

## CONIFEROUS OVULATE CONES FROM THE LOWER CRETACEOUS OF SANTA CRUZ PROVINCE, ARGENTINA

Georgina M. Del Fueyo,<sup>1,\*</sup> Sergio Archangelsky,<sup>2,\*</sup> Magdalena Llorens,<sup>3,†</sup> and Rubén Cúneo<sup>4,†</sup>

\*División Paleobotánica, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Avenida Angel Gallardo 470, 1405 Buenos Aires, Argentina; and †Museo Egidio Feruglio, Avenida Fontana 140, 9100 Trelew, Chubut, Argentina

Two types of coniferous ovulate cones borne on leafy twigs are described from the Lower Cretaceous Kachaiké Formation in Santa Cruz Province, Argentina. The fossils are impressions and compressions with well-preserved cuticles. Morphology, anatomy, and ultrastructure were studied using LM, SEM, and TEM. Ovulate cones were assigned to *Athrotaxis ungeri* (Halle) Florin of the taxodiaceous Cupressaceae and *Kachaikastrobus acuminatus* gen. et sp. nov. of the Cheirolepidiaceae. This latter taxon is characterized by terminal elongate cones borne on twigs with *Brachyphyllum* leaves, cone scales densely and helically disposed, broad bracts with an accentuated acuminate apex fused at their bases to eight-lobed ovuliferous dwarf shoots shorter than the bracts, and an epimatium covering at least one ovule that has preserved only the outer integument and the megaspore membrane. The ultrastructure of the bract and ovuliferous dwarf shoot cuticle is composed of three layers. Comparisons of *K. acuminatus* with other cheirolepidiacean ovulate cones showed closest resemblance to *Hirmeriella muensteri* (Schenk) Jung. These Patagonian cone scales appear to have some of the most ancestral characters in the family. By the early Albian, *A. ungeri* and *K. acuminatus* were part of a plant assemblage dominated by ferns and a few subordinate angiosperms. The finding of *A. ungeri* in the Kachaiké Formation extends its distribution during the Lower Cretaceous in Patagonia. These fossils also show that at that time, the taxodiaceous Cupressaceae and the Cheirolepidiaceae still were well represented in southern South America.

**Keywords:** Argentina, Cheirolepidiaceae, conifers, Kachaiké Formation, Lower Cretaceous, ovulate cones, Patagonia, taxodiaceous Cupressaceae.

### Introduction

The occurrence of coniferous ovulate cones in the Mesozoic of Patagonia is well documented with families such as Araucariaceae, Podocarpaceae, Cheirolepidiaceae, and taxodiaceous Cupressaceae (Archangelsky 1966). Unique remains, such as *Araucaria mirabilis* (Spegazzini) Windhausen (Stockey 1978) in the Araucariaceae, are found in the famous Jurassic Cerro Cuadrado petrified forest. Also present is *Pararaucaria patagonica* Wieland, which may represent an intermediate position between the taxodiaceous Cupressaceae and Pinaceae, according to Calder (1953) and Stockey (1977), or within the Voltziaceae, in the opinion of Miller (1999).

*Romeroites argentinesis* is another permineralized seed cone from the Upper Jurassic Vaca Muerta Formation attributed to taxodiaceous Cupressaceae (Spegazzini 1924a). In addition, several Cretaceous megasporangiate cones based on compressions were studied from the Aptian Anfiteatro de Ticó Formation (Baqueró Group): *Trisacocladius tigrensis* (Archangelsky 1966) and *Squamastrobus tigrensis* (Archangelsky and Del Fueyo 1989) of the Podocarpaceae and *Tomaxellia biforme* (Archangelsky and Gamero 1967; Archangelsky 1968) of the

Cheirolepidiaceae. *Athrotaxis ungeri* (Halle 1913; Florin 1940) referred to the taxodiaceous Cupressaceae was found at the Río de los Fósiles locality from the Albian Kachaiké Formation. This unit that holds the coniferous reproductive structures studied here is characterized by having diverse plant assemblages, including Bennettitales, Cycadales, Pteridophytes, and Coniferales (Frenguelli 1935; Baldoni and Ramos 1981; Longobucco et al. 1985; Llorens and Del Fueyo 2003). Few Bryophytes and uncertain conifer remains are also present (Halle 1913; Rebasá 1982), while angiosperms are represented by at least seven leaf morphotypes (Cúneo and Gandolfo 2005). Palynological data further confirm that the Kachaiké Formation contains a high number of species belonging to several major groups: Algae, Dinoflagellate cysts, Bryophytes, Pteridophytes, Coniferophytes, and Angiosperms (Gamero 1982; Archangelsky and Llorens 2003, 2005; Barreda and Archangelsky 2006; Guler and Archangelsky 2006).

In this article, coniferous ovulate cones organically connected to branches and recovered from the Caballo Muerto Creek locality are described. The fossils were studied using LM, SEM, and TEM. Individual cones were assigned to *A. ungeri* (Halle) Florin, taxodiaceous Cupressaceae, or *Kachaikastrobus acuminatus* gen. et sp. nov. within the Cheirolepidiaceae.

### Material and Methods

Ovulate cones were collected in the uppermost part of the Kachaiké Formation at the Arroyo Caballo Muerto Creek locality

<sup>1</sup> E-mail: gdelfueyo@macn.gov.ar.

<sup>2</sup> E-mail: sarcang@fibertel.com.ar.

<sup>3</sup> E-mail: mlllorens@mef.org.ar.

<sup>4</sup> E-mail: rcuneo@mef.org.ar.

(Estancia Kachaike) in Santa Cruz Province, Argentina (see location map and stratigraphical section in Cúneo and Gandolfo 2005). The age of the Kachaike Formation varies from Late Aptian to Late Albian, according to stratigraphic and geographic locations and the fossil content. The lower section is marine and has yielded ammonites at Estancia La Federica of Late Aptian age (Aguirre Urreta 2002) and dinoflagellates at Bajo de La Comisión of early Albian age (Guler and Archangelsky 2006). Angiosperm pollen from the upper part of the unit at Bajo de la Comisión suggests a Late Albian age (Barreda and Archangelsky 2006). Palynological data (Gamerro 1982; Baldoni et al. 2001) and angiosperm leaf assemblages (Cúneo and Gandolfo 2005) at Estancia Kachaike suggest a Late Aptian/early Albian age. Our fossils were found in the same horizon with the angiosperm leaves, which most probably is early Albian.

The fossils are impressions and compressions of coniferous twigs bearing ovulate cones with well-preserved cuticles of leaves, bracts, and ovuliferous dwarf shoots that belong to the Cheirolepidiaceae and taxodiaceous Cupressaceae, the only conifers found in the fossiliferous bed. Other components of the assemblage are the ferns *Nathorstia alata* Halle, *Cladophlebis* spp., *Coniopteris* sp., and several morphotypes of angiosperm leaves (Cúneo and Gandolfo 2005).

Leaves, bracts, and cone scale cuticles of the new Cheirolepidiaceae conifer were removed from the matrix and macerated in hydrochloric acid (20%), followed by hydrofluoric acid (70%). Some cuticles were treated with 40% nitric acid, followed by 5% ammonium hydroxide, while others were cleared with sodium hypochlorite. An incomplete ovulate cone was macerated in hydrofluoric acid, yielding parts of two cone scales. Cuticles were mounted in glycerine jelly for LM observation. For SEM, cuticles of leaves, bracts, and scales were mounted on double-sided adhesive tape fixed to stubs and were coated with gold-palladium. Observations were made under an SEM Jeol-T 100 at 15.1 kV. For TEM, selected fragments of leaves, bracts, and scales were stained with 2% OsO<sub>4</sub> for 2 h at room temperature. After that, they were washed for 30 min in distilled water and dehydrated in an ascending alcohol series (25%, 50%, 70%, 96%, and 100%; 15 min each and twice with 100%), followed by 100% acetone. The material was then infiltrated with acetone-Spurr's 3 : 1 for 6 h, acetone-Spurr's 1 : 1 for 16 h, and twice in Spurr's for 24 h. It was finally included in molds and vacuum-dried at 70°C for 48 h. Ultrathin sections (~800 Å thick) were made with a diamond knife using a Sorval automatic ultramicrotome. Individual sections were mounted in single-hole grids coated with Formvar, stained with lead citrate (1 min) and uranyl acetate (10 min), and observed under a TEM Jeol JEM 100C at 85.0 kV.

The cuticle in compressed specimens of *Athrotaxis ungeri* is strongly carbonized, and treatments with sodium hypochlorite (50%, 80%, and 100%) were unsuccessful. No cellular details were observed in leaves or reproductive structures. The terminology for the ovulate cones follows that of Clement-Westerhof and van Konijnenburg-van Cittert (1991). Specimens, microscope slides, and samples for SEM and TEM are deposited in the paleobotanical collection of the Paleontological Museum Egidio Feruglio, Chubut Province, Argentina (using the prefixes MPEF-Pb, MPEF-Pb PM, MPEF-Pb MEB, and MPEF-Pb MET).

## Systematic Paleobotany

### Order—Coniferales

#### Family—Cheirolepidiaceae Takhtajan

#### Genus—Kachaikostrobus Del Fueyo, Archangelsky, Llorens, et Cúneo gen. nov.

*Diagnosis.* Conifer branches of penultimate order terminally bifurcate, in last-order twigs bearing terminal ovulate cones. Leaves scalelike, decurrent, and with acuminate apex; spirally disposed and adpressed to twigs. Stomata on both surfaces randomly placed; sparse in apex. Stomatal apparatus monocyclic. Anticlinal flanges straight. Ovulate cones elongate, with cone scales helically arranged on central axis, composed of acuminate bracts subtending ovuliferous dwarf shoots, fused at bases. Ovuliferous dwarf shoots broad, shorter than bracts, each consisting of eight scales. Papillae present on both surfaces of scale. Ovuliferous dwarf shoots and bracts amphistomatic; stomatal characters as for leaves. Epimatium covering at least one(?) ovule. Bract and ovuliferous dwarf shoot cuticle ultrastructure composed of three layers.

*Etymology.* The generic name is a combination of *Kachaike*, after the Kachaike Formation, and *strobos*, conelike.

*Type species.* *Kachaikostrobus acuminatus* Del Fueyo, Archangelsky, Llorens, et Cúneo gen. et sp. nov. (figs. 1–5).

*Holotypes.* MPEF-Pb 859A, MPEF-Pb PM 859A 1–5, MPEF-Pb MEB 859A 1, and MPEF-Pb MET 859A 1–2.

*Paratypes.* MPEF-Pb 859B, MPEF-Pb PM 859B 1–16, MPEF-Pb MEB 859B 1–4, MPEF-Pb MET 859B 1–3, MPEF-Pb 863, and MPEF-Pb PM 863 1–11.

*Type locality.* Arroyo Caballo Muerto Creek (Estancia Kachaike), Santa Cruz Province, Argentina.

