A new Cheirolepidiaceae (Coniferales) from the Early Jurassic of Patagonia (Argentina): Reconciling the records of impression and permineralized fossils[1]

Ignacio Escapa[2,4] and Andrew Leslie[3]

PREMISE OF THE STUDY: Plants preserved in different fossil modes provide complementary data concerning the paleobiology and evolutionary relationships among plant groups. New material from the Early Jurassic of Patagonia shows the importance of combining these sources of information, as we describe the first compression/impression fossils of *Pararaucaria*, a genus of the extinct conifer family Cheirolepidiaceae previously known from permineralized fossils. These fossils extend the temporal range of this genus and may allow its wider recognition in the fossil record.

METHODS: We studied fossil plants from the Early Jurassic (Pleinsbachian-Toarcian) locality of Taquetrén in Patagonia, Argentina using standard paleobotanical preparation and description techniques.

KEY RESULTS: *Pararaucaria taquetrensis* consists of isolated ovuliferous scales and small seed cones with helically arranged bract-scale complexes attached to scale-leaf foliage. Bract-scale complexes consist of separated bracts and ovuliferous scales with two seeds and three broad distal lobes.

CONCLUSIONS: *Pararaucaria taquetrensis* represents the oldest known Cheirolepidiaceae seed cones from the Southern Hemisphere, and this material highlights the importance of compression and impression fossils in understanding the distribution of fossil taxa. This material also suggests that Cheirolepidiaceae cone scales can be easily confused with those of another common conifer family, the Araucariaceae, which has important implications for accurately understanding Mesozoic conifer diversity and paleoecology.

KEY WORDS conifer; paleobotany; *Pararaucaria*; seed cone

The Cheirolepidiaceae are an extinct family of conifers known from the Late Triassic up to the Late Cretaceous (early Paleogene in Patagonia; Barreda et al., 2012). The group was highly diverse in the Mesozoic, particularly in lower latitudes, although their numbers began to decline in many areas from the Middle to Late Cretaceous (Watson, 1988; van der Ham et al., 2003). Species of Cheirolepidiaceae genera appear to have been ecologically distinctive among living and extinct conifers, as their common occurrence in arid coastal settings suggests they could tolerate drought stress as well as high salinity (Alvin, 1982; Watson, 1988; Moreau et al., 2015). The unusual leaf morphology of many Cheirolepidiaceae species, which is reminiscent of angiosperm halophytes such as *Salicornia* (Alvin, 1982; Watson, 1988), further suggests they inhabited extremely xeric or water-stressed environments. Members of the Cheirolepidiaceae also have distinctive reproductive morphology among conifers; the characteristic pollen grains that define the group (*Classopollis*) are perhaps the most complex of any known gymnosperm (Srivastava, 1976; Alvin, 1982; Taylor and Alvin, 1984) and their seed cones have a complex morphology that may have facilitated insect pollination in at least some species (Labandeira et al., 2007). Yet despite the importance of this group in Mesozoic ecosystems and its significance for understanding the ecological, anatomical, and morphological diversity of conifers, the origins and phylogenetic relationships of Cheirolepidiaceae remain unclear.

Resolving these relationships is important because they may help to answer fundamental questions about conifer evolution. Although molecular data support a consistent set of relationships among the major extant conifer groups (see e.g., Rai et al., 2008; Leslie et al., 2012), it is difficult to reconstruct deep patterns of

character evolution among conifers because the major groups are highly divergent morphologically and anatomically. Cheirolepidiaceae may help to bridge this gap by essentially breaking up long morphological branches among living clades. For example, molecular evidence supports a sister relationship between the Araucariaceae and Podocarpaceae clades (Chaw et al., 2000; Rai et al., 2008) and many extant representatives of both groups possess characteristic tissues that partially or fully cover their seeds (see e.g., Owens et al., 1995; Tomlinson et al., 1991; Tomlinson and Takaso, 2002). It is unclear if these structures are truly homologous, however, because they differ substantially in anatomical structure and position. Cheirolepidiaceae also have a flap of tissue covering their seeds (the "pocket forming tissue" of Escapa et al., 2012) that may suggest a relationship among these three groups (i.e., Araucariaceae, Podocorpaceae and Cheirolepidiaceae), although it has alternatively been suggested that this structure is homologous to the seed wing of Pinaceae (see Escapa et al., 2013). A detailed phylogenetic analysis of Cheirolepidiaceae is necessary to provide clues to the origins and potential homologies of these "covering tissues", and thus a more accurate understanding of the morphological differences and similarities among extant and extinct conifer groups. A crucial first step, however, is a better understanding of the basic morphology, anatomy, diversity, temporal distribution, and geographic distribution of the Cheirolepidiaceae.

With these goals in mind, we describe a new species of the Cheirolepidiaceae genus *Pararaucaria* from the Early Jurassic of Patagonia. *Pararaucaria* was originally created for permineralized seed cones of uncertain affinity from Jurassic deposits in Santa Cruz Province (Wieland, 1929, 1935; Stockey, 1977), but has recently been placed in the Cheirolepidiaceae due to similarities in its seed cone morphology (Escapa et al., 2012). In particular, *Pararaucaria* bract-scale complexes (the typical scales of a conifer cone that consist of a bract subtending a modified shoot, or ovuliferous scale) have the characteristic lobes and "pocket-forming tissue" that characterize the Cheirolepidiaceae (Escapa et al., 2012). Subsequent work has shown that *Pararaucaria* was widespread and diverse in the Jurassic, with multiple species of permineralized seed cones now known from Patagonia (Escapa et al., 2013), the western United States (Stockey and Rothwell, 2013; Gee et al., 2014) and England (Steart et al., 2014). In this study, we describe the first compression/impression remains of the genus, which extends its range into the Early Jurassic. These attached branches, foliage, and seed cones represent the oldest known reproductive macrofossil remains of the Cheirolepidiaceae from South America and probably the Southern Hemisphere in general (depending on the exact age of our locality; see Hieger et al., 2015).

A further goal of this study was to integrate information from compression and impression fossils, such as those described here, with data derived from permineralized fossils. Permineralized fossils are relatively rare in the fossil record but are a major paleobotanical focus because their three-dimensional cellular preservation records a wealth of morphological and anatomical information (see e.g., Rothwell and Stockey, 2002; Taylor et al., 2005; Friis et al., 2007; Schwendemann et al., 2010). Compression and impression fossils, on the other hand, preserve less structural information but are much more widespread and can therefore provide key data regarding the temporal, spatial, and environmental distribution of fossil species (see e.g., DiMichele et al., 2007; Falcon-Lang et al., 2009; Escapa et al., 2011). Compression and impression fossils also provide valuable information regarding connections between different plant organs and parts (see e.g., Rothwell and Serbet, 1994; Yao et al., 1998), as permineralized fossils often preserve only isolated organs. Reconciling information from these different preservational modes is then crucial to understanding plant evolution because their combination facilitates the development of progressively more complete plant concepts for use in phylogenetic analyses (see e.g., Hernandez-Castillo et al., 2009; Escapa et al., 2010; Bomfleur et al., 2013, 2014).

MATERIALS AND METHODS

Geologic setting—The fossil impressions, molds, and casts described here were collected in Argentina in the Cañadón del Zaino area, near the town of Paso del Sapo, Chubut Province. Fossils were collected at two localities in close proximity, "Taquetrén" and "Taquetrén B", which are separated by 3.5 km but are found on a stratigraphically equivalent level (Fig. 1). Plant-bearing sediments at the original "Taquetrén" locality were first assigned to the Taquetrén Formation (Nullo and Proserpio, 1975) but were subsequently placed in the broader Lonco Trapial Group (see Lizuain and Silva Nieto, 2005; Escapa et al., 2008; Cúneo et al., 2013; Figari et al., 2015). The Lonco Trapial Group (Lesta and Ferello, 1972) has an estimated thickness of 500-800 meters (Figari, 2005; Figari et al., 2015) and is dominated by poorly stratified agglomerates, breccias, and basaltic lavas with associated volcaniclastic conglomerates, sandstones, and lahar deposits. The fossiliferous levels are found near the base of the Lonco Trapial Group, a few meters above the contact with the underlying Las Leoneras Formation.

The age of the fossil floras at Taquetrén were originally based on their fossil content and comparisons with other Mesozoic floras from South America and Antarctica, which generally supported a Middle-Late Jurassic age (see e.g., Bonetti, 1964; Herbst and Anzótegui, 1968; Nullo and Proserpio, 1975). Escapa et al. (2008) suggested an earlier age for the Taquetrén localities due to the presence of taxa that are characteristic of the Early Jurassic of Gondwana (e.g., *Goeppertella*, *Clathropteris*, *Sagenopteris*; see e.g., Escapa et al., 2008). More recently, Cúneo et al. (2013) obtained radiometric ages for the upper part of Las Leoneras Formation (188.9 Ma) and for the transition between the Lonco Trapial Group and the overlying Cañadon Asfalto Formation (178.8 Ma), thereby bracketing the age of the Taquetrén flora to the Early Jurassic. Given its stratigraphic position at the base of the Lonco Trapial Group, Taquetrén most likely dates to the older end of this age range, probably to the Pliensbachian.

