (Del Fueyo et al., 2008), but all of the genera except *Pseudohirmerella* Arndt are characterized by an ovuliferous scale that is either attached to the bract only at the base or free throughout its length (Table 1). A bract is not known for *Pseudohirmerella* (Axsmith et al., 2004). All genera of the Cheirolepidiaceae have either one or two seeds. All genera except *Pseudohirmerella* also have inverted seeds attached proximal to a broad central lobe that is positioned somewhat more abaxially than the other terminal lobes and is either simple or divided into as many as four units (Table 1). In *Pseudohirmerella*, all of the scale lobes appear to be in a single plane, and the seed orientation is not known (Axsmith et al., 2004; Table 1). In all of the genera except *Pseudohirmerella*, the seeds are inverted, attached at the chalaza, and occur beneath either a flap of scale tissue or within a pocket of scale tissue that is located on the adaxial surface of the scale (Table 1). Due to incomplete preservation, it is not known whether ovule-covering tissue is absent from the scales of *P. delawarensis* (Bock) Axsmith, Andrews et Fraser and other species of *Pseudohirmerella* seed cones or whether it has simply not been observed (Axsmith et al., 2004), and assignment of this genus to the Cheirolepidiaceae remains in doubt (Axsmith et al., 2004).

Among the species of cheirolepidiaceous seed cones with a broad central scale lobe (Table 1), the ovuliferous scales show a range of variation in the number and positions of distal scale

lobes. All have two lateral lobes and a broad central lobe that is positioned in a somewhat more abaxial plane with respect to the lateral lobes (Table 1). The central lobe is undivided in *Pararaucaria*, *Alvinia* Kvaček and *Pseudohirmerella*, but it is divided into two to four tips in Hirmeriella Hörhammer, *Kachaikestrobus* Del Fueyo, Archangelsky, Llorens, et Cuneo, and *Tomaxellia* Archangelsky (Table 1). In addition, *Hirmeriella muensteri* (Schenk) Jung has two small lobes that are in a somewhat more adaxial plane than the lateral lobes (Clement-Westerhof and van Konijnenburg-van Cittert, 1991) and are not known for the other cheirolepidiaceous seed cones. The best-known species, *Hirmeriella muensteri*, also shares with *P. patagonica* the presence of external striations on the surface of the scale lobes (cf. Figs. 1, 2 of present study with fig. 1 of Clement-Westerhof and van Konijnenburg-van Cittert, 1991).
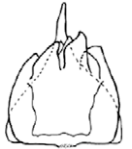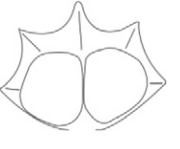
As emphasized earlier, the number of seeds per ovuliferous scale varies from one to two in cheirolepidiaceous cones (Table 1). On the basis of well-preserved specimens of *Hirmeriella muensteri*, Clement-Westerhof and van Konijnenburg-van Cittert (1991) interpreted this difference of seed number to result from only one of a pair of seeds developing to maturity in many specimens, while both seeds mature in others. In both types of cones, there are two sites of seed attachment, side by side, on the adaxial surface immediately proximal to the large abaxially positioned central scale lobe (cf. figs. 1, 2 of Clement-Westerhof and van Konijnenburg-van Cittert, 1991). The ovuliferous scale of *P. patagonica* also appears to conform to this interpretation, as a few cones show ovuliferous scales with two seeds that are attached side-by-side proximal to the central scale lobe and oriented parallel to the long axis of the scale. By contrast, single-seeded ovuliferous scales of *P. patagonica* have their seed rotated from the long axis of the scale with the micropyle oriented to the side of the cone axis. This orientation is consistent with each single seed of *P. patagonica* being borne at one of two off-center attachment sights that are each lateral to the central axis of the ovuliferous scale, thus accounting for the seed micropyle being rotated away from the long axis of the ovuliferous scale.

In contrast to several compressed cheirolepidiaceous seed cone species (e.g., Archangelsky, 1968; Harris, 1979; Krassilov, 1982; Kvaček, 2000), none of our specimens of *P. patagonica* show evidence of pollen within the ovules or bract/scale complexes of the cones. Inverted seeds with micropyles facing the cone axis of *P. patagonica* are similar in that respect to many species of Pinaceae and Cupressaceae, which are wind-pollinated. Also, there is no trichome-lined channel through the ovuliferous scales of *P. patagonica* like that described for *Alvinia bohemica* (Velenovský) J. Kvaček and interpreted as evidence for insect pollination within the Cheirolepidiaceae (Kvaček, 2000; see Labandeira et al., 2007 for a thorough discussion of that interpretaton). At present, the mode of pollination for *P. patagonica* remains unknown.