*Stratigraphic horizon.* Uppermost part of the Kachaike Formation, early Albian.

*Etymology.* The specific epithet *acuminatus* refers to the acute apex of leaves and bracts.

*Diagnosis.* Conifer branches bearing scalelike leaves, adpressed, helically arranged, ovate with distinctive acuminate apex; 3.6–4 mm long and 2 mm wide. Leaf margins entire at basal part and serrate toward apex. Papillae present on distal part of leaves; more numerous on adaxial than on abaxial epidermis. Leaves amphistomatic, stomata randomly disposed, sparse at apex; apertures parallel, obliquely and transversely oriented. Stomatal apparatus elliptical-rounded; monocyclic, with four or five subsidiary cells, radially placed; up to 35 μm long and 27 μm wide. Suprastomatal aperture elliptical, 26 μm long and 13 μm wide. Florin ring present. Guard cells sunken, 41 μm long and 7 μm wide. Epidermal cells of leaves isodiametric, 27 μm long and 24 μm wide, and rectangular-elongate, 62 μm long and 15 μm wide. Ovulate cones single and terminal on twigs up to 1.6 cm long and 3.5 mm wide, cylindrical elongate, 1.7 cm long and 1 cm wide. Cone axes bearing 40 cone scales, dense and helically disposed. Bracts acuminate, overlapping adjacent bracts, 4–5 mm wide and 7 mm long; amphistomatic, stomata in rows with features as for leaves. Common epidermal cells of three shapes: rectangular-elongate, 64 μm long and 18 μm wide; quadrangular, 24 μm long and 20 μm wide; rectangular-narrow elongate, 105 μm long and 14 μm wide. Ovuliferous dwarf shoots broadly elliptical,

5 mm long and 4–5 mm wide, shorter than and fused to bracts at base; consisting of eight scales, two small and six large; two large, probably fertile, emerging laterally; three emerging adaxially and three abaxially. Scale apices triangular, acute to blunt, 0.8 mm long and 0.7 mm wide. Apices with serrate margins and papillae. Ovuliferous dwarf shoots amphistomatic; stomata scarce, random, present only on distal part. Stomatal features as for leaves and bracts. Epidermal cells quadrangular, 26  $\mu\text{m}$  long and 18  $\mu\text{m}$  wide. Epimatium emerging as outgrowth of two adaxial larger scales,  $\sim 3.2$  mm long and 2.0 mm wide, formed by two layers of rectangular-elongate cells; outer layer, 51  $\mu\text{m}$  long and 18  $\mu\text{m}$  wide; inner layer, 64  $\mu\text{m}$  long and 10  $\mu\text{m}$  wide. Epimatium covering one ovule, which has an outer integument layer with rectangular cells, 69  $\mu\text{m}$  long and 12  $\mu\text{m}$  wide. A thick structureless megaspore membrane is present. Cuticle ultrastructure of bracts and ovuliferous dwarf shoot scales composed of three layers: external layer with loosely disposed fibrillar elements; middle layer with compactly arranged fibrils; inner layer with fibrillar element, more dense and of parallel disposition.

*Description.* The specimens consist of penultimate, incomplete twigs up to 6 mm long and 3.5 mm wide and terminally bifurcate ultimate-order fertile twigs,  $\sim 1.6$  cm long and up to 3.5 mm wide, each bearing a single ovulate cone (fig. 1A, 1B).

Leaves are helically arranged and addressed to twigs. They are scalelike and ovate, with a decurrent oval base and a distinctive acuminate apex (fig. 1C). Leaves are 3.6–4 mm long and up to 2 mm wide, with a base cushion 2 mm long and 1.5 mm wide (fig. 1D). The free parts of the leaves are markedly convex, 1.8 mm long and 0.7 mm wide (fig. 1A). Leaf margins are entire up to the midregion, where they become irregularly serrate, and are formed by rectangular-elongate cells (71  $\mu\text{m}$  long and 14  $\mu\text{m}$  wide), mostly obliquely but also perpendicularly oriented, with rounded to sharp-pointed contour (fig. 1H, 1K). Papillae are present distally on both leaf surfaces, being more abundant on the adaxial side, and mostly close to the leaf margin (fig. 1E). Papillae are rounded,  $\sim 9$   $\mu\text{m}$  in diameter (fig. 1J).

Leaves are amphistomatic, with stomata randomly placed and apertures parallel and oblique or transversely oriented to the leaf axis. Most stomata are in the basal part of the leaf and become fewer distally (fig. 1F, 1H, 1I, 1L). Stomatal density varies according to the leaf surface: on the abaxial epidermis, it is 10–12 per  $\text{mm}^2$ , and on the adaxial epidermis, it is 4–7 per  $\text{mm}^2$ . The stomatal apparatus is elliptical to rounded and is composed of one cycle of four or five subsidiary cells radially placed, isodiametric (30  $\mu\text{m}$  long and 27  $\mu\text{m}$  wide) to oblong (35  $\mu\text{m}$  long and 14  $\mu\text{m}$  wide), with rounded sides. The subsidiary cells comprise an elliptical suprastomatal aperture (26  $\mu\text{m}$  long and 13  $\mu\text{m}$  wide), and they have a 3.5- $\mu\text{m}$  cuticular thickening, the so-called Florin ring (fig. 1G). Anticlinal flanges of the subsidiary cells are straight and 3–3.5  $\mu\text{m}$  thick, and their inner surfaces are smooth. The guard cells are preserved in few stomata; they are sunken and linear (41  $\mu\text{m}$  long and 7  $\mu\text{m}$  wide) and thin toward the poles, with curved inner and outer lateral sides. The anticlinal flanges between them are 1  $\mu\text{m}$  thick (figs. 1G, 2C).

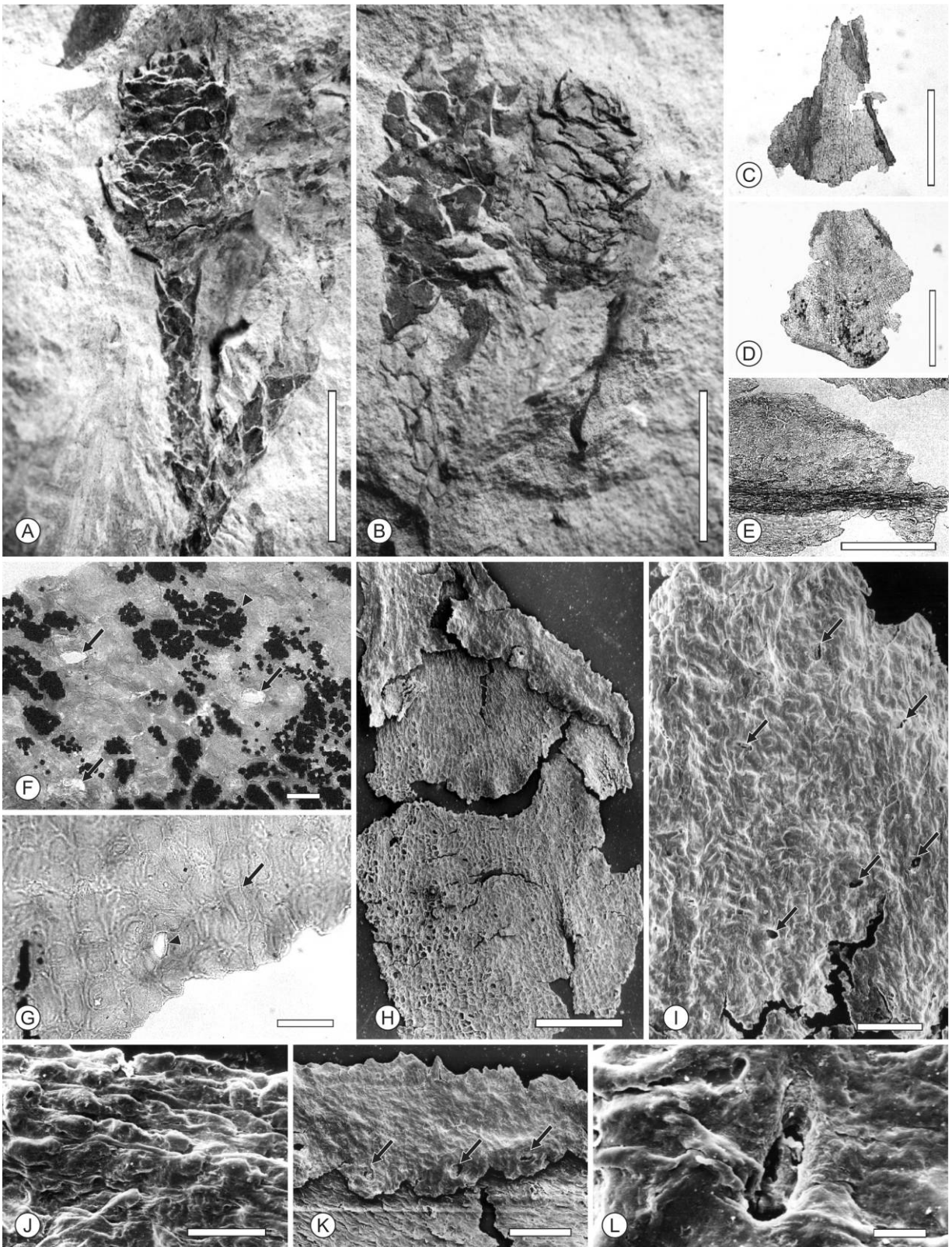
The epidermal cells have the same abaxial and adaxial characters: isodiametric (27  $\mu\text{m}$  long and 24  $\mu\text{m}$  wide) from the basal to the midregions of the leaf and rectangular-elongate

(62  $\mu\text{m}$  long and 15  $\mu\text{m}$  wide) distally. Anticlinal flanges of these cells are straight and 3.5–4  $\mu\text{m}$  thick. Remains of cutinized hypodermal cells were observed in all studied leaves, and they had a thin anticlinal flange  $< 1$   $\mu\text{m}$  thick (figs. 1G, 2A). Some epidermal cells contain polyhedral bodies 3–7  $\mu\text{m}$  wide that were not removed after the acid treatments; these are probably resins present also inside the subsidiary cells (figs. 1F, 2B).

The cuticle in transverse section has periclinal walls 2.8  $\mu\text{m}$  thick and anticlinal walls 3.3  $\mu\text{m}$  deep (fig. 5A). The ultrastructure of the cuticle shows a unique and compact layer of disorganized fibrils that show patches of dark and less electron-dense areas (fig. 5B). This organization may be attributed to poor preservation of the cuticle.