The fossil content of Taquetrén has been the subject of several taxonomic studies in the past (Bonetti, 1964; Herbst and Anzótegui, 1968), while Taquetrén B has only recently been discovered. The flora at both localities generally consists of Equisetales, ferns, seed ferns, Bennettitales, and conifers (Bonetti, 1964; Herbst and Anzótegui, 1968). In total, 20 taxa have been preliminarily identified described from both vegetative and reproductive remains.

Fossil preparation and illustration—Standard paleobotanical techniques were used in the preparation and study of the specimens described here, which are deposited at the Museo Paleontológico Egidio Feruglio Paleobotanical Collection in Trelew, Argentina (hereafter MPEF-PB). Fossils were examined using a Zeiss MC80DX
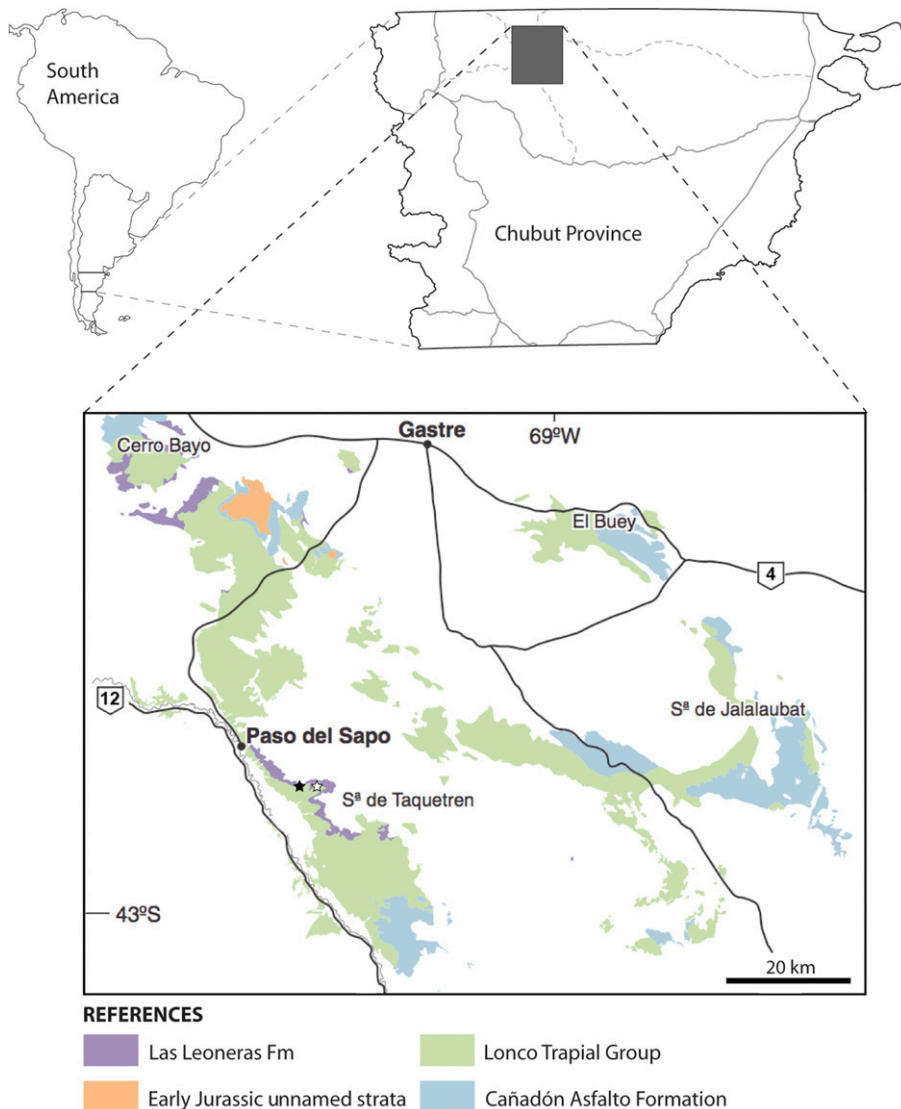
FIGURE 1 Location and geology of Taquetrén (white star) and Taquetrén B (black star) localities, Chubut Province, Argentina. Modified from Cúneo et al., 2013.

stereoscope (Carl Zeiss, Oberkochen, Germany) with camera lucida attached and photographed using a Canon Mark 7D digital camera with a 60 mm macro lens. Higher magnifications were obtained using extension tubes attached to the lens. To generate clear, fully focused images of three-dimensional material, some specimens were photographed in multiple planes of focus, and the images were subsequently stacked using the auto-align and auto-blend functions of Adobe Photoshop (Adobe Systems, San Jose, California, USA).

Previously described specimens from Taquetrén were revised. Specimens originally described by Bonetti (1964) are deposited in the Palaeobotanical collection of the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Buenos Aires, Argentina (hereafter Ba Pb), while specimens described by Herbst and Anzotegui (1968) are deposited in the Paleontological Collection of the 'Facultad de Ciencias Exactas y Naturales y Agrimensura de la Universidad Nacional del Nordeste,' Corrientes, Argentina (hereafter CTES-Pb).

SYSTEMATICS

Order—Coniferales sensu Farjon, 2010

Family—Cheirolepidiaceae Tahktajan, 1963

Genus—*Pararaucaria* Wieland, 1929, *emend.* Escapa, Rothwell, Stockey et Cúneo

Remarks—The genus *Pararaucaria* originally described permineralized seed cones from the Middle-Late Jurassic of Patagonia with uncertain systematic affinities (Wieland, 1929, 1935). *Pararaucaria* has been linked with or assigned to the Araucariaceae, Cheirolepidiaceae, Cupressaceae, Pinaceae, Voltziales, or in its own family by various authors (Wieland, 1935; Calder, 1953; Stockey, 1977; Miller, 1999; Smith and Stockey, 2001), but the genus was recently emended and placed more firmly in the Cheirolepidiaceae following a reinterpretation of its morphology and anatomy (Escapa et al., 2012). Here we expand the concept of *Pararaucaria* to also include seed cone impressions that are morphologically similar to anatomically preserved seed cones from the Jurassic of Patagonia (Escapa et al., 2012, 2013), specifically in terms of the presence of three ovuliferous scale lobes. This material also extends the concept of *Pararaucaria* to include vegetative branches with scale-leaf morphology.

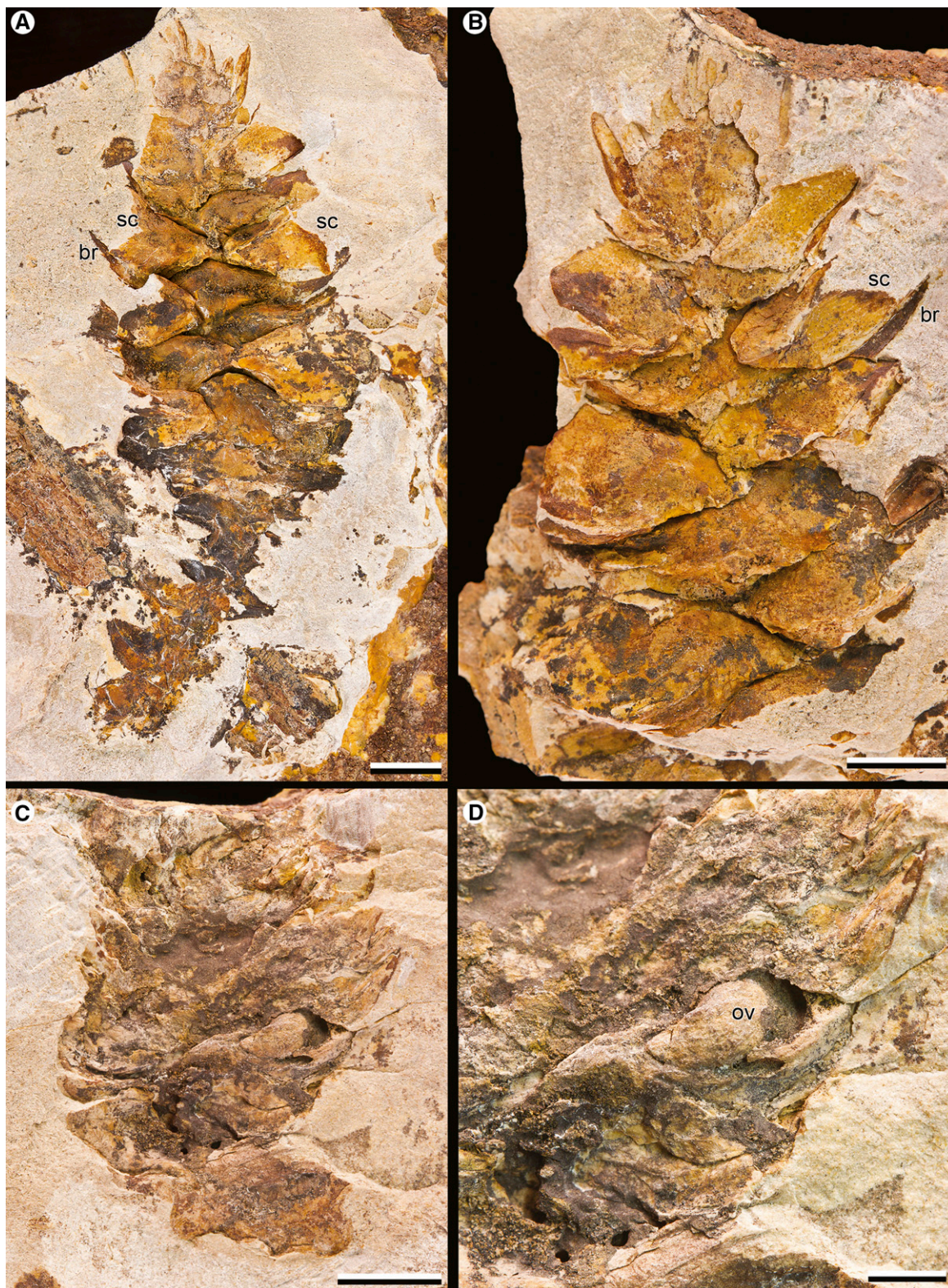**Species**—*Pararaucaria taquetrensis* Escapa et Leslie, sp. nov.