Cheirolepidiaceous conifers comprise one of the most important components of global vegetation worldwide for much of the Mesozoic, being present in abundance on all continents in both the northern and southern hemispheres (Alvin, 1982; Francis, 1983; Watson, 1988; Taylor et al., 2009). Such plants also have played a crucial role in the phylogenetic radiation of conifers. Therefore, the Cheirolepidiaceae has great potential for either meaningfully extending or dramatically altering current understanding of conifer phylogeny by providing important new data to test hypotheses that have been developed from systematic analyses of only living species (e.g., Rai et al., 2008; Mathews, 2009). In the past, this potential was highly restricted by the paucity of permineralized fossil Cheirolepidiaceae that could provide anatomical characters for phylogenetic analyses. The discovery that *Pararaucaria patagonica* seed cones represent cheirolepidiaceous conifers makes available, for the first time, a large suite of such characters. While it is beyond the scope of the present study to conduct a comprehensive phylogenetic analysis of conifer relationships, these data are being employed in

TABLE 1. Comparison of morphological features of selected cheirolepidaceous seed cones.

Character	*Pararaucaria patagonica*	*Hirmeriella muensteri*	*Kachaikestrobus acuminatus*	*Tomaxellia biforme*	*Alvinia bohemica*	*Pseudohirmeriella delawarensis*
Age, distribution	Jurassic, S. America	Jurassic, Europe	Cretaceous, S. America	Cretaceous, S. America	Cretaceous, Europe	Triassic, N. America
PFT	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 [a]	1 central (div.) (?)
OS abaxial	absent	present (1)	present (3)	absent (?)	absent	absent
Bract	present	present	present	present	present	absent
Bract/scale fusion	present at base only	present at base only	present at base only	absent, or fused at base only	present at base only	absent
Ovules per OS	1 or 2	1 or 2	? (1–2)	2	1 or 2	2

Notes: Reconstruction credits: *Hirmeriella muensteri*, modified from (Clement-Westerhof and van Knonijnenburg-van Cittert, 1991); *Kachaikestrobus acuminata*, taken from Del Fueyo et al. (2008); *Tomaxellia biforme*, line drawings based on original description and illustrated specimens (plate 1, figs. 4, 5, Archangelsky, 1968); *Alvinia bohemica* taken from Kvaček (2000) and *Pseudohirmeriallla delawarensis*, modified from Axsmith at al. (2004). *Abbreviations:* N. = North, OS = ovuliferous scale, PFT = pocket-forming tissue, S. = South.

[a] Kvaček (2000) considered the two lateral lobes of *Alvinia bohemica* as abaxial; however, they are comparable to the lateral adaxial lobes considered for the other species.

ongoing studies (e.g., Rothwell et al., 2009, 2011), with the ultimate goal of resolving the overall pattern of conifer phylogeny.

LITERATURE CITED

ALVIN, K. L. 1982. Cheirolepidiaceae: Biology, structure and paleoecology. *Review of Palaeobotany and Palynology* 37: 71–98.

ARCHANGELSKY, S. 1968. On the genus *Tomaxellia* (Coniferae) from the Lower Cretaceous of Patagonia (Argentina) and its male and female cones. *Botanical Journal of the Linnean Society* 61: 153–165.

AXSMITH, B. A., F. M. ANDREWS, AND N. C. FRASER. 2004. The structure and phylogenetic significance of the conifer *Pseudohirmerella delawarensis* nov. comb. from the Upper Triassic of North America. *Review of Palaeobotany and Palynology* 129: 251–263.

AXSMITH, B. J., AND B. F. JACOBS. 2005. The conifer *Frenelopsis ramosissima* (Cheirolepidiaceae) in the Lower Cretaceous of Texas: systematic, biogeographical, and paleoecological implications. *International Journal of Plant Sciences* 166: 327–337.

CALDER, M. G. 1953. A coniferous petrified forest in Patagonia. *Bulletin of the British Museum of Natural History, London, Geology* 2: 97–137.

CHAMBERLAIN, C. J. 1935 Gymnosperms, structure and evolution. AC Black, London, UK.

CLEMENT-WESTERHOF, J. H. A., AND J. H. A. VAN KONIJNENBURG-VAN CITTERT. 1991. *Hirmeriella muensteri*: New data on the fertile organs leading to a revised concept of Cheirolepidiaceae. *Review of Palaeobotany and Palynology* 68: 147–179.

DE BARRIO, R. E., J. L. PANZA, AND F. E. NULLO. 2000. Jurásico y Cretácico del Macizo del Deseado, Provincia de Santa Cruz. *In* R. Caminos [ed], Geología Argentina, Servicio Geológico Minero Argentino, SEGEMAR, Anales 29: 511-527.