Ovulate cones are borne singly, terminally on twigs of last order, and are cylindrical and elongate (up to 1.7 cm long and 1 cm wide), narrowing slightly toward the base and apex. Each bears  $\sim 40$  cone scales, densely and helically disposed on the cone axis, whose characters are not available because of the compact cone organization (fig. 1A, 1B; fig. 4A). Each cone scale consists of an acuminate bract subtending an ovuliferous dwarf shoot (fig. 2D) that is free from the bract along most of its length; both seem to be fused only at their bases. Neither bracts nor ovuliferous dwarf shoots were found isolated in the fossiliferous bed. The holotype MPEF-Pb 859 A (fig. 1A) shows on one twig a complete seed cone with the bracts broken away and on the other, the ghost of another cone. The counterpart holotype MPEF-Pb 859 B (fig. 1B) shows the cone with complete bracts in one twig and remnants of a cone in the other.

*Bracts.* Bracts are ovate with entire margins, a broad base, and a gradually tapering apex ending in a round point. They are 4–5 mm wide and up to 7 mm long, and the free part appears to be 6 mm long (fig. 2E, 2G; fig. 4B). The most distal part is strongly curved on both abaxial and adaxial sides, overlapping the adjacent cone scales (figs. 1B, 2F). The bracts have the same adaxial and abaxial epidermal characters. They are amphistomatic, with stomata arranged in rows in the bract midregions. Distally, stomata become gradually fewer, and none are seen in the apex (fig. 2H, 2I). Stomatal rows are separated by four to seven lines of cells and within the stomatal rows by at least four cells. Neighboring stomata with subsidiary cells in contact are rare. The stomatal apparatus is rounded to elliptical and monocyclic, with four or five subsidiary cells (fig. 2J, 2K) that show characters similar to those seen in the leaves. Subsidiary cells have two shapes: isodiametric (17  $\mu\text{m}$  long and 14  $\mu\text{m}$  wide) and oblong (45  $\mu\text{m}$  long and 14  $\mu\text{m}$  wide). The anticlinal flanges between these cells are straight and 2  $\mu\text{m}$  thick, forming an elliptical suprastomatal aperture (31  $\mu\text{m}$  long and 14  $\mu\text{m}$  wide). Most of the apertures are parallel oriented, while a few are transverse or oblique. The guard cells are not preserved. The shape of epidermal cells varies according to their disposition in the bract; between stomatal rows, cells are rectangular-elongate (64  $\mu\text{m}$  long and 18  $\mu\text{m}$  wide), while in the stomatal rows, cells are quadrangular (24  $\mu\text{m}$  long and 20  $\mu\text{m}$  wide; fig. 2H). The anticlinal flanges in both cell types are straight, 2–2.5  $\mu\text{m}$  thick. At the apex, in the nonstomatiferous area, the rectangular cells become longer and narrower (105  $\mu\text{m}$  long and 14  $\mu\text{m}$  wide), and the anticlinal flanges are straight (3  $\mu\text{m}$  thick; fig. 2I, 2L). Remnants of hypodermal cells are also present (fig. 2M). Resin bodies similar to those observed in the leaves are also found in the bract cells (fig. 2N).



**Fig. 1** *Kachaikastrobus acuminatus* ovulate cones and leaves. All specimen numbers have the prefix MPEF-Pb. *A, B*, Ovulate cones in organic connection to bifurcate twigs. *A*, Holotype; 859A, scale = 1 cm. *B*, Counterpart; 859B, scale = 1 cm. *C–L*, Leaves. *C–G*, LM. *C*, Acuminate leaf apex; PM 859A 3, scale = 0.5 mm. *D*, Abaxial middle and basal leaf fragment; PM 859A 1, scale = 1 mm. *E*, Adaxial distal surface showing papillae; PM 859A 4, scale = 0.2 mm. *F*, Stomata (arrows) and probable resin bodies inside cells (arrowhead); PM 859A 3, scale = 20  $\mu\text{m}$ . *G*,

Epidermal cells of the bract in transverse section have periclinal walls with an average thickness of  $4.5\ \mu\text{m}$  ( $3\text{--}6\ \mu\text{m}$ ) and anticlinal walls  $\sim 8\ \mu\text{m}$  deep (fig. 5C). The cuticle consists of three layers. The external layer ( $\sim 1200\ \text{nm}$  thick) shows fibrillar elements loosely and randomly arranged, giving the appearance of a somewhat reticulate disposition. These fibrils become slightly more compact toward the middle layer (fig. 5D). In this layer ( $\sim 2100\ \text{nm}$  thick), the fibrils turn almost to a parallel and compact disposition: most are interconnected and in some areas perpendicular to the cuticle surface. The innermost layer is the thinnest ( $\sim 600\text{--}800\ \text{nm}$  thick) and has dense and almost parallel fibrillar elements (fig. 5D).

*Ovuliferous dwarf shoots.* Ovuliferous dwarf shoots are broadly elliptical, shorter than the bracts, and  $\sim 5\ \text{mm}$  long, and they appear to have the same width,  $4\text{--}5\ \text{mm}$  (fig. 3A, 3B; fig. 4C, 4D). These consist of eight scales, two smaller and six larger, emerging in two planes (fig. 3C, 3D). Two of the scales, probably fertile, are larger and emerge laterally. Of the remaining six, three emerge adaxially, and the smaller of these appears to be placed behind the two larger scales; the other three emerge abaxially, with the two larger ones overlapping each other and the smaller appearing to be placed ahead of them. These six scales are sterile (fig. 4D). The scale apices are more or less triangular in shape, with the acute ones on the larger lobes and the blunt ones on the smaller lobes (fig. 3C, 3E). Each scale apex has a keel. They are  $1.3\text{--}0.4\ \text{mm}$  long and  $0.6\text{--}1.6\ \text{mm}$  wide, averaging  $\sim 0.8\ \text{mm}$  long and  $0.7\ \text{mm}$  wide. Lobes from an ovuliferous dwarf shoot in specimen MPEF-Pb 863 are  $\sim 0.44\ \text{mm}$  long and  $0.40\ \text{mm}$  wide, with all the scale apices still round, suggesting that the dwarf shoot was at an early developmental stage at the time of fossilization (fig. 3D). Margins of scale apices are serrate toward the distal end and are markedly crenulated in the two abaxial larger scales (fig. 3F). Papillae are present in both sterile and fertile scales and on both adaxial and abaxial epidermis. Papillae are  $17\ \mu\text{m}$  high and rounded,  $\sim 17\ \mu\text{m}$  in diameter (fig. 3I). Pollen of the *Classopollis* type (average  $28\ \mu\text{m}$  in diameter) is observed adhering to the scale apex surfaces (fig. 3J, 3K). Only one *Araucariacites* type of pollen was also found on the scale epidermis (fig. 3L).

The ovuliferous dwarf shoots are amphistomatic, with scattered stomata randomly disposed and the apertures ( $28\ \mu\text{m}$  long and  $12\ \mu\text{m}$  wide) mostly oblique and transversely oriented. Stomata are in the distal part of scales and share the same characters as described for leaves and bracts. The stomatal apparatus is rounded and monocyclic, with four or five subsidiary cells of two shapes (isodiametric [ $17\ \mu\text{m}$  long and  $17\ \mu\text{m}$  wide] and oblong [ $21\ \mu\text{m}$  long and  $14\ \mu\text{m}$  wide]), with straight anticlinal flanges ( $4\text{--}7\ \mu\text{m}$  thick). A Florin ring is present,  $5\ \mu\text{m}$  thick. Guard cells are not preserved (fig. 3H).

Epidermal cells of scales, of both adaxial and abaxial surfaces, are quadrangular ( $26\ \mu\text{m}$  long and  $18\ \mu\text{m}$  wide), with straight anticlinal flanges ( $3.5\text{--}5\ \mu\text{m}$  thick; fig. 3G). These cells grade gradually to rectangular-elongate ( $33\ \mu\text{m}$  long and  $8\ \mu\text{m}$

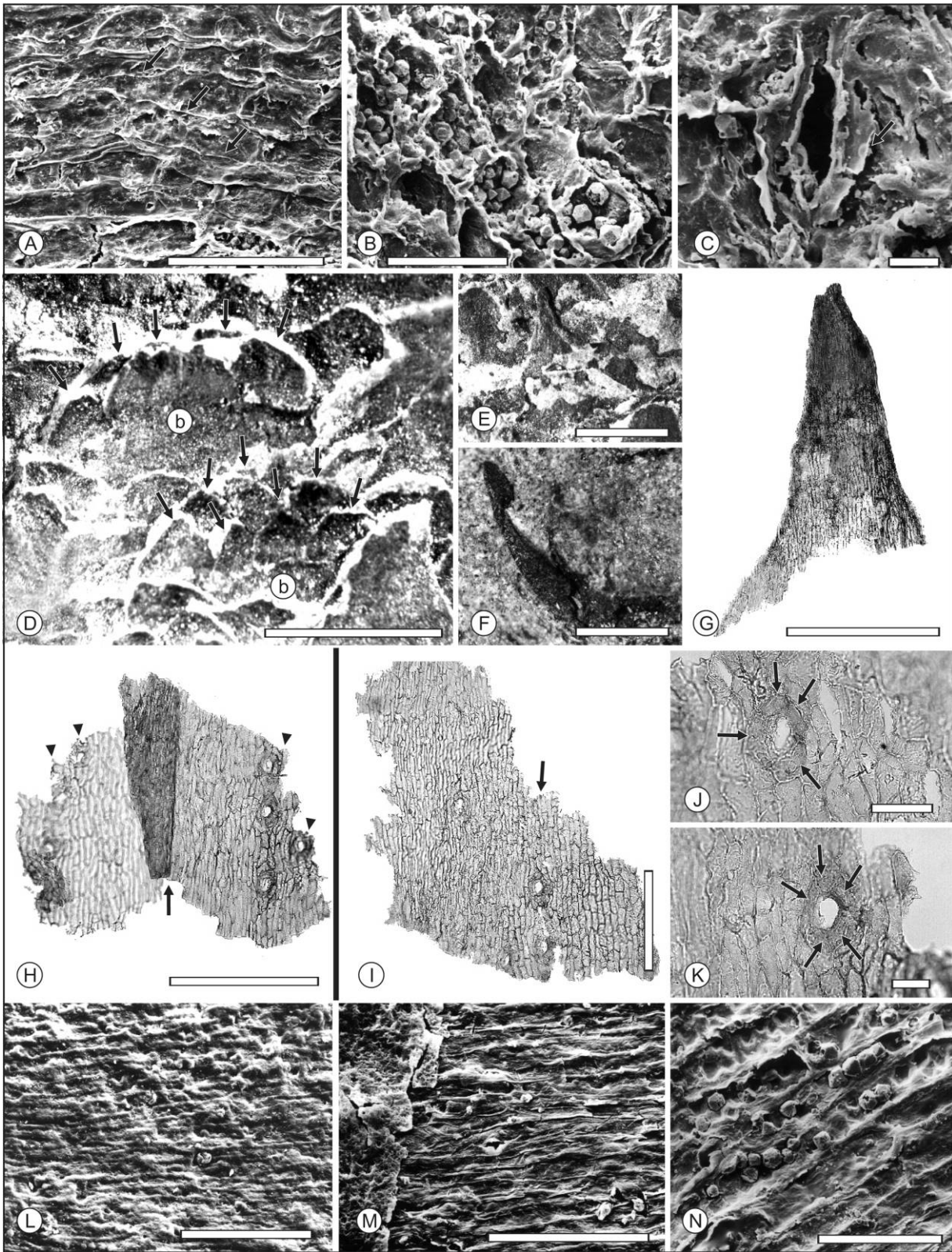
wide) toward the margins, where they comprise three layers of longer rectangular cells ( $53\ \mu\text{m}$  long and  $12\ \mu\text{m}$  wide) with straight anticlinal flanges ( $3.5\ \mu\text{m}$  thick). Cells of the outer layer, especially those situated at the scale apices, end in a very acute or blunt contour (fig. 3F). Remains of cutinized hypodermal cells are also found (fig. 3G).