Specific diagnosis—Seed cones at least 22 mm long and up to 18 mm in diameter, bearing helically arranged bract-scale complexes 6.6–13.7 mm in length by 6.25–11.8 mm in width on a thin axis around 1.5 mm in diameter. Ovuliferous scales with three broad lobes, 0.5–1.0 mm long and 2–4 mm wide, arranged in two ranks with a single adaxially positioned central lobe. Ovuliferous scales bear one or two seeds measuring 3.9 mm long by 2.2 mm wide in a broad central depression covered by a flap of tissue. Ovulate cones borne terminally on relatively thick, ramified branches 2–4 mm in diameter bearing imbricated, *Brachyphyllum*-type scale leaves 1.8–3.0 mm long.

Holotype—MPEF-Pb 1893a,b, here designated (Fig. 2A, B; 4B; 7B). Deposited in the Museo Paleontologico Egidio Feruglio, Trelew, Chubut Province, Argentina.

Other illustrated material—*Pararaucaria taquetrensis* MPEF-Pb 2163 (Fig. 2C, D), MPEF-Pb 1894b (Fig. 3A), MPEF-Pb 1894a (Fig. 3B; 6D), MPEF-Pb 8901 (Fig. 3C), MPEF-Pb 2088 (Fig. 3D), MPEF-Pb 1903 (Fig. 3E; 6F), MPEF-Pb 2145 (Fig. 3F), MPEF-Pb 1908 (Fig. 3G), MPEF-Pb 1889 (Fig. 3H), MPEF-Pb 1869 (Fig. 4A), MPEF-Pb 1884 (Fig. 4C). *Pararaucaria delfueyoi* Escapa et al.
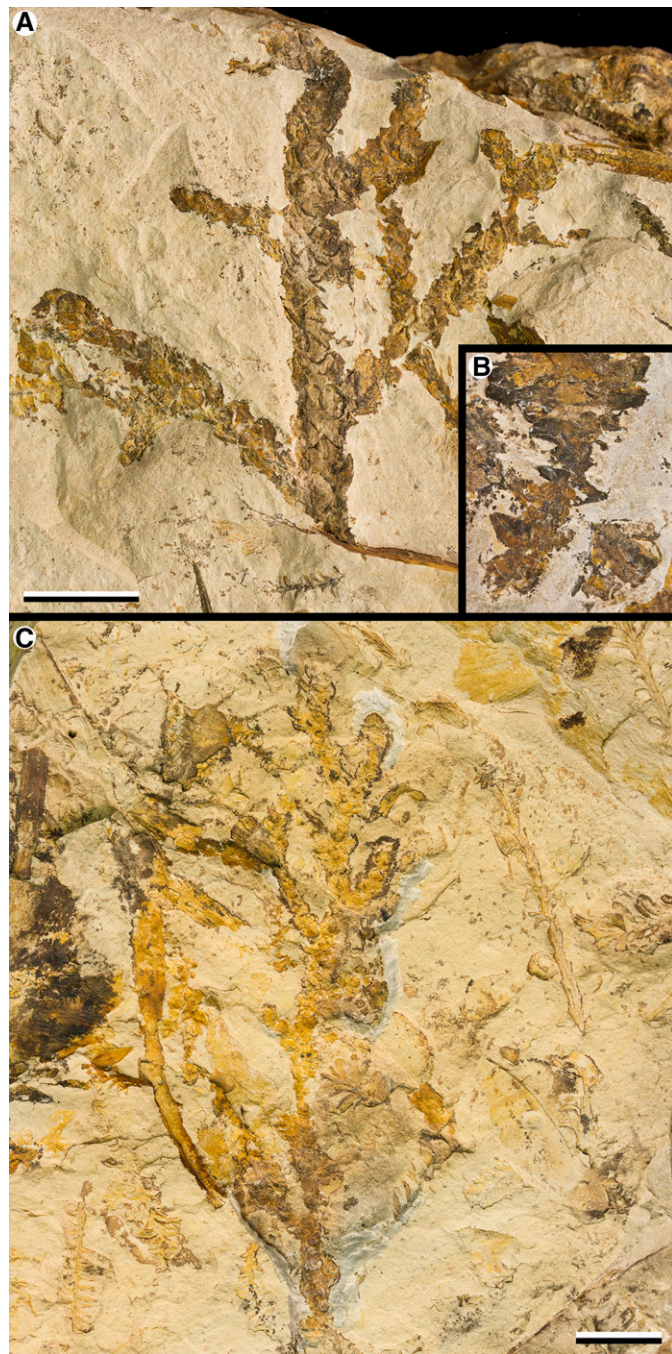
FIGURE 2 *Pararaucaria taquetrensis* Escapa et Leslie. (A). Articulated cone preserved in lateral view attached to *Brachyphyllum*-type foliage. Note the bracts subtending the ovuliferous scale, which together form a rhomboidal bract-scale complex impression. MPEF-Pb 1893a. Scale bar = 3 mm. (B) Counterpart of (A), showing separate bract and ovuliferous scale impressions. MPEF-Pb 1893b. Scale bar = 3 mm. (C) Articulated cone attached to *Brachyphyllum*-type foliage and containing the impression of either an individual seed or the entire pocket containing the seeds. MPEF-Pb 2163. Scale bar = 5 mm. (D) Close-up of (C). Scale bar = 2 mm. Note: sc = ovuliferous scale, br = bract; ov = ovule.
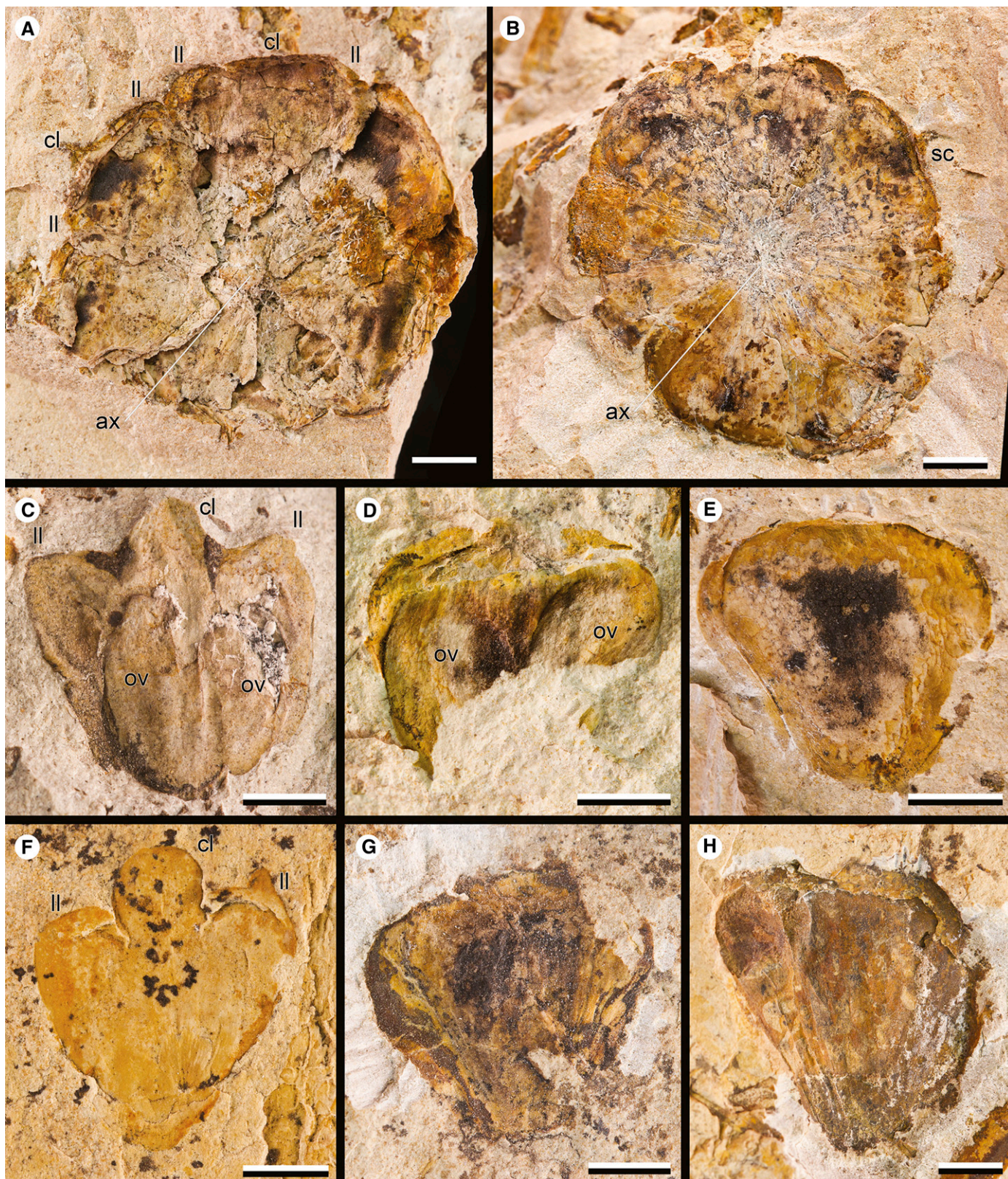
FIGURE 3 *Pararaucaria taquetrensis* Escapa et Leslie. (A) Articulated cone preserved in transverse section. This specimen is a three-dimensional cast that has been fractured through a single plane, therefore exposing the adaxial surfaces of the bract-scale complex on the part and the abaxial surfaces of the counterpart. MPEF-Pb 1894b. Scale bar = 3 mm. (B) Counterpart of (A), showing the abaxial surface of bracts subtending the ovuliferous scales. MPEF-Pb 1894a. Scale bar = 3 mm. (C) Isolated ovuliferous scale showing impressions of two seeds and the distal three. MPEF-Pb 8901. Scale bar = 2 mm.