DE LAUBENFELS, D. J. 1988. Coniferales. *Flora Malesiana Series I* 10: 337–453.

DEL FUEYO, G. M., S. ARCHANGELSKY, M. LLORENS, AND N. R. CÚNEO. 2008. Coniferous ovulate cones from the Lower Cretaceous of Santa Cruz Province, Argentina. *International Journal of Plant Sciences* 169: 799–813.

ESCAPA, I. H. 2009. La tafoflora de la formación Cañadón Asfalto, Jurásico Medio Superior de Chubut. Taxonomía, Bioestratigrafía y Paleofitogeografía. Ph.D. dissertation, Universidad Nacional del Comahue, Bariloche, Argentina.

ESCAPA, I. H., N. R. CÚNEO, AND B. AXSMITH. 2008. A new genus of Cupressaceae (*sensu lato*) from the Jurassic of Patagonia: Implications for conifer megasporangiate cone homologies. *Review of Palaeobotany and Palynology* 151: 110–122.

FALASCHI, P., J. GROSFELD, A. B. ZAMUNER, N. FOIX, AND S. M. RIVERA. 2011. Growth architecture and silhouette of Jurassic conifers from La Matilde Formation, Patagonia, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 302: 122–141.

FARJON, A., AND S. ORTIZ-GARCIA. 2003. Cone and ovule development in *Cunninghamia* and *Taiwania* (Cupressaceae sensu lato) and its significance for conifer evolution. *American Journal of Botany* 90: 8–16.

FLORIN, R. 1938–1945. Die Koniferen des Oberkarbons und des unteren Perms. I-VII. *Palaeontographica B* 85: 1–729.

FLORIN, R. 1951. Evolution of cordaites and conifers. *Acta Horti Bergiani* 15: 285–388.

FLORIN, R. 1963. The distribution of conifer and taxad genera in time and space. *Acta Horti Bergiani* 20: 122–312.

FRANCIS, J. E. 1983. The dominant conifer of the Jurassic Purbeck Formation, England. *Palaeontology* 26: 277–294.

GUIDO, D. M. 2004. Subdivisión litofacial e interpretación del volcanismo jurásico (Grupo Bahía Laura) en el Este del Macizo del Deseado, provincia de Santa Cruz. *Revista de la Asociación Geológica Argentina* 59: 727–742.

HARRIS, T. M. 1979. The Yorkshire Jurassic flora, V. Coniferales. British Museum of Natural History, London, UK.

HERNANDEZ-CASTILLO, G. R., G. W. ROTHWELL, AND G. MAPES. 2001. Thucydiaceae fam. nov. with a review and reevaluation of Paleozoic walchian conifers. *International Journal of Plant Sciences* 162: 1155–1185.

HIRMER, M., AND L. HÖRHAMMER. 1934. Zur weiteren Kenntnis von *Cheirolepis* Schimper und *Hirmeriella* Hörhammer mit Bemerkungen über deren systematische Stellung. *Palaeontographica B* 79: 67–84.

HÖRHAMMER, L. 1933. Über die Coniferen-Gattungen *Cheirolepis* Schimper und *Hirmeriella* nov. gen. aus dem Rhät-Lias von Franken. *Bibliotheca Botanica* 107: 1–33.

JUNG, W. 1968. *Hirmerella münsteri* (Schenk) Jung nov. comb., eine bedeutsame Konifere des Mesozoikums. *Palaeontographica B* 122: 55–93.

KAY, S., V. A. RAMOS, C. MPODOZIS, AND P. SRUOGA. 1989. Late Paleozoic to Jurassic silicic magmatism at the Gondwana margin: Analogy to the Middle Proterozoic in North America. *Geology* 17: 324–328.

KRASSILOV, V. A. 1982. On the ovuliferous organ of *Hirmeriella*. *Phyta* 1: 141–144.

KVAČEK, J. 2000. *Frenelopsis alata* and its microsporangiate and ovuliferous reproductive structures from the Cenomanian of Bohemia (Czech Republic, Central Europe). *Review of Palaeobotany and Palynology* 112: 51–78.

LABANDEIRA, C. C., J. KVAČEK, AND M. B. MOSTOVSKI. 2007. Pollination drops, pollen, and insect pollination of Mesozoic gymnosperms. *Taxon* 56: 663–695.

MATHEWS, S. 2009. Phylogenetic relationships among seed plants: Persistent questions and the limits of molecular data. *American Journal of Botany* 96: 228–236.

MILLER, C. N. 1977. Mesozoic conifers. *Botanical Review* 43: 217–280.

MILLER, C. N. 1999. Implication of fossil conifers for the phylogenetic: Relationships of the living families. *Botanical Review* 65: 239–277.