At the basal part of dwarf shoots, due to preservation, neither abaxial nor adaxial cuticles are present ( $d_1$  and  $d_2$ , respectively, in the terminology of Clement-Westerhof and van Konijnenburg-van Cittert [1991]). On the adaxial cuticle of the dwarf shoot and at its distal part, the quadrangular cells of the two larger and sterile scales pass into rectangular-elongated cells of what is interpreted to be the epimatium (fig. 3C). This structure is  $\sim 3.2\ \text{mm}$  long and  $2.0\ \text{mm}$  wide; its lateral margins appear to be almost straight, and at the bottom, the margin is somewhat irregular (figs. 3C, 4D). The epimatium consists of two layers: an inner and an outer cuticle ( $d_3$  and  $d_4$ , respectively, according to Clement-Westerhof and van Konijnenburg-van Cittert [1991]). The outer cuticle shows rectangular-elongate cells ( $51\ \mu\text{m}$  long and  $18\ \mu\text{m}$  wide), longitudinally oriented, with diagonal to blunt end walls. These cells, especially at the bottom of the epimatium, may be arranged in groups of sister cells (fig. 3M, 3N). The inner cuticle shows similar characters but differs in the size and shape of cells, which are narrower and larger ( $64\ \mu\text{m}$  long and  $10\ \mu\text{m}$  wide). Both cuticles have cells with straight anticlinal walls  $\sim 2\ \mu\text{m}$  thick. These inner and outer cuticles are nonstomatiferous, and papillae are absent. At the bottom part of the inner cuticle, a crossing-cells layer is observed, characterized by rectangular cells ( $69\ \mu\text{m}$  long and  $12\ \mu\text{m}$  wide) with straight and very thin anticlinal walls ( $<1\ \mu\text{m}$  thick), possibly corresponding to an outer integumentary layer ( $O_4$  of Clement-Westerhof and van Konijnenburg-van Cittert [1991]; fig. 3O). Part of what is assumed to be a poorly preserved ovule was obtained from the dwarf shoot maceration. The ovule is spindle shaped and measures  $0.66\ \text{mm}$  in length and  $0.17\ \text{mm}$  in width. A thick and structureless megaspore membrane ( $O_1$  of Clement-Westerhof and van Konijnenburg-van Cittert [1991]) appears to be covered by two distinct layers of the epimatium (fig. 3P). No remains of the nucellus or inner layer of the integument have been identified. The site of the ovule attachment remains unknown in the Patagonian material.

Observations with TEM of the scale apices in transverse section show periclinal walls with an average thickness of  $7\ \mu\text{m}$  ( $3\text{--}11\ \mu\text{m}$ ), while anticlinal walls are up to  $15\ \mu\text{m}$  deep (fig. 5E). The cuticle has three layers with the same ultrastructural features as those observed in the bracts. Only the external layer is thicker ( $\sim 1800\ \text{nm}$  thick), and the middle and innermost layers are thinner ( $\sim 1200$  and  $500\ \text{nm}$  thick, respectively; fig. 5F). In the papillae, the external layer has a thickness similar to that of the epidermal cells; the middle layer is more developed (up to  $3700\ \text{nm}$  thick), and the inner layer is poorly developed ( $<400\ \text{nm}$  thick; fig. 5G).

---

Detail of stoma, with guard cells preserved (arrowhead) and remains of cutinized hypodermal cells (arrow); PM 859A 3, scale =  $100\ \mu\text{m}$ . H–L, SEM; all MEB 859A 1. H, General leaf view showing abaxial cuticle inner surface and adaxial cuticle outer surface; scale =  $0.5\ \text{mm}$ . I–L, Cuticle outer surface. I, Cuticle showing stomata randomly placed (arrows); scale =  $0.1\ \text{mm}$ . J, Detail of papillae; scale =  $50\ \mu\text{m}$ . K, Serrulate leaf margin and stomata on adaxial cuticle (arrows); scale =  $0.1\ \text{mm}$ . L, Detail of stomata aperture; scale =  $10\ \mu\text{m}$ .



**Fig. 2** *Kachaikestrobus acuminatus* leaves and cone scales. All specimen numbers have the prefix MPEF-Pb. A–C, SEM of leaf cuticle inner surface; all MEB 859A 1. A, Epidermal cells and remains of cutinized hypodermal cells (arrows); scale = 0.1 mm. B, Resin bodies in epidermal cells; scale = 0.05 mm. C, Stomata with guard cells preserved (arrow); scale = 10  $\mu$ m. D, Detail of two cone scales showing the bracts (*b*) and scales (arrows); note that the apex of the upper bract is broken and five scales are seen, and also most of the lower bract is broken and seven scales are shown; 859A, scale = 3 mm. E–N, Bract. E–G,

Family—Cupressaceae Bartling

Genus—Athrotaxis (Unger) Florin

Type Species—Athrotaxis lycopodioides (Unger) Florin

Athrotaxis ungeri (Halle) Florin (Fig. 6)

**Description.** The fossils are impressions and compressions of penultimate, incomplete shoots up to 2.5  $\mu\text{m}$  wide and 110  $\mu\text{m}$  long that end in bifurcate ultimate-order fertile twigs 1.5–2 mm wide and 13 mm long, each bearing a single ovulate cone (fig. 6C). Leaves are helically arranged, adpressed to twigs, scale-like, ovate, with decurrent rhomboidal base cushion and acute apex, 1.5–2.5 mm long and 1–2 mm wide (fig. 6A, 6C). Ovulate cones are elongate, cylindrical, 7–17 mm wide and 12–18 mm long (fig. 6A, 6B). Most specimens are longitudinal sections split through a robust central axis, 1.5 mm wide and 11 mm long (fig. 6A), while others are split in a somewhat transverse-oblique section (fig. 6C). The axis bears  $\sim$ 30 spirally disposed woody, lax cone scales. Most cone scales are seen in paradermal and some in oblique view (fig. 6A). The subtending bract is equal in length and completely fused to the scale. Each cone scale is peltate and  $\sim$ 5 mm long and has a cuneate base broadly attached to the axis ( $\sim$ 1.5 mm wide). Each has a spatulate distal portion 3 mm wide that ends in a short acute appendage  $<$ 0.5 mm in width that forms the free distal part of the subtending bract (fig. 6B). There is no evidence of seeds, and it is assumed that they were shed at the time of fossilization.

**Studied material.** MPEF-Pb 543B, 544, 859B, and 859C.

**Locality.** Arroyo Caballo Muerto Creek (Estancia Kachaike), Santa Cruz Province, Argentina.

**Stratigraphic horizon.** Uppermost part of the Kachaike Formation, early Albian.

## Discussion

### Comparisons among Cheirolepidiaceae Species

Ovuliferous cones of the Cheirolepidiaceae are characterized by flattened bilateral dwarf shoots with several scales. Commonly, two fertile lateral scales and a variable number of middle sterile scales are fused between them over almost their entire length, except the scale apex. Two adaxially attached ovules covered by an epimatium and bracts are fused at the base of the dwarf shoots (Clement-Westerhof and van Konijnenburg-van Cittert 1991).

*Kachaikastrobus acuminatus* has large ovulate cones, borne terminally on bifurcate shoots with distinctly acuminate scale-like leaves with stomata randomly placed and papillae distally placed, cone scales densely and helically arranged, subtending acuminate bracts fused at their bases to ovuliferous dwarf shoots with eight scales, two lateral, three adaxially and three abax-

ially emerging, with an epimatium covering at least one ovule. These characters allow us to place *K. acuminatus* within the Cheirolepidiaceae. On the other hand, the combination of characters shown by *K. acuminatus* differs from that of other previously described cheirolepidiaceae seed cones.