FIGURE 4 *Pararaucaria taquetrensis* Escapa et Leslie. (A) Vegetative branch with *Brachyphyllum*-type foliage. MPEF-Pb 1869. Scale Bar = 10 mm. (B) Cone from Fig. 2A attached to Brachyphyllum-type foliage. MPEF-Pb 1893a. (C) Vegetative branch with Brachyphyllum-type foliage. MPEF-Pb 1884. Scale bar = 20 mm.

MPEF-Pb 1953, MPEF-Pb 5342, MPEF-Pb 1954. Deposited in the Museo Paleontologico Egidio Feruglio, Trelew, Chubut Province, Argentina.

Locality—Taquetrén and Taquetrén B localities in Chubut Province, Patagonia, Argentina. Coordinates available upon request.

Stratigraphic position and age—Lonco Trapial Group, Pleinsbachian to Toarcian stage (188.9–178.8 Ma), Early Jurassic.

Etymology—The species epithet refers to the Taquetrén localities where the material was discovered.

RESULTS

Seed cones—Four articulated seed cones of *Pararaucaria taquetrensis* were found in the material; although only three are preserved well enough to be described in detail. The first cone is preserved in lateral view and consists of a three-dimensional part and counterpart that preserves half of the exterior surface of a cone that is attached terminally to a leaf-bearing branch (Fig. 2A, B). The cone measures 22.9 mm long by 12.2 mm wide and it shows impressions of approximately 16 bract-scale complexes; the total number of bract-scale complexes was then probably between 30 and 40, although this is not known with certainty. The free tips of the bracts and ovuliferous scales are separated and visible at the edges of the cone where they bend upward (Fig. 2B). The visible exterior surface of the cone is therefore formed by the abaxial surface of the bract and ovuliferous scale, which together create a rhomboidal or diamond shaped impression (Fig. 2A, B).

A second cone is also preserved in lateral view and attached to foliage, but is not well preserved (Fig. 2C, D). This cone measures 17.2 mm long by 13.7 mm wide, but its length is probably not completely preserved. The specimen is broken in longitudinal section and shows imbricated bract-scale complexes (Fig. 2C, D), one of which preserves a wedge-shaped body that is likely either a seed or a mold of the internal seed-containing pocket (Fig. 2D). This body measures 3.75 mm long by 1.5 mm deep.

The third cone is well-preserved in transverse section, with a split between part and counterpart that is perpendicular to the cone axis (Fig. 3A, B). This cone is three-dimensionally preserved as a cast and does not appear to be flattened or otherwise altered during preservation. It measures 17.8 mm in diameter with a small central axis 1.5 mm in diameter, around which tightly imbricated cone scales are arranged. As in conifers generally, these cone scales represent bract-scale complexes where a bract subtends a modified shoot, called an ovuliferous scale, which produces seeds. Ovuliferous scales in this particular cone are wedge-shaped and measure between 7 and 8 mm in length by 6.5-8 mm in width. As in isolated ovuliferous scales (see paragraph below), three lobes are visible, i.e.,

(D) Isolated ovuliferous scale where the plane of section passes through the central pocket, showing impressions of two seeds with the base of the central lobe compressed and flattened over the lateral lobes. MPEF-Pb 2088. Scale bar = 3 mm. (E) Counterpart of (D), where the specimen shows the underside of the upper surface of the ovuliferous scale. In this case, there appears to be a single large central area, which corresponds to the entire pocket housing the seeds. MPEF-Pb 1903. Scale bar = 3 mm. (F) Isolated ovuliferous scale showing three distal lobes. MPEF-Pb 2145. Scale bar = 3 mm. (G) Isolated ovuliferous scale in adaxial view showing broad central region. In this specimen, distal lobes are not preserved. MPEF-Pb 1908. Scale bar = 3 mm (H) Large ovuliferous scale. MPEF-Pb 1889. Scale bar = 3 mm. Note: ax = central axis; cl = central lobe of the ovuliferous scale; ll = lateral lobe of the ovuliferous scale; ov = ovule; sc = ovuliferous scale.

two lateral lobes and one broad central lobe ending in a pointed apex (Fig. 3A). The bract-scale complexes also appear to form a helix; poor preservation makes this difficult to observe definitely but there is no evidence of a true decussate arrangement or of any other phyllotaxy.

Ovuliferous scales—Isolated ovuliferous scales measure 6.6–13.7 mm in length by 6.25–11.8 mm in width. They are cuneate in outline with three lobes fused for approximately 3/4 or more of their length (Fig. 3C-H). The unfused portions of the three lobes are arranged in two ranks, with a central lobe positioned above two lateral lobes (Fig. 3D, F). The central lobe has a pointed apex and measures between 0.5 and 1.0 mm in height by 2–4 mm in width, while lateral lobes are generally more rounded and measuring between 0.5 and 1.0 mm in height by 2–3 mm in width (Fig. 3C, D, F). It can be difficult to consistently determine the relative position and size of the lobes, however, because of differences in preservation coupled with the partial three-dimensional nature of the specimens. The specific plane of section through the specimen may expose different parts of the scale depending on where it passes through, and the scale itself may be partially deformed by compression prior to fossilization. For example, the part and counterpart of one specimen (Fig. 3D, E) is broken through the middle of the scale; the counterpart shows little evidence of lobation because it represents the upper, or adaxial, surface of the ovuliferous scale with the remains of only the central, highest, lobe (Fig. 3E). The lateral lobes, which occur below the central lobe, are only visible in the part (Fig. 3D) and which also appears to be partially flattened as well, based on the visible crease between the base of the central lobe and the distal ends of the lateral lobes (Fig. 3D).

Seeds—Seeds are preserved in three of the isolated ovuliferous scales; in all known cases two seeds are present per ovuliferous scale (Fig. 3C, D) although we cannot rule out the possibility that single seeds were produced in some fraction of the scales. A broad, wedge-shaped central depression measuring 4.7–5.7 by 4.0–5.1 mm is also present on many of the ovuliferous scales (Fig. 3E, G, H). This depression housed the seeds and is located in roughly the center of the ovuliferous complex, although it is deepest distally where it forms a steep indentation that abuts the distal end of the ovuliferous scale (Figs. 2D, 3D). Individual seeds measure 3.9 mm long by 2.2 mm wide, and are positioned within the central pocket so that their chalazal ends point somewhat laterally, away from the midline of the ovuliferous scale (Fig. 3C, D).

Vegetative remains—Branches with attached foliage similar to that found in organic connection with seed cones (see Fig. 2A) are common in the Taquetrén localities (Fig. 4A, B). We assign them to the form genus *Brachyphyllum* due to their relatively short, imbricated, and tightly clasping leaves. This foliage consists of impressions of ramifying axes with up to three orders of branching. These branches are relatively thick, with ultimate twigs between 2–4 mm in diameter when including the thick decurrent leaf bases. All orders of preserved branching bear helically arranged, imbricated, and tightly clasping scale leaves. Leaves measure 1.8–3.0 mm long by 1.8–2.7 mm wide, and have a pointed apex and apparently smooth margins, although preservation of the leaves is not great. Cuticle and stomata are not preserved in the foliage specimens.

Assignment to **Pararaucaria**—The genus *Pararaucaria* originally included only permineralized seed cones (Wieland, 1929, 1935; Stockey, 1977) and some of the diagnostic characters for the genus relate to anatomical features that are not preserved in *P. taquetrensis*. Nevertheless, we are confident in assigning this material to *Pararaucaria* due to its morphological similarity with previously described permineralized species from Patagonia (Escapa et al., 2012; Escapa et al., 2013), and thus expanding the concept of the genus to include impressions and molds. This assignment is primarily based on the morphology of the ovuliferous scale, particularly the presence of three broad distal lobes, a feature that is unique to *Pararaucaria* among described Cheirolepidiaceae (Clement-Westerhof and van Konijnenburg-van Cittert, 1991; Kvaček, 2000; Del Fueyo et al., 2008; Escapa et al., 2012). Like other described permineralized *Pararaucaria* (Escapa et al., 2012; Escapa et al., 2013), the lateral lobes of *P. taquetrensis* are slightly abaxial to the central lobe, and they are partially fused to it as well (Figs. 3D, F; 5).