PAGE, C. N. 1990. Coniferophytina. *In* K. Kubitzki [ed.], The families and genera of vascular plants; vol. 1, K. U. Kramer and P.S. Green [eds.], Pteridophytes and gymnosperms, 282–361. Springer, Berlin, Germany.

PANKHURST, R., P. T. LEAT, P. SRUOGA, C. W. RAPELA, M. MÁRQUEZ, B. C. STOREY, AND T. R. RILEY. 1998. The Chon Aike province of Patagonia and related rocks in West Antarctica: a silicic large igneous province. *Journal of Volcanology and Geothermal Research* 81: 113–136.

PANKHURST, R., T. RILEY, C. FANNING, AND S. KELLEY. 2000. Episodic silicic volcanism in Patagonia and the Antarctic Peninsula: Chronology of magmatism associated with the break-up of Gondwana. *Journal of Petrology* 41: 605–625.

PANZA, J. L., AND A. GENINI. 2001. Hoja Geológica 4769-IV Monumento Natural Bosques Petrificados. *Instituto de Geología y Recursos Mineros, Servicio Geológico Minero Argentino; Boletin (Instituto de Estudios de Poblacion y Desarrollo (Dominican Republic))* 258: 1–112.

QUATTROCCHIO, M. E., M. A. MARTINEZ, AND W. VOLKHEIMER. 2007. Las floras jurásicas de la Argentina. *Ameghiniana Publicación Especial* 11: 87–100.

RAI, H. S., P. A. REEVES, R. PEAKALL, R. G. OLMSTEAD, AND S. W. GRAHAM. 2008. Inference of higher order conifer relationships from a multi-locus plastid data set. *Botany* 86: 658–669.

ROTHWELL, G. W., G. MAPES, J. HILTON, AND N. T. HOLLINGWOTH. 2007. Pollen cone anatomy of *Classostrobus crossii* sp. nov. (Cheirolepidiaceae). *International Journal of Coal Geology* 69: 55–67.

ROTHWELL, G. W., G. MAPES, R. A. STOCKEY, J. HILTON, AND R. BATEMAN. 2009. "Descent with modification", transformational series, and phylogenetic analyses to infer the evolution of modern conifer families. Geological Society of America, 2009 annual meeting, Portland, Oregon, USA. *Abstracts with Programs* 41(7): 563 [online asbtract http://gsa.confex.com/gsa/2009AM/finalprogram/abstract_165301.htm].

ROTHWELL, G. W., R. A. STOCKEY, G. MAPES, AND J. HILTON. 2011. Structure and relationships of the Jurassic conifer seed cone *Hugmillerites juddii* gen. et comb. nov.: Implications for the origin and evolution of Cupressaceae. *Review of Palaeobotany and Palynology* 164: 45–59.

SERBET, R., I. ESCAPA, T. N. TAYLOR, E. L. TAYLOR, AND N. R. CUNEO. 2010. Additional observations on the enigmatic Permian plant *Buriadia* and implications on early coniferophyte evolution. *Review of Palaeobotany and Palynology* 161: 168–178.

SMITH, S. Y., AND R. A. STOCKEY. 2001. A new species of *Pityostrobus* from the Lower Cretaceous of California and its bearing on the evolution of Pinaceae. *International Journal of Plant Sciences* 162: 669–681.

SMITH, S. Y., AND R. A. STOCKEY. 2002. Permineralized pine cones from the Cretaceous of Vancouver Island, British Columbia. *International Journal of Plant Sciences* 163: 185–196.

STIPANICIC, P., AND M. BONETTI. 1970. Posiciones estratigráficas y edades de las principales floras jurásicas argentinas. II. Floras doggerianas y málmicas. *Ameghiniana* 7: 101–118.

STOCKEY, R. A. 1977. Reproductive biology of the Cerro Cuadrado (Jurassic) fossil conifers: *Pararaucaria patagonica. American Journal of Botany* 64: 733–744.

TAYLOR, T. N., E. L. TAYLOR, AND M. KRINGS. 2009. The biology and evolution of fossil plants, 2nd ed. Academic Press, Amsterdam, Netherlands.

TOMLINSON, P. B., AND T. TAKASO. 2002. Seed cone structure in conifers in relation to development and pollination: A biological approach. *Canadian Journal of Botany* 80: 1250–1273.

WATSON, J. 1988. The Cheirolepidiaceae. *In* C. B. Beck [ed.], Origin and evolution of gymnosperms, 382–447. Columbia University Press, New York, New York, USA.

WIELAND, G. R. 1929. The world's two greatest petrified forests. *Science* 69: 60–63.

WIELAND, G. R. 1935. The Cerro Cuadrado petrified forest. Carnegie Institution of Washington, Washington, D.C., USA.