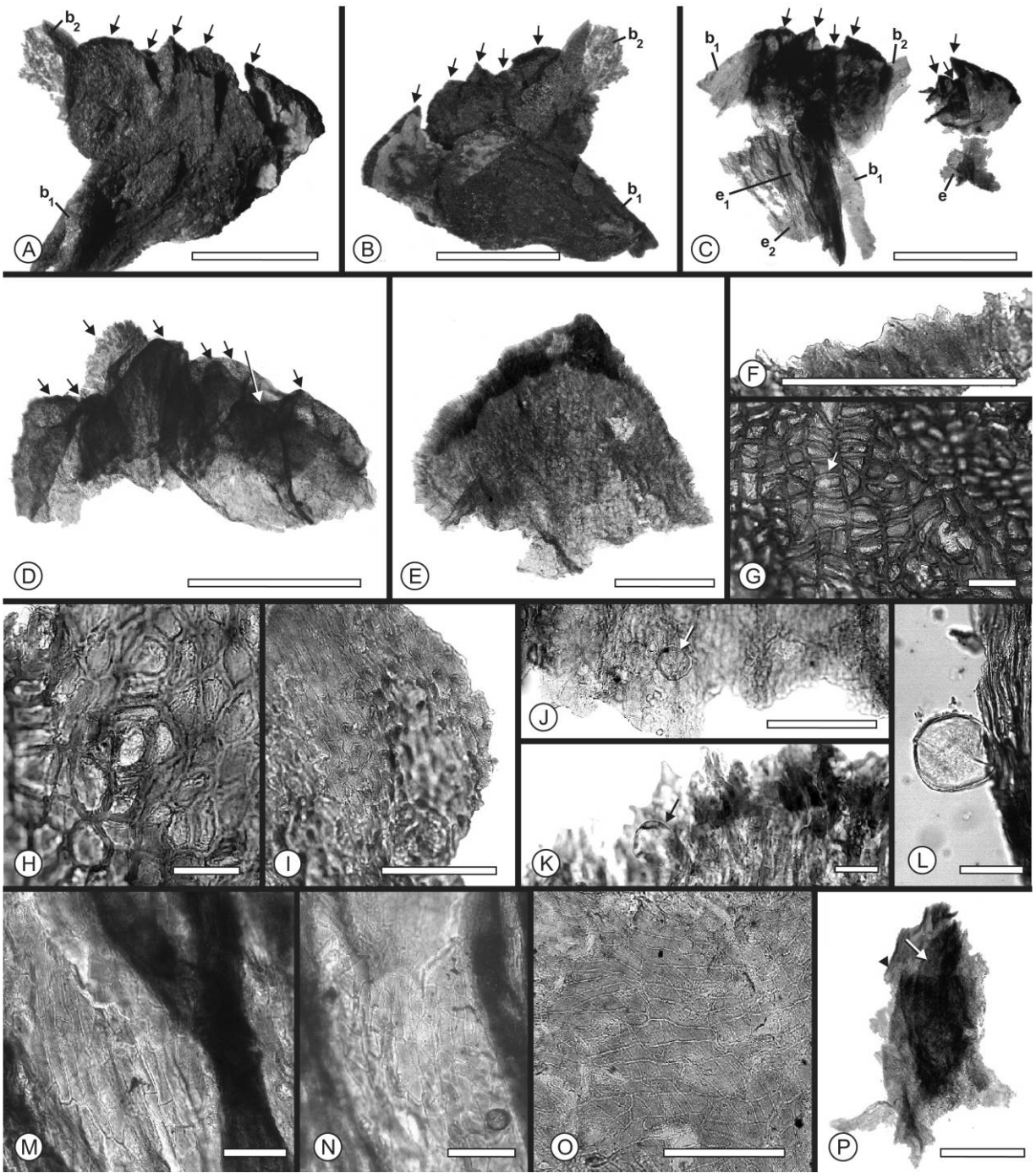
Ovulate cones belonging to the Cheirolepidiaceae are found in only a few species, in contrast to the well-known and abundant *Classopollis*-bearing pollen cones (Alvin et al. 1994). Within the two major groups recognized for the family (Alvin 1982; Watson 1988), taxa based on complete ovuliferous cones are *Hirmeriella muensteri* (Schenk) Jung and *Pseudohirmeriella delawarensis* (Arndt) Axsmith, Andrews, et Franser among the “brachyphylls” and *Alvinia bohémica* (Velenovský) Kvaček and *Frenelopsis ramosissima* (Fontaine) Watson among the “frenelopsids.” Another cheirolepid, *Tomaxellia biforme* Archang, is not considered to be within either of these two groups because of its dimorphic leaves (Archangelsky 1968).

*Kachaikastrobus acuminatus* shares vegetative and reproductive features with *H. muensteri* from the Late Triassic–Early Jurassic of Germany (Jung 1967, 1968). They share the *Brachyphyllum* type of leaf. However, in the German species, leaves are larger (2–5 mm wide and 4–8 mm long), the apex is much less acuminate, stomata are arranged in rows, and papillae are absent (Guignard et al. 1998). The differences are more evident when comparing the cuticle ultrastructural features. In this case, the better-preserved leaf cuticle of *H. muensteri* shows four layers: an outer polylamellate layer beneath a granular layer, a middle layer of parallel-oriented fibrils, and an innermost granular layer (Guignard et al. 1998). The disorganized fibrils of the unique layer in the leaf cuticle of *K. acuminatus* are not comparable to the parallel fibrils of the middle layer of *H. muensteri*. This disposition, however, slightly resembles the structure of the innermost layer of the bract and scale cuticles of the Patagonian taxon. Vegetative and reproductive organs of *K. acuminatus* have a different cuticle preservation (very poor and very good, respectively), although both organs were buried and underwent the same diagenetic process. A probable explanation for this may be that cone scale cuticles were better protected due to their tight disposition and overlapping in the cones.

At a reproductive level, among the Cheirolepidiaceae, *Hirmeriella* is perhaps the taxon with the largest record, represented by several early Jurassic European species based mostly on isolated ovuliferous dwarf shoots and a few incomplete cones (Harris 1979; Krassilov 1982; Thévenard 1993). Complete ovulate cones of *H. muensteri* redescribed by Jung (1968) resemble *K. acuminatus* in gross morphology but are much more elongated (4.5 cm long and 1.5 cm wide).

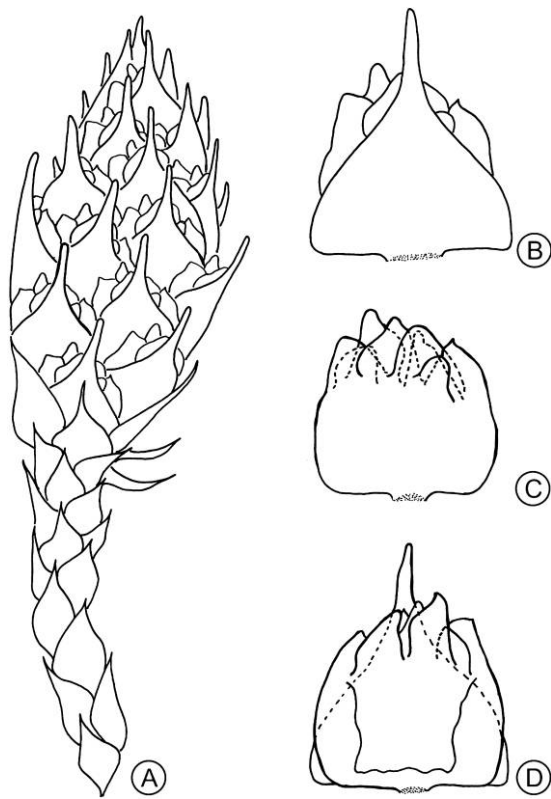
Clement-Westerhof and van Konijnenburg-van Cittert (1991), based on a detailed study of the cone scale outer and inner cuticles of well-preserved *H. muensteri* specimens from the German Liassic, gave a novel interpretation of the ovulate cone structure

Distal part. E, Acuminate apex in abaxial view; 859B, scale = 2 mm. F, Free distal part in lateral view; 859B, scale = 1.5 mm. G–K, LM; all from PM 859B. G, Detail of cuticle apex; 10, scale = 0.5 mm. H, Middle amphistomatic bract cuticle with stomata in rows (arrowheads) and bract margin (arrow); 9, scale = 350  $\mu\text{m}$ . I, Transition of the form of cells near the bract apex; note longer and narrower cells to the left of the stomatal row (arrow); 9, scale = 350  $\mu\text{m}$ . J, K, Detail of two stomata and subsidiary cells (arrows); 9. J, Scale = 60  $\mu\text{m}$ . K, Scale = 35  $\mu\text{m}$ . L–N, SEM; all from MEB 859 B. L, Cuticle outer surface with rectangular elongate cells; 2, scale = 0.1 mm. M, N, Cuticle inner surface. M, Detail of the rectangular elongate cells with remnants of cutinized hypodermal cells; 1, scale = 0.1 mm. N, Cells containing resin bodies; 4, scale = 0.05 mm.



**Fig. 3** *Kchaikestrobos acuminatus* ovuliferous dwarf shoot. All specimen numbers have the prefix MPEF-Pb. **A, B**, General aspect of the ovuliferous dwarf shoot after maceration; 863, scale = 1.5 mm. **A**, Abaxial view showing a bract with its apex broken ( $b_1$ ) and scales (arrows) of the subtended ovuliferous dwarf shoot and remains of an adjacent bract ( $b_2$ ). **B**, Adaxial view of the same ovuliferous dwarf shoot. **C**, Ovuliferous dwarf shoot in adaxial view with seven scales (arrows) and the epimatium ( $e$ ) partially broken, with differential areas shown in **M**, **N** ( $e_1$ ), and **O** ( $e_2$ ), and fragments of the subtending bract ( $b_1$ ) and adjacent bract ( $b_2$ ); detached scales and epimatium were broken during treatment; PM 863 4, scale = 1 mm. **D**, Eight scales (arrows) of an immature ovuliferous dwarf shoot; PM 863 6, scale = 1 mm. **E**, Single lobe; 859 B 4, scale = 350  $\mu\text{m}$ . **F–I**, Cuticular scale features. **F**, Serrulate margin; 859 B 5, scale = 120  $\mu\text{m}$ . **G**, Detail of quadrangular cells, with remnants of cutinized hypodermal cells (arrow); PM 863 7, scale = 15  $\mu\text{m}$ . **H**, Detail of stoma; PM 859 B 1, scale = 50  $\mu\text{m}$ . **I**, Detail of papillae; PM 859 B 5, scale = 160  $\mu\text{m}$ . **J–L**, Pollen grains adhered to the scale cuticle surface. **J**, *Classopollis* sp. **J**, Grain adhered to adaxial cuticle; PM 859 B 6, scale = 100  $\mu\text{m}$ . **K**, Grain (arrow) adhered to serrulate margin; PM 859 B 7, scale = 35  $\mu\text{m}$ . **L**, *Araucariacites* sp. adhered to adaxial cuticle; PM 863 8, scale = 56  $\mu\text{m}$ . **M–O**, Epimatium. **M**, **N**, Detail of groups of sister cells of the outer layer, corresponding to  $e_1$  of **C**; PM 863 4, scale = 70  $\mu\text{m}$ . **O**, Detail of the inner layer with crossing cells, corresponding to the area  $e_2$  of **C**; PM 863 10, scale = 60  $\mu\text{m}$ . **P**, Remnants of an ovule showing part of the megaspore membrane (arrow) and epimatium (arrowhead); PM 859 B 14, scale = 350  $\mu\text{m}$ .





**Fig. 4** *Kachaikostrobus acuminatus* suggested reconstruction. A, General aspect of ovulate cone attached to the leafy shoot. B, Ovuliferous dwarf shoot and subtending bract in abaxial view. C, Ovuliferous dwarf shoot in abaxial view without subtending bract. D, Ovuliferous dwarf shoot in adaxial view showing the epimatium.

and proposed this new organization as being representative for the Cheirolepidiaceae. Therefore, the comparisons between the Patagonian seed cone and that of *Hirmeriella* are focused on *H. muensteri*.

Cone scales of *H. muensteri* are similar to those of *K. acuminatus*. However, the bracts of *H. muensteri* are broader (8 mm wide), have a less acuminate apex, and are amphistomatic, and stomata are arranged in rows. The ovuliferous dwarf shoots are larger (13 mm wide and 8 mm long), with fewer scales (six), and they have stomata and scattered papillae only on the abaxial surfaces of fertile and sterile scales. The epimatium of *H. muensteri* is larger (6.5 mm wide and 4.5 mm long) than that of *K. acuminatus*, though the epidermal characters are similar in the two taxa. The distal part of the epimatium adaxial surface in *H. muensteri* has quadrangular epidermal cells, with few stomata and some papillae. In the basal part of both adaxial and abaxial surfaces, the cells are rectangular but longer and narrower (100  $\mu\text{m}$  long and 12  $\mu\text{m}$  wide). The outer layer of the integument in *H. muensteri* has rectangular cells that are longitudinally oriented, but they are narrower (20  $\mu\text{m}$  long and 100  $\mu\text{m}$  wide) than those of *K. acuminatus* and have crenulate anticlinal walls. The number of ovules per scale in *H. muensteri* appears to be two.