This material is also consistent with *Pararaucaria* and in other respects, including the small overall size of the seed cones and their roughly cylindrical shape, a proportionally thin central cone axis, a prominent bract that is separated from the ovuliferous scale for most of its length, the presence of one or two seeds in a centrally located depression on the ovuliferous scale. Although ovuliferous scales in *P. taquetrensis* do not obviously show the "pocket-forming tissue" characteristic of Cheirolepidiaceae (see Clement-Westerhof and van Konijnenburg-van Cittert, 1991; Escapa et al., 2012), we would not expect to clearly see this delicate tissue given the preservation mode of these fossils. With the assignment to *Pararaucaria*, these fossils extend the range of this genus to the Lower Jurassic (most likely to the Pliensbachian), and provide the earliest macrofossil evidence of Cheirolepidiaceae reproductive structures in South America. The age of this material is also consistent with other aspects of the Cheirolepidiaceae fossil record from the Southern Hemisphere, including pollen cones (*Classostrobus* species) from the Early Jurassic (Toarcian) of Antarctica (Hieger et al., 2015) and the appearance of cheirolepidiaceous pollen (*Classopolis*) in the Southern Hemisphere in the Late Triassic and Early Jurassic (see e.g., Quattrocchio et al., 2011.

DISCUSSION

Comparison to Cheirolepidiaceae—*Pararaucaria taquetrensis* is similar in its general morphology to other *Pararaucaria* species, but it differs in size. Among South American species, *Pararaucaria patagonica* Wieland from the Middle-Late Jurassic La Matilde Formation of Santa Cruz Province of Argentina (Wieland, 1929; Stockey, 1977) is larger than *P. taquetrensis*, measuring up to 5 cm long and up to 2.6 cm wide (Stockey, 1977). Likewise, seed cones of *P. delfueyoi* from the Late Jurassic Cañadón Calcáreo Formation of Chubut Province (Escapa et al., 2013) are up to 8 cm long by 4 cm wide, with ovuliferous scales approximately twice the width of *P. taquetrensis* (Escapa et al., 2013). The largest isolated *P. taquetrensis* ovuliferous scale (13.7 mm long) suggests that some cones of this species may have reached up to 3 cm in width, but most dispersed scales are much smaller. Among Northern Hemisphere species, *Pararaucaria carrii* Stockey and Rothwell from the Middle Jurassic (Callovian) of Oregon (Stockey and Rothwell, 2013) also appears to be larger than *P. taquetrensis*, with a central axis up to 3.5 mm in diameter. Like many permineralized conifer cones, the true size of
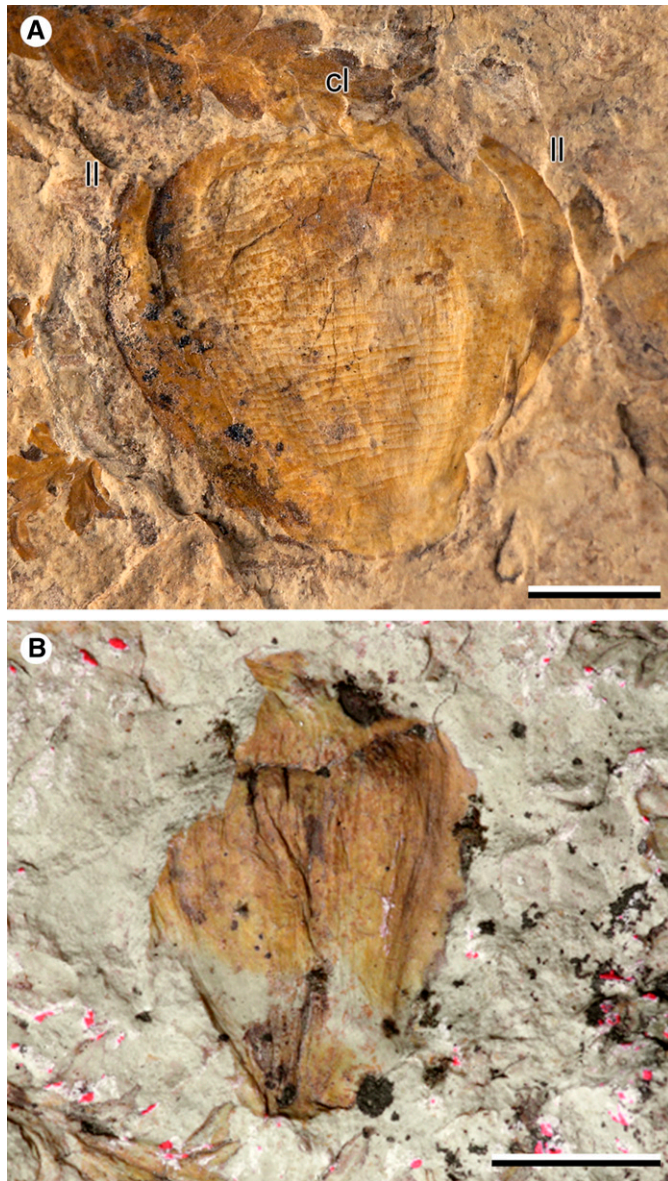
FIGURE 5 Previously described and illustrated specimens synonymous with *Pararaucaria taquetrensis*. (A) *Araucarites sp.* (Herbst and Anzótegui, 1968), specimen CTES-PB 113. (B) *Feruglio sp.* (Bonetti, 1964), specimen BA Pb 7785. Note: cl = central lobe of the ovuliferous scale; ll= lateral lobe of the ovuliferous scale.

this species is incompletely known because its surface was abraded prior to fossilization. *Pararaucaria collinsonae* Steart, Spencer, Kenrick, Needham & Hilton from the Late Jurassic (Tithonian) of England (Steart et al., 2014) is also abraded, but in this case the species appears to have had smaller cones than *P. taquetrensis;* they were unlikely to be more than 1.5 cm in length or width (Steart et al., 2014). Finally, an unnamed *Pararaucaria* species from the Late Jurassic Morrison Formation of Utah, USA (Morphotype 5; Gee et al., 2014) is close in size to *P. taquentrensis*, but it appears to be somewhat larger (central cone axis around 2.5 mm in diameter with seeds around 5 mm long).

In comparison to other Cheirolepidiaceae, *Pararaucaria* differs from all other genera in having fewer and less clearly distinct ovuliferous scale lobes (Fig. 6). For example, the younger Patagonian Cheirolepidiaceae genera *Kachaikestrobus* and *Tomaxellia* from the Early Cretaceous of Santa Cruz Province both have either four or five lobes rather than three (Archangelsky, 1968; Del Fueyo et al., 2008). Late Triassic *Pseudohirmeriella* from North America had five pointed lobes arranged in a single rank (Axsmith et al., 2004) and the well-known Late Triassic—Middle Jurassic European genus *Hirmeriella* has two sets of lateral lobes in addition to a small central lobe on its ovuliferous scale (Clement-Westerhof and van Konijnenburg-van Cittert, 1991). Seed cones of *Alvinia bohemica* (Velenovský) Kvaček from the Cenomanian of Europe (Kvaček, 2000) have ovuliferous scales with a similar arrangement, although the specific morphology of the lobes is distinctive and may reflect specialized pollination biology. Despite these differences, *Pararaucaria* species share a number of basic structural similarities with other Cheirolepidiaceae seed cones that suggest they belong to the same lineage. In particular, their bract and ovuliferous scales are separated across their length, their ovuliferous scales appear to be shed as units because they are commonly found isolated and not associated with bracts (see Clement-Westerhof and van Konijnenburg-van Cittert, 1991), and they all possess a similar flap of "pocket-forming tissue" that loosely covers the seeds. Even stronger evidence of a cheirolepidiaceous affinity for *Pararaucaria* would be provided by pollen (the presence of *Classopollis*) and cuticular morphology (Florin rings around a sunken stomatal pit), but these are not currently known.