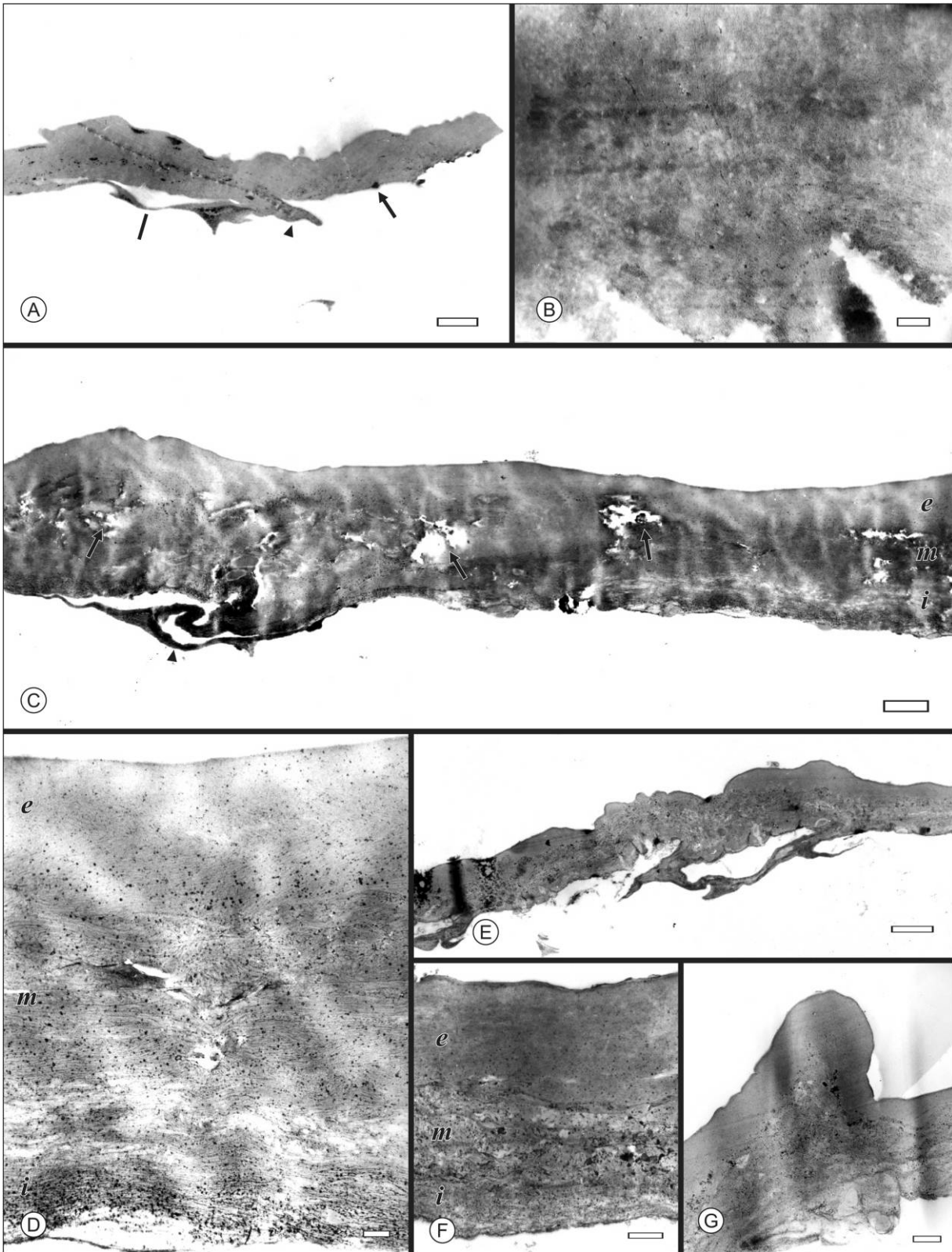
*Pseudohirmeriella delawarensis* from the Upper Triassic of North America was based on impressions of ovulate cones

associated with pollen cones and twigs with *Pagiophyllum-Brachyphyllum*-type leaves (Axsmith et al. 2004). Although this material provides no information for cuticular comparison with *K. acuminatus*, leaves in both species share almost the same morphology, being larger in *P. delawarensis* (2.7–8 mm long and 1.4–2.5 mm wide). Also, ovulate cones in *P. delawarensis* are larger (32 mm long and 15 mm wide) and have fewer cone scales, which are laxly disposed on the cone axis, and bracts are completely fused to five-lobed and larger ovuliferous dwarf shoots (9 mm long and 12 mm wide).

*Alvinia bohemia* from the Cenomanian of the Czech Republic (Kvaček 2000) and *F. ramosissima* from the Lower Cretaceous of North America (Axsmith and Jacobs 2005) differ from *K. acuminatus* in their characteristic “frenelopsid”-type leaves. Ovulate cones and cone scales of *A. bohemia* and *F. ramosissima* resemble in some aspects the Patagonian material, although they also show marked differences. *Alvinia bohemia* has larger ovoid cones (40 mm long and 40 mm wide). Its bracts are broadly elliptical (1.8 mm long and 5 mm wide), with blunt apices, and its ovuliferous dwarf shoots have fewer scales (three), which form a distinctly “protostigmatic” structure lined by trichomes (Kvaček 2000). On the other hand, *F. ramosissima* has larger cones (40 mm long and 2.4 mm wide). Its bracts are rhomboidal (15 mm long and 175 mm wide in the midpoint), with a rounded apex, and the ovuliferous dwarf shoots are smaller (~2.2 mm long and 4.0 mm wide), with no distal lobes.

*Tomaxellia biforme*, described from the Aptian of Patagonia (Archangelsky 1968), differs from *K. acuminatus* in its dimorphic leaves borne on the same branch. The short *Brachyphyllum*-type leaves are smaller (1.5 mm long and 0.8 mm wide), while the long leaves, distinctly different, are linear, with the free distal end spreading at almost 90° to the axis. The overall morphology of ovulate cones of both Cretaceous taxa is similar, except that in *T. biforme*, cones are larger (2.7 cm long and 1.5 cm wide). Ovuliferous dwarf shoots of *K. acuminatus* and *T. biforme* are fused at the base of bracts; however, bracts in *T. biforme* are slightly longer (1 cm long) and have scattered stomata on the distal end of the adaxial surface. Other differences between the two Patagonian species are that the ovuliferous dwarf shoots in *T. biforme* are smaller (0.7 mm long and 11 mm wide) and have fewer scales (six), stomata are present only on the abaxial surface and have two ovules, and the outer layer of the integument has quadrangular to rectangular cells.

Apparently, a common feature for all members of the Cheirolepidiaceae is that when ovulate cones were ripe, the ovuliferous dwarf shoots were shed from the cone axis as disseminules while the bracts remained persistent. This characteristic has been recorded in *H. muensteri* (Jung 1968; Harris 1979; Clement-Westerhof and van Konijnenburg-van Cittert 1991), *T. biforme* (Archangelsky 1968), *P. delawarensis* (Axsmith et al. 2004), *A. bohemia* (Kvaček 2000), and *F. ramosissima* (Axsmith and Jacobs 2005). However, isolated ovuliferous dwarf shoots have not been found in the same sediments as *K. acuminatus*, suggesting that, as in previously mentioned cheirolepids, this taxon may have shed its ovuliferous dwarf shoots at maturity. In addition, cuticles such as the nucellus and the inner layer of the integument surrounding the megaspore have not been found in *K. acuminatus*. Therefore, we assume that the ovulate cones were immature or in an early stage of development at the time of fossilization.



**Fig. 5** *Kchaikastrobus acuminatus* leaves and cone scale cuticles. TEM. All specimen numbers have the prefix MPEF-Pb MET. A, B, Leaf cuticle; 859A 1. A, Cuticle in transverse section; note thick periclinal walls (arrow), anticlinal wall (arrowhead), and remains of hypodermal cells (bar); scale = 2  $\mu$ m. B, Detail of disorganized fibrils in the innermost part of the cuticle; scale = 0.2  $\mu$ m. C–G, Cone scale cuticles. C, D, Bract; 859B 1. C, Cuticle showing three layers: external (*e*), middle (*m*), and inner (*i*); note degraded areas in periclinal walls (arrows) and extended hypodermal cells remains

### Pollination

Alvin (1982) suggested that pollination in the Cheirolepidiaceae was anemophilous because of the abundance of *Classopollis* pollen in sediments all over the world. Accordingly, this taxon is one of the main components of the pollen assemblage studied by Gamero (1982) from the Caballo Muerto locality, as in many Mesozoic deposits in Patagonia (Archangelsky et al. 1994). The finding of *Classopollis* adhered to the external surfaces of *K. acuminatus* scales may suggest that pollen germination occurred on the scale surfaces and that pollen tubes could have grown toward the nucellus. This pollination mechanism is similar to what has been mentioned by Clement-Westerhof and van Konijnenburg-van Cittert (1991) for other members of the Cheirolepidiaceae, such as *H. muensteri* and *T. biforme*. Exceptions are *A. bohémica* (Kvaček 2000) and *F. ramosissima* (Axsmith and Jacobs 2005), in which, respectively, a stigmalike pollen reception area lined by trichomes in the distal lobes or the distal area of the ovuliferous dwarf shoots has been suggested. Alvin (1982) and Clement-Westerhof and van Konijnenburg-van Cittert (1991) have indicated that these advanced pollination mechanisms in the Cheirolepidiaceae could be comparable with those observed by Doyle (1945) in several extant conifers, such as *Saxegothaea* of the Podocarpaceae, *Tsuga* of the Pinaceae, and *Araucaria* and *Agathis* of the Araucariaceae.

### Evolutionary Trends

If we take into account the evolutionary trends that involved the reduction of scales in the ovuliferous dwarf shoot and the shortening in the bract length of Mesozoic conifers (Miller 1999), *K. acuminatus* has, within the Cheirolepidiaceae described to date, the largest number of scales and bracts that are longer than the ovuliferous dwarf shoot. This shows that the ovuliferous cone scales of *K. acuminatus* have primitive characters among cheirolepids in spite of its Albian age (*T. biforme* and *H. muensteri* are of Aptian and Liassic age, respectively). On the other hand, Axsmith et al. (2004), when considering the evolutionary trends of the flattening of fertile and sterile scales and the loss or fusion of bracts (Miller 1999), have noted that in the Triassic *P. delawarensis*, the distal lobes of the ovuliferous cone scale are all oriented in a single plane, and the subtending bract is absent. Axsmith et al. (2004) pointed out that the presence of such advanced features in *P. delawarensis* may represent a substantial Triassic diversification of the Cheirolepidiaceae. *Kachaikestrobis acuminatus* is a cheirolepid of a southern alliance, and the eventual primitive characters may be the result of a different evolutionary trend related to its Gondwanic origin.