Comparison to other conifers—*Pararaucaria* cones and bract scale complexes are morphologically distinctive from those of every major conifer clade (including the Cupressaceae, Pinaceae, Podocarpaceae, Sciadopityaceae, and Taxaceae) except the Araucariaceae, which also have wedge-shaped complexes whose seeds are covered by flaps of tissue. The central lobe of the *Pararaucaria* ovuliferous scale can also be easily confused with the free tip of the ovuliferous scale (often referred as the 'ligule') in *Araucaria*, further contributing to potential misidentification. In fact, the first publications of the Taquetrén flora described isolated conifer cone scales identical to *Pararaucaria taquetrensis* as *Araucarites* (Bonetti, 1964; Herbst and Anzótegui, 1968; see Fig. 5A, B), a form genus used for bract-scale complexes belonging to Araucariaceae (Pant and Srivastava, 1968; Mildenhall and Johnston, 1971; Zijlstra and van-Konijnenburg van-Cittert, 2000). The gross morphological similarities among these taxa are misleading, however; the isolated cone scales of *Pararaucaria taquetrensis* are the ovuliferous scales alone while those of *Araucarites* and other Araucariaceae are the remains of the entire bract-scale complex, where the bract and ovuliferous scale are fused for nearly their entire length. The apparent central lobe of some *Araucarites* and modern *Araucaria* bract-scale complexes then represents the remains of a small, unfused portion of the ovuliferous scale, while the basic shape of the complex reflects the morphology of the bract. Unambiguous araucarian bract-scale complexes are also typically larger than Cheirolepidiaceae scales, and have more tissue between the central seed body and the distal margin of the complex. In contrast, the seed pocket of *Pararaucaria* is more centrally located because there is little scale tissue either distal or proximal to the seed. Finally, *Pararaucaria* may contain two seeds rather than one as in all extinct and extant Araucariaceae genera, although as noted above, the number of seeds can be difficult to determine from impressions of *Pararaucaria* scales.
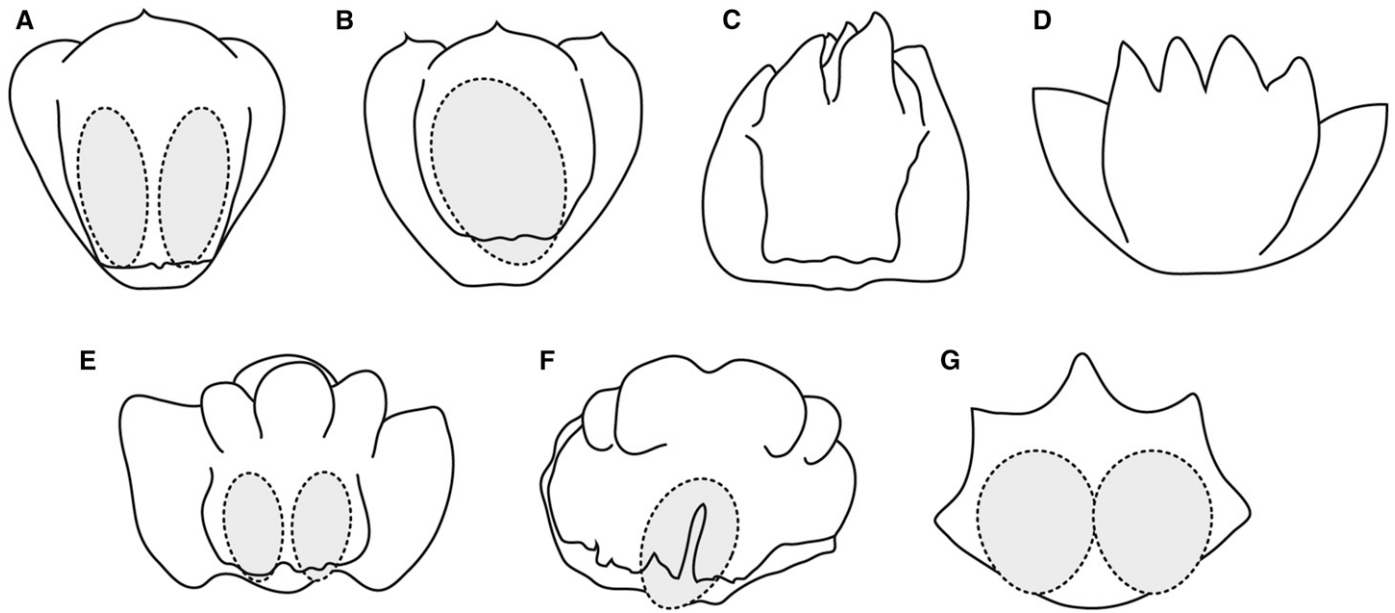
FIGURE 6 Comparison of ovuliferous scale morphology in selected Cheirolepidiaceae. (A) *Pararaucaria taquetrensis*. (B) *Pararaucaria patagonica* (after Escapa et al., 2012). (C) *Kachaikestrobus acuminatus* Del Fueyo, Archangelsky, Llorens & Cúneo, (after Del Fueyo et al., 2008). (D) *Tomaxellia biforme* Archangelsky (after Archangelsky, 1968). (E) *Hirmeriella muensteri* (Schenk) Jung (after Clement-Westerhof and van Konijnenburg-van Cittert, 1991). (F) *Alvinia bohemica* (Velenovský) Kvaček (after Kvaček). (G) *Pseudohirmeriella delawarensis* Axsmith, F.M. Andrews & N.C. Fraser (after Axsmith et al., 2004). Ovuliferous scales are now shown to scale, and bracts are not illustrated. Seeds are indicated in light gray.

The basic differences in the structure of bract-scale complexes between Araucariaceae and all Cheirolepidiaceae, particularly in terms of the degree of fusion between the ovuliferous scale and the bract, suggest that these are distinctive lineages and that *Pararaucaria* is more closely related to the Cheirolepidiaceae. Beyond individual bract-scale complexes, Araucariaceae also differ in reproductive morphology from Cheirolepidiaceae. Araucariaceae cones typically have a thick axis with a large pith that contributes to their generally globose shape, while in contrast, Cheirolepidiaceae often have cylindrical cones (at least among the larger species) with a very thin central cone axis (Stockey, 1977; Escapa et al., 2012). Araucariaceae seed cones are also generally larger than those of Cheirolepidiaceae, although individual Araucariaceae bract-scale complexes are proportionally smaller relative to the whole seed cone. This generates distinctive differences in phyllotaxy between the groups; for example, the numerous, relatively small Araucariaceae bract-scale complexes form clear parastiches (see Stockey, 1978) while these are not as visible in *Pararaucaria*, where the bract scale complexes almost appear to form orthostiches as if the scales were decussate (Fig. 2A, B; 7A, B). Such differences in cone structure and phyllotaxy may be important for distinguishing Cheirolepidiaceae from Araucariaceae in future studies of compression or impression material.

Broader Implications—The specimens from the Lonco Trapial Formation illustrate the importance of comparing permineralized and compression/impression fossils, as the initial determination that this material belonged to the Cheirolepidiaceae rather than the Araucariaceae was based on comparison to permineralized *Pararaucaria* cones from the Late Jurassic (Fig. 7). Permineralized specimens suggested that the overall shape and distinctive phyllotaxy of the impression cones (Fig. 7A-D) were more consistent with

Cheirolepidiaceae than Araucariaceae, which then allowed us to reinterpret of the morphology of the isolated cone scales as three lobes of an ovuliferous scale (Fig. 7A) rather than as an araucarian bract-scale complex with a central "ligule". Potential confusion between the reproductive structures of Araucariaceae and Cheirolepidiaceae is also exacerbated by preservation as compressions or impressions, which can obscure relevant information like the presence of lobes and "pocket-forming tissues" needed to distinguish the groups. Our results imply that at least some *Araucarites* may actually belong to *Pararaucaria* or to *Pararaucaria*-like Cheirolepidiaceae, and that careful measurements of the size and relative position of the seeds are necessary to distinguish between the groups. Just as the insight that permineralized *Pararaucaria* belonged to the Cheirolepidiaceae (Escapa et al., 2012) was followed by wider recognition of the genus in other permineralized cones (Escapa et al., 2013; Stockey and Rothwell, 2013; Steart et al., 2014, identifying the compression/impression form of *Pararaucaria* and distinguishing it from *Araucarites* may facilitate a wider recognition of the genus and therefore a better understanding of its temporal and ecological range.