### Phylogeny

Clement-Westerhof and van Konijnenburg-van Cittert (1991) have found that among the three Late Paleozoic genera of the family Majoniceae (*Pseudovoltzia*, *Dolomita*, and *Majonica*), the organization of *H. muensteri* ovuliferous dwarf shoots is

most like that of *Majonica alpina* Clement-Westerhof, except in the lateral attachment of the winged ovules and the presence of a pollen chamber. Accordingly, these authors suggested that the Cheirolepidiaceae may have originated from or may have had a common ancestor with the Majoniceae. Miller (1999) showed the same results with his cladistic treatment of conifers based on 11 ovuliferous cone characters and also suggested that the Cheirolepidiaceae are not directly related to any of the modern conifer families. However, other authors have considered that the Cheirolepidiaceae could have a common ancestor with the Araucariaceae and Podocarpaceae, mainly because of their enclosed ovules (Krassilov 1982; Clement-Westerhof and van Konijnenburg-van Cittert 1991). Recently, Ewin (2006), using the leaf characters of 96 extant conifer species plotted for a conifer phylogeny, concluded that the Cheirolepidiaceae leaf cuticles resemble most closely those of the Araucariaceae.

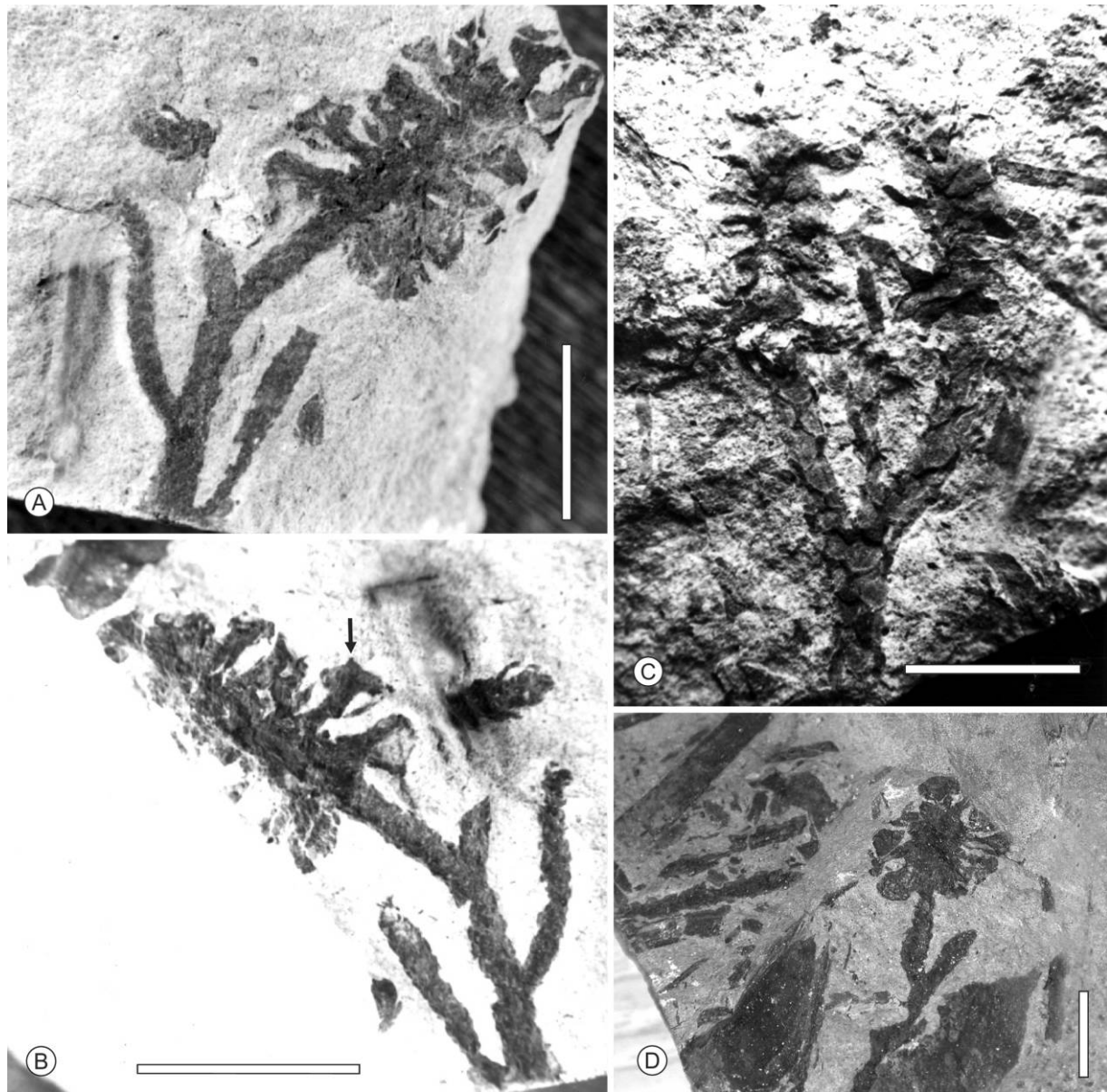
In the Southern Hemisphere, there are no records of Majoniceae, a family with several genera in the Permian of Europe (Clement-Westerhof 1988) and North America (Looy 2007). The only Permian conifers described from Gondwana are the Ferugliocladaeae from Patagonia (Archangelsky and Cúneo 1987), characterized by lanceolate leaves with acute apices, ovoid and simple ovuliferous cones (up to 4 cm long and 1 cm wide), and orthotropous ovules borne axillary on lanceolate bracts (up to 7 cm long). According to Archangelsky and Cúneo (1987), the dwarf shoot in this family is not recognizable because it is entirely fused to the ovule, suggesting a highly advanced stage of the ovuliferous cone evolution. In the opinion of these authors, the Ferugliocladaeae probably represents a line of evolution parallel to that of the northern conifers, which led to the Voltziaceae. Thus, a possible ancestor for *K. acuminatus*, and so for *T. biforme*, cannot be recognized among the Permian families.

*Pararaucaria patagonica* from the Jurassic of Santa Cruz Province in Argentina, recently included within the Voltziaceae by Miller (1999), could have had a common origin with or could have been the ancestor of *K. acuminatus* and *T. biforme*. However, the ovuliferous scales of *Pararaucaria* lack distal lobes and are entirely free from subtending bracts (Calder 1953; Stockey 1977), features not shown by *Kachaikestrobis* and *Tomaxellia*. An interesting ovulate cone that may be considered as a possible ancestor is that of *Telemachus*, a genus that has been found exclusively in the Triassic of Gondwana, South America (Morel 1991; Lutz 2006), South Africa (Anderson and Anderson 1989), Antarctica (Yao et al. 1993), and New Zealand (Retallack 1981) and that has been provisionally assigned to the Voltziaceae. Although the ovulate cone of *Telemachus* is similar in gross morphology to that of the two Patagonian taxa, its bract is elongate and fused to the five-lobed ovuliferous scales for about half of their length.

### Comparison among Athrotaxis Species

The material of *Athrotaxis ungeri* here studied shows helically arranged ovate and scalelike leaves and ovulate cones

(arrowhead); scale = 2  $\mu\text{m}$ . D, Detail of fibrillar elements arrangement in the external (*e*), middle (*m*), and internal (*i*) layers; scale = 0.2  $\mu\text{m}$ . E–G, Ovuliferous dwarf shoot; 859B 2. E, Cuticle at the distal papillate area; scale = 2  $\mu\text{m}$ . F, Detail of the external (*e*), middle (*m*), and internal (*i*) layers of the cuticle; scale = 0.5  $\mu\text{m}$ . G, Section through a papilla; scale = 0.5  $\mu\text{m}$ .



**Fig. 6** *Athrotaxis ungeri* (Halle) Florin ovulate cones in connection to shoots. All specimen numbers have the prefix MPEF-Pb. A, B, Ovulate cones in longitudinal section showing thick central axis and cone scales spirally disposed; scale = 1 cm. A, Entire ovulate cone; 859 C. B, Counter-part showing cone scale spatulate distal part (arrow); 859 B. C, Ovulate cones borne on bifurcate shoots; 543 B, scale = 1 cm. D, Ovulate cone in transverse-oblique section; 544, scale = 1 cm.

with a distinctive cone scale. These features are the same as those described from the Kachaiké Formation at the Río de los Fósiles locality by Halle (1913), who first defined the species. The main differences are that in Halle's specimens, the leaves are up to 3 mm wide, and the cones are spherical and 10–15 mm in diameter and mostly were found detached from the stems. The striking feature of the material from the Caballo Muerto locality described here is that the ovulate cones are borne on bifurcate ultimate-order twigs.

In Patagonia, *A. ungeri* has also been found at two other Lower Cretaceous sites that, including the Río de los Fósiles and Caballo

Muerto localities, occur within an extensive area of ~250 km<sup>2</sup>. Piatnitzky (1938) mentioned a list of fossil plants from probable Aptian-Albian sediments near Lago Cardiel, in which he included *A. ungeri*, with no description or illustration. Archangelsky (1963) found vegetative remains in the Aptian Anfiteatro de Ticó Formation, at the homonymous locality, with leaves of *A. ungeri* that resemble those of the Caballo Muerto locality specimens in morphology and size (2 mm long and 1.5 mm wide).

In the opinion of Halle (1913), *A. ungeri* is identical to the living Tasmanian *Athrotaxis cupressoides* D. Don in external

morphology of both sterile foliage (crowded, helically arranged leaves) and spherical ovulate cones. This resemblance was also pointed out by Florin (1940) and later confirmed by Archangelsky (1963), with studies made on the leaf cuticle with LM that showed a similar cuticular structure in both taxa, especially at the stomata level. Later, Villar de Seoane (1998), using both SEM and TEM of the leaf cuticle of *A. ungeri* from the Aptian Anfiteatro de Ticó Formation, also stressed the similarities between this species and *A. cupressoides*.

In the well-known Patagonian Deseado Massif in Eocene sediments located 200 km west of the Deseado River mouth, Spegazzini (1924b, pl. 4, p. 105) described *Athrotaxis? ameghinoana*, based on a twig impression showing adpressed rhomboidal leaves (4–5 mm long and 1.5–1.7 mm wide) and a probable detached ovulate cone. This record remains doubtful until new and better-preserved material from the same locality is found.