Properly identifying Cheirolepidiaceae in the compression record will provide a clearer picture of the relative diversity and abundance of major Mesozoic conifer groups in fossil floras. This is important from a paleoecological perspective because different conifers are often thought to indicate different environmental conditions; the Cheirolepidiaceae in particular are often associated with indicators of high temperature, water stress, and salinity (Alvin, 1982; Watson, 1988; Axsmith and Jacobs, 2005; Moreau et al., 2015). Distinguishing between Cheirolepidiaceae and Araucariaceae in a given fossil assemblage may then substantially alter the paleoecological interpretation of a given flora, although care must be taken with such an assessment because Cheirolepidiaceae are
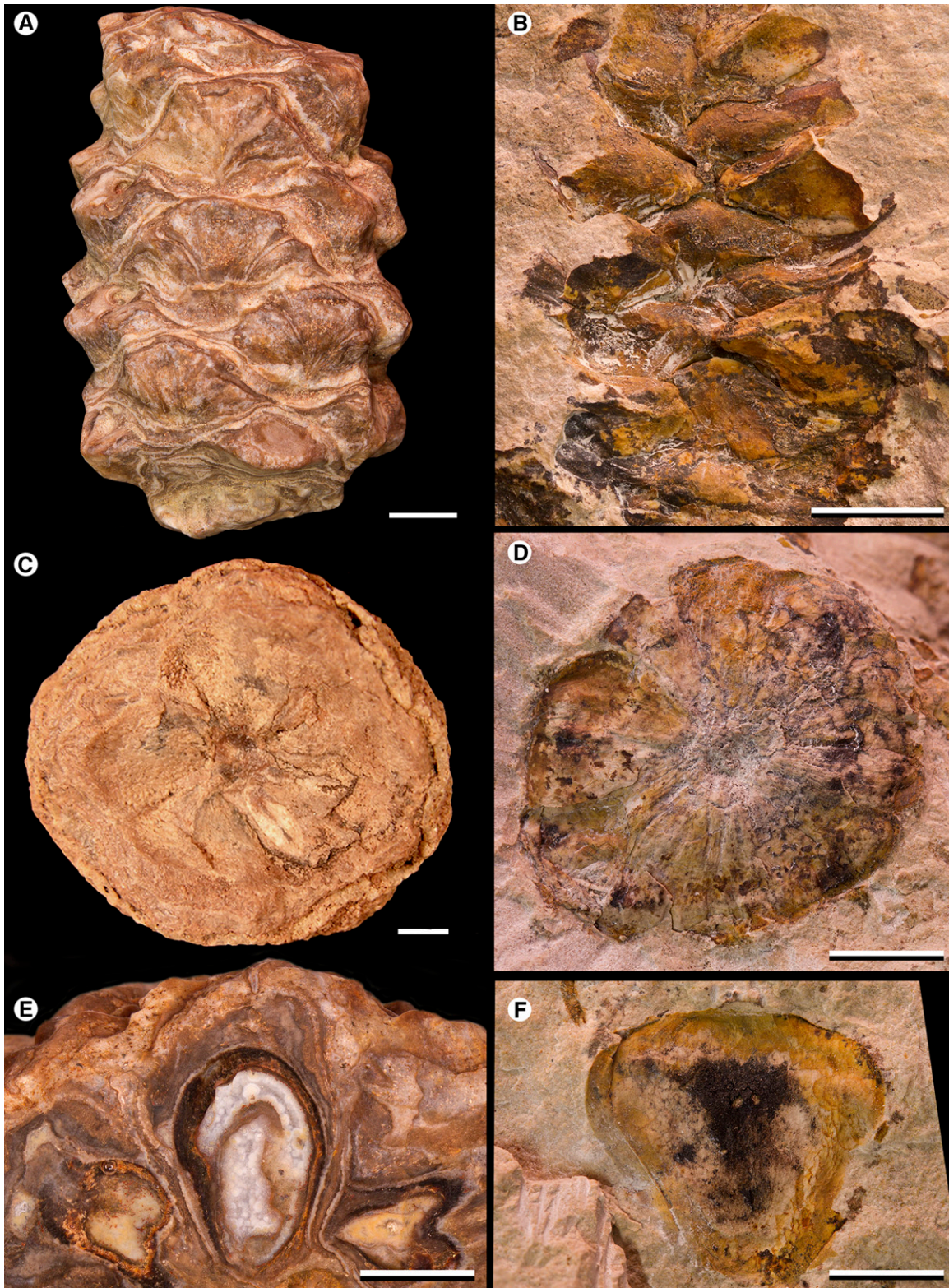
FIGURE 7 Comparison of *Pararaucaria taquetrensis* to permineralized *Pararaucaria delfueyoi*. Note the similarity in the phyllotaxy of the cones, the visible separation between the bracts and the ovuliferous scales, and the similarity in the relation position of the seed on the ovuliferous scale. (A) *Pararaucaria delfueyoi*. MPEF-Pb 1953. Scale bar = 5 mm. (B) *Pararaucaria taquetrensis*. MPEF-Pb 1893a. Scale bar = 3 mm. (C) *Pararaucaria delfueyoi*. Scale bar = 3 mm. (D) *Pararaucaria taquetrensis*. MPEF-Pb 1894a. Scale bar = 3 mm (E) MPEF-Pb 1954. *Pararaucaria delfueyoi*. Scale bar = 5 mm. (F) *Pararaucaria taquetrensis*. MPEF-Pb 1903. Scale bar = 3 mm.

not uniform in their ecology and may appear in wetter environments as well (see e.g., Upchurch and Doyle, 1981). This appears to be the case in Taquetrén itself, where *Pararaucaria* occurs in association with a high diversity of ferns, seed ferns, and early members of Cupressaceae that suggest a fairly mesic environment. Regardless of their exact ecology, our material shows that Cheirolepidiaceae were a component of Patagonian forests by the Early Jurassic.

From a phylogenetic perspective, the shoots, leaves, and seed cones preserved here in organic connection provide an important step toward reconstructing the *Pararaucaria* plant. Such whole-plant reconstructions are crucial for morphological phylogenetic analyses because they provide much richer and more complete character information for taxa, which help to increase resolution and support for phylogenetic relationships. Although a more detailed understanding of *Pararaucaria* cuticular morphology and leaf anatomy would be ideal, the present material shows that at least some species of *Pararaucaria* produced scale-leaf foliage on ramified branches. *Pararaucaria* is then similar in overall vegetative morphology to known Cheirolepidiaceae, despite its reduced ovuliferous scale with only three lobes. This material further suggests that Cheirolepidiaceae with reduced ovuliferous scales appear in the fossil record at nearly the time as those with more complex scales such as *Hirmeriella*, which makes it difficult to assess the likely ancestral state for the group. A reduced ovuliferous scale with only a few lobes is similar to some Triassic "voltzialean" conifers such as *Telemachus* (Escapa et al., 2010; Bomfleur et al., 2013). Whether this implies any direct relationship is unclear, but better reconstructions of fossil taxa are a necessary step in untangling the phylogenetic relationships among the Cheirolepidiaceae, Araucariaceae, "voltzialeans," and conifers more generally. The *Pararaucaria taquetrensis* material described here provides an important step in that direction by linking vegetative and reproductive organs for the first time.

CONCLUSIONS

Given the age of the Taquetrén localities (well-constrained to be Early Jurassic and most likely Pleinsbachian), *Pararaucaria taquetrensis* represents the earliest known Cheirolepidiaceae seed-cone macrofossils in South America, and they are among the oldest known seed-cone macrofossils for the group as a whole. These fossils expand the temporal range of the *Pararaucaria* genus to the Lower Jurassic, and they show for the first time an organic connection between seed cones of this genus and *Brachyphyllum*-type scale-leaf foliage. This material highlights the need to link compression and impression remains of conifers with permineralized counterparts, to more fully understand the morphological, spatial, and temporal distribution of taxa. This material also suggests that isolated seed cone scales of Araucariaceae and Cheirolepidiaceae may easily be confused, which has important implications for understanding broad conifer diversity patterns and paleoecological interpretations.

ACKNOWLEDGEMENTS

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. *Journal of the Linnean Society of London. Botany* 61: 153–165.

Axsmith, B. J., 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.

Barreda, V. D., N. R. Cúneo, P. Wilf, E. D. Currano, R. A. Scasso, and H. Brinkhuis. 2012. Cretaceous/Paleogene floral turnover in Patagonia: Drop in diversity, low extinction, and a *Classopollis* spike. *PLoS One* 7: e52455.

Bomfleur, B., A. L. Decombeix, I. H. Escapa, A. B. Schwendemann, and B. Axsmith. 2013. Whole-plant concept and environment reconstruction of a Telemachus conifer (Voltziales) from the Triassic of Antarctica. *International Journal of Plant Sciences* 174: 425–444.

Bomfleur, B., A. L. Decombeix, A. B. Schwendemann, I. H. Escapa, E. L. Taylor, T. N. Taylor, and S. McLoughlin. 2014. Habit and ecology of the *Petriellales*, an unusual group of seed plants from the Triassic of Gondwana. *International Journal of Plant Sciences* 175: 1062–1075.

Bonetti, M. I. R. 1964. Flórula Mesojurásica de la zona de Taquetrén (Cañadón del Zaino) Chubut. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". *Paleontología* 1: 23–43.

Calder, M. G. 1953. A coniferous petrified forest in Patagonia. *Bulletin of the British Museum (Natural History). Geology* 2: 97–138.

Chaw, S. M., C. L. Parkinson, Y. Cheng, T. M. Vincent, and J. D. Palmer. 2000. Seed plant phylogeny inferred from all three plant genomes: Monophyly of extant gymnosperms and origin of Gnetales from conifers. *Proceedings of the National Academy of Sciences, USA* 97: 4086–4091.

Clement-Westerhof, J. A., and J. H. A. van Konijnenburg-van Cittert. 1991. *Hirmeriella muensteri*: New data on the fertile organs leading to a revised concept of the Cheiroleopiaceae. *Review of Palaeobotany and Palynology* 68: 147–179.

Cúneo, R., J. Ramezani, R. Scasso, D. Pol, I. Escapa, A. M. Zavattieri, and S. A. Bowring. 2013. High-precision U–Pb geochronology and a new chronostratigraphy for the Cañadón Asfalto Basin, Chubut, central Patagonia: Implications for terrestrial faunal and floral evolution in Jurassic. *Gondwana Research* 24: 1267–1275.

Del Fueyo, G. M., S. Archangelsky, M. Llorens, and R. Cúneo. 2008. Coniferous ovulate cones from the Lower Cretaceous of Santa Cruz Province, Argentina. *International Journal of Plant Sciences* 169: 799–813.

DiMichele, W. A., H. J. Falcon-Lang, W. J. Nelson, S. D. Elrick, and P. R. Ames. 2007. Ecological gradients within a Pennsylvanian mire forest. *Geology* 35: 415–418.

Escapa, I. H., R. Cúneo, and G. Cladera. 2008. New evidence for the age of the Jurassic Flora from Cañadón del Zaino, Sierra de Taquetrén, Chubut. *Ameghiniana* 45: 633–637.

Escapa, I. H., N. R. Cúneo, G. W. Rothwell, and R. A. Stockey. 2013. *Pararaucaria delfueyoi* sp. nov. from the Late Jurassic Cañadón Calcáreo Formation, Chubut, Argentina: Insights into the evolution of the Cheirolepidiaceae. *International Journal of Plant Sciences* 174: 458–470.

Escapa, I. H., A. L. Decombeix, E. L. Taylor, and T. N. Taylor. 2010. Evolution and relationships of the conifer seed cone *Telemachus*: Evidence from the Triassic of Antarctica. *International Journal of Plant Sciences* 171: 560–573.

Escapa, I. H., G. W. Rothwell, R. A. Stockey, and N. R. Cúneo. 2012. Seed cone anatomy of Cheirolepidiaceae (Coniferales): Reinterpreting *Pararaucaria patagonica* Wieland. *American Journal of Botany* 99: 1058–1068.

Escapa, I. H., E. L. Taylor, R. Cúneo, B. Bomfleur, J. Bergene, R. Serbet, and T. N. Taylor. 2011. Triassic floras of Antarctica: Plant diversity and distribution in high paleolatitude communities. *Palaios* 26: 522–544.

Falcon-Lang, H. J., W. J. Nelson, S. Elrick, C. V. Looy, P. R. Ames, and W. A. DiMichele. 2009. Incised channel fills containing conifers indicate that seasonally dry vegetation dominated Pennsylvanian tropical lowlands. *Geology* 37: 923–926.

Farjon, A. 2010. A handbook of the world's conifers. Brill, Leiden, Netherlands.

Figari, E. G. 2005. Evolución Tectónica de la Cuenca de Cañadón Asfalto. Ph.D. dissertation, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Buenos Aires, Buenos Aires, Argentina.

Figari, E. G., R. A. Scasso, N. R. Cúneo, and I. H. Escapa. 2015. Estratigrafía y evolución geológica de la Cuenca de Cañadón Asfalto, Provincia del Chubut, Argentina. *Latin American Journal of Sedimentology and Basin Analysis* 22: 135–169.

Friis, E. M., P. R. Crane, K. R. Pedersen, S. Bengtson, P. C. Donoghue, G. W. Grimm, and M. Stampanoni. 2007. Phase-contrast X-ray microtomography links Cretaceous seeds with Gnetales and Bennettitales. *Nature* 450: 549–552.

Gee, C. T., R. D. Dayvault, R. A. Stockey, and W. D. Tidwell. 2014. Greater palaeobiodiversity in conifer seed cones in the Upper Jurassic Morrison Formation of Utah, USA. *Palaeobiodiversity and Palaeoenvironments* 94: 363–375.

Herbst, R., and M. L. Anzótegui. 1968. Nuevas plantas de la flora del Jurásico Medio (Matildense) de Taquetrén, Provincia de Chubut. *Ameghiniana* 5: 183–190.

Hernandez-Castillo, G. R., R. A. Stockey, G. W. Rothwell, and G. Mapes. 2009. Reconstructing *Emporia lockardii* (Voltziales: Emporiaceae) and initial thoughts on Paleozoic conifer ecology. *International Journal of Plant Sciences* 170: 1056–1074.

Hieger, T. J., R. Serbet, C. J. Harper, T. N. Taylor, E. L. Taylor, and E. L. Gulbranson. 2015. Cheirolepidiaceous diversity: An anatomically preserved pollen cone from the Lower Jurassic of southern Victoria Land, Antarctica. *Review of Palaeobotany and Palynology* 220: 78–87.

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.

Leslie, A. B., J. M. Beaulieu, H. S. Rai, P. R. Crane, M. J. Donoghue, and S. Mathews. 2012. Hemisphere-scale differences in conifer evolutionary dynamics. *Proceedings of the National Academy of Sciences, USA* 109: 16217–16221.

Lesta, P. J., and R. Ferello. 1972. Región extrandina de Chubut y norte de Santa Cruz. *In* A. F. Leanza [ed.], Geología Regional Argentina, 601-653. Academia Nacional de Ciencias, Córdoba, Argentina.

Lizuain, A., and D. Silva Nieto. 2005. Observaciones geológicas en la region del río Chico, Gastre, Río Chubut Medio. Provincia de Chubut. *16° Congreso Geológico Argentino, La Plata, Actas* 1: 133–139.

Mildenhall, D. C., and M. R. Johnston. 1971. A megastrobilus belonging to the genus *Araucarites* from the upper Motuan (upper Albian), Wairarapa, North Island, New Zealand. *New Zealand Journal of Botany* 9: 67–79.

Miller, C. N. 1999. Implications of fossil conifers for the phylogenetic relationships of living families. *Botanical Review* 65: 239–277.

Moreau, J. D., D. Néraudeau, P. Tafforeau, and É. Dépré. 2015. Study of the histology of leafy axes and male cones of *Glenrosa carentonensis* sp. nov. (Cenomanian flints of Charente-Maritime, France) using synchrotron microtomography linked with palaeoecology. *PLoS One* 10: e0134515.

Nullo, F., and C. Proserpio. 1975. La Formación Taquetrén en Cañadón del Zaino (Chubut) y sus relaciones estratigráficas en el ámbito de la Patagonia, de acuerdo a la flora, República Argentina. *Revista de la Asociación Geológica Argentina* 30: 133–150.

Owens, J. N., G. L. Catalano, S. J. Morris, and J. Aitken-Christie. 1995. The reproductive biology of Kauri (*Agathis australis*). I. Pollination and prefertilization development. *International Journal of Plant Sciences* 156: 257–269.

Pant, D. D., and G. K. Srivastava. 1968. On the cuticular structure of *Araucaria* (*Araucarites*) *cutchensis* (Feistmantel) comb. nov. from the Jabalpur Series, India. *Journal of the Linnean Society of London. Botany* 61: 201–206.

Quattrocchio, M. E., W. Volkheimer, A. M. Borromei, and M. Martínez. 2011. Changes of the palynobiotas in the Mesozoic and Cenozoic of Patagonia: A review. *Biological Journal of the Linnean Society. Linnean Society of London* 103: 380–396.

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., and R. Serbet. 1994. Lignophyte phylogeny and the evolution of spermatophytes: A numerical cladistic analysis. *Systematic Botany* 19: 443–482.

Rothwell, G. W., and R. A. Stockey. 2002. Anatomically preserved *Cycadeoidea* (Cycadeoidaceae), with a reevaluation of systematic characters for the seed cones of Bennettitales. *American Journal of Botany* 89: 1447–1458.

Schwendemann, A. B., T. N. Taylor, E. L. Taylor, and M. Krings. 2010. Organization, anatomy, and fungal endophytes of a Triassic conifer embryo. *American Journal of Botany* 97: 1873–1883.

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.

Srivastava, S. K. 1976. The fossil pollen genus *Classopollis*. *Lethaia* 9: 437–457.

Steart, D. C., A. R. Spencer, R. J. Garwood, J. Hilton, M. C. Munt, J. Needham, and P. Kenrick. 2014. X-ray synchrotron microtomography of a silicified Jurassic Cheirolepidiaceae (Conifer) cone: Histology and morphology of *Pararaucaria collinsonae* sp. nov. *PeerJ* 2: e624.

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

Stockey, R. A. 1978. Reproductive biology of Cerro Cuadrado fossil conifers: Ontogeny and reproductive strategies in *Araucaria mirabilis* (Spegazzini) Windhausen. *Palaeontographica , B. Paläophytologie* 166: 1–15.

Stockey, R. A., and G. W. Rothwell. 2013. *Pararaucaria carrii sp. nov.*, anatomically preserved evidence for the conifer family Cheirolepidiaceae in the Northern Hemisphere. *International Journal of Plant Sciences* 174: 445–457.

Takhtajan, A. L. 1963. Gymnosperms and angiosperms. *Osnovy Paleontologii* 15:1–743. (In Russian).

Taylor, T. N., and K. L. Alvin. 1984. Ultrastructure and development of Mesozoic pollen: *Classopollis. American Journal of Botany* 71: 575–587.

Taylor, T. N., H. Kerp, and H. Hass. 2005. Life history biology of early land plants: Deciphering the gametophyte phase. *Proceedings of the National Academy of Sciences, USA* 102: 5892–5897.

Tomlinson, P. B., J. E. Braggins, and J. A. Rattenbury. 1991. Pollination drop in relation to cone morphology in Podocarpaceae: A novel reproductive mechanism. *American Journal of Botany* 78: 1289–1303.

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.

Upchurch, G. R., and J. A. Doyle. 1981. Paleoecology of the conifers *Frenelopsis* and *Pseudofrenelopsis* (Cheirolepidiaceae) from the Cretaceous Potomac Group of Maryland and Virginia. *In* R.C. Romans [ed.], Geobotany II, 167-202. Plenum Press, New York, New York, USA.

van der Ham, R. W. J. M., J. H. A. van Konijnenburg-van Cittert, R. W. Dortangs, G. F. W. Herngreen, and J. van der Burgh. 2003. *Brachyphyllum patens* (Miquel) comb. nov.(Cheirolepidiaceae?): Remarkable conifer foliage from the Maastrichtian type area (Late Cretaceous, NE Belgium, SE Netherlands). *Review of Palaeobotany and Palynology* 127: 77–97.

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, District of Columbia, USA.

Yao, X., Z. Zhou, and B. Zhang. 1998. Reconstruction of the Jurassic conifer *Sewardiodendron laxum* (Taxodiaceae). *American Journal of Botany* 85: 1289–1300.

Zijlstra, G., and J. H. A. van Konijnenburg-van Cittert. 2000. Proposal to conserve the name *Araucarites* C. Presl (Fossil Gymnospermae, Coniferales, Araucariaceae) against *Araucarites* Endl.(Fossil Gymnospermae, Coniferales). *Taxon* 49: 279–280.