*Athrotaxis* species that differ from *A. ungeri* in gross morphology have been found in New Zealand and Tasmania, ranging from the Cretaceous to the Pleistocene. *Athrotaxis novae-zeelandiae* (Florin 1940, 1960), from the Late Cretaceous of Otago in New Zealand, includes compressions of foliage remains with unidentified seed cones. The leaves are imbricate, scalelike, and markedly smaller (0.5 mm and ~1.5 mm long) than those in *A. ungeri*. According to Pole (1995), *A. novae-zeelandiae* should be placed into *Sequoiadendron* because the shoot, leaf, and stomata shapes are closely comparable with those of the extant *Sequoiadendron giganteum* Buchholz. This generic transfer was rejected by Hill and Brodribb (1999) and Hill (2001) on the basis that stomata are much more similar to those of the *Athrotaxis* type.

Townrow (1965, 1967) described *Athrotaxis tasmanica* from the Early Eocene of Buckland, Tasmania, based on compressions of shoots with spirally arranged leaves. The leaves are ovate, adpressed, and larger (2.5 mm wide and 3 mm long) than those of *A. ungeri*.

From the Early Oligocene–earliest Miocene of several localities in Tasmania, Hill et al. (1993) described twig compressions with leaves of *Athrotaxis mesibovii* and *Athrotaxis rhomboidea* and incomplete immature ovulate cones. The former species shows clear differences from *A. ungeri* in foliar characters. The leaves are larger (3–8 mm long), loosely spreading, and strongly keeled, while *A. rhomboidea* appears to have the same smaller leaf shape as the Caballo Muerto specimens (1.8–2.2 mm long and 0.7–0.9 mm wide).

Leaves and ovulate cones of *Athrotaxis* cf. *laxifolia* were recovered at Regatta Point, in the Early Pleistocene of Tasmania, by Hill et al. (1993) and Jordan (1995). This species is quite distinct from *A. ungeri*. Its leaves are larger (4–6 mm long) and oblong-lanceolate, with a strong keel. The ovulate cones are slightly smaller (12 mm in diameter), and the bracts are larger than the ovuliferous scale.

#### Distribution of *Athrotaxis*

Florin (1960, 1963) and others (Miller and La Pasha 1983; Hill 1995; Hill and Brodribb 1999) have suggested that the distribution of *Athrotaxis* in the past is restricted solely to the Southern Hemisphere and that all Northern Hemisphere records (such as those of Canada, Europe, or Russia) must be considered doubtful or wrong. However, Srinivasan (1995) described vege-

tative remains attributed to *A. cf. ungeri* from the Early Cretaceous Potomac Group in eastern North America. The leaves are much smaller (0.6–1.5 mm long and 0.6–1 mm wide) than any of those of the Patagonian specimens. Documentation of ovulate cones in organic connection with twigs is necessary to confirm their assignment to *A. ungeri*.

According to the fossil record, *Athrotaxis* was a more widespread genus during the Mesozoic than it is at present. Particularly during the Lower Cretaceous in Patagonia, *Athrotaxis* had an important regional distribution and probably became extinct during the Tertiary. At present, *Athrotaxis* is confined to Tasmania, represented by three species (*A. cupressoides* D. Don, *Athrotaxis selaginoides* D. Don, and *A. laxifolia* Hook [considered to be a hybrid between the two former species]; Hill et al. 1993). These taxa grow on moist slopes and around lakes in mountain regions at an elevation of ~750–1300 m (Sporne 1965; Gibson et al. 1995).

#### Paleoenvironment at the Arroyo Caballo Muerto Creek Section

*Kachaikostrobus acuminatus* and *A. ungeri* were found in the same fossiliferous bed, with both entire vegetative and entire reproductive structures, suggesting the parent plants were not very far from the site of deposition. This completeness was also observed in the other components of the plant assemblage represented by ferns, which dominate the taphocoenosis, with 79%; the two conifers, with 15%; and the subordinate angiosperm leaves, with 6% (Cúneo and Gandolfo 2005). According to Rebas (1982), the paleotopography at the Arroyo Caballo Muerto Creek section, where this plant community was deposited, may be interpreted as a delta flood plain with a fluvial dominance; the climate in the area was humid and temperate. Similar environmental conditions, but with a hot to temperate climate, were inferred for the other Patagonian cheirolepid, *T. biforme* (Archangelsky 1968). Therefore, both *K. acuminatus* and *T. biforme* could be considered thermophilous. This interpretation agrees closely with what has largely been established for most of the cheirolepids (Hluštik 1978; Alvin 1982; Watson 1988). However, among this group, *H. muensteri* has been shown to be adapted to a brackish-water environment (Guignard et al. 1998), while *P. delawarensis* is associated with lacustrine conditions (Axsmith et al. 2004).

Accordingly, it can be suggested that *K. acuminatus* and *T. biforme* successfully inhabited Patagonia by the early Albian and early Aptian, respectively. However, the reasons *Athrotaxis* and the Cheirolepidiaceae have not persisted through geologic time in that area while conifer families such as the Podocarpaceae and Araucariaceae have declined only in numbers of taxa still remain obscure. As has been pointed out by Archangelsky (2001), this may be attributed to changes in the climatic conditions caused by extensive volcanic activity that occurred in Patagonia and other regions during the Lower Cretaceous.

#### Acknowledgments

The work was partially funded by grants BID 1201 PICT 99/6044 (Cretácico Inferior de la Patagonia Austral, Fitoestra-

tigrafía de Áreas Seleccionadas) and PIP CONICET 5093 (Estudios Paleobotánicos y Palinológicos en el Cretácico Inferior de la Cuenca Austral, Santa Cruz). Valuable suggestions for

improving the manuscript were provided by two anonymous reviewers. We thank Orlando Cárdenas for technical assistance in ovulate cone maceration.

### Literature Cited

- Aguirre Urreta MB 2002 Invertebrados del Cretácico inferior. Pages 439–459 in MJ Haller, ed. Geología y recursos naturales de Santa Cruz. Relatorio XV Congreso Geológico Argentino, Calafate.
- Alvin KL 1982 Cheirolepidiaceae: biology, structure and paleoecology. *Rev Palaeobot Palynol* 37:71–98.
- Alvin KL, J Watson, RA Spicer 1994 A new coniferous male cone from the English Wealden and a discussion of pollination in the Cheirolepidiaceae. *Palaeontology* 37:173–180.
- Anderson JM, HM Anderson 1989 Palaeoflora of southern Africa, Molteno Formation (Triassic). II. Gymnosperms (excluding *Dicroidium*). Balkema, Rotterdam. 576 pp.
- Archangelsky A, M Llorens 2003 Palinología de la Formación Kachaika, Cretácico inferior de la Cuenca Austral, Provincia de Santa Cruz. I. Esporas lisas y cinguladas. *Ameghiniana* 40:71–80.
- 2005 Palinología de la Formación Kachaika, Cretácico inferior de la Cuenca Austral, Provincia de Santa Cruz. II. Esporas. *Ameghiniana* 42:311–328.
- Archangelsky S 1963 A new Mesozoic flora from Ticó, Santa Cruz Province, Argentina. *Bull Br Mus (Nat Hist) Geol* 8:48–92.
- 1966 New gymnosperms from the Ticó flora, Santa Cruz Province, Argentina. *Bull Br Mus (Nat Hist) Geol* 13:262–295.
- 1968 On the genus *Tomaxellia* (Coniferae) from the Lower Cretaceous of Patagonia (Argentina) and its male and female cones. *Bot J Linn Soc* 61:153–165.
- 2001 The Ticó flora (Patagonia) and the Aptian extinction event. *Acta Palaeobot* 42:115–122.
- Archangelsky S, ES Bellosi, GA Jalfin, C Perrot 1994 Palynology and alluvial facies from the mid-Cretaceous of Patagonia, subsurface of San Jorge Basin, Argentina. *Cretaceous Res* 15:127–142.
- Archangelsky S, NR Cúneo 1987 Ferugioladaceae, a new conifer family from the Permian of Gondwana. *Rev Palaeobot Palynol* 51:3–30.
- Archangelsky S, GM Del Fueyo 1989 *Squamastrobos* gen. nov., a fertile podocarp from the early Cretaceous of Patagonia, Argentina. *Rev Palaeobot Palynol* 59:109–126.
- Archangelsky S, JC Gamarro 1967 Pollen grains found in coniferous cones from the Lower Cretaceous of Patagonia (Argentina). *Rev Palaeobot Palynol* 5:179–182.
- Axsmith BJ, FM Andrews, NC Fraser 2004 The structure and phylogenetic significance of the conifer *Pseudohirmerella delawarensis* nov. comb. from the Upper Triassic of North America. *Rev Palaeobot Palynol* 129:251–263.
- Axsmith BJ, BF Jacobs 2005 The conifer *Frenelopsis ramosissima* (Cheirolepidiaceae) in the Lower Cretaceous of Texas: systematic, biogeographical, and paleocological implications. *Int J Plant Sci* 166:327–337.
- Baldoni AM, RA Askin, D Ragona 2001 Palynology of the Lower Cretaceous Kachaika Formation, Santa Cruz Province, Argentina. Pages 191–200 in DK Goodman, RT Clark, eds. Proceedings of the IX International Palynological Congress, American Association of Stratigraphic Palynologists, Houston, June 1996. American Association of Stratigraphic Palynologists, Dallas.
- Baldoni AM, VA Ramos 1981 Nuevas localidades con plantas fósiles Cretácicas en la cordillera Patagónica (Provincia de Santa Cruz, República Argentina). Pages 743–759 in *Actas VII Congreso Geológico Argentino*, San Luis. Sociedad Geológica Argentina, Buenos Aires.
- Barreda V, S Archangelsky 2006 The southernmost record of tropical pollen grains in the Cretaceous of Patagonia, Argentina. *Cretaceous Res* 27:778–787.
- Calder MG 1953 A coniferous petrified forest in Patagonia. *Bull Br Mus (Nat Hist) Geol* 2:99–138.
- Clement-Westerhof JA 1988 Morphology and phylogeny of Paleozoic conifers. Pages 298–337 in CB Beck, ed. *Origin and evolution of gymnosperms*. Columbia University Press, New York.
- Clement-Westerhof JA, JHA van Konijnenburg-van Cittert 1991 *Hirmeriella muensteri*: new data on the fertile organs leading to a revised concept of the Cheirolepidiaceae. *Rev Palaeobot Palynol* 68:147–179.
- Cúneo R, MA Gandolfo 2005 Angiosperm leaves from the Kachaika Formation, Lower Cretaceous of Patagonia, Argentina. *Rev Palaeobot Palynol* 133:169–178.
- Doyle J 1945 Developmental lines in pollination mechanisms in the Coniferales. *Sci Proc R Dublin Soc* 24:43–63.
- Ewin TAM 2006 Distinguishing the Cheirolepidiaceae from extant conifer families using leaf cuticle characters. Paper presented at the 7th European Paleobotany-Palynology Conference, Prague, September 6–11.
- Florin R 1940 The Tertiary fossil conifers of south Chile and their phytogeographical significance. *K Sven Vetenskapsakad Handl* 19:1–107.
- 1960 Die frühere Verbreitung der Konifergattung *Athrotaxis* D Don. *Senckenb Lethaea* 41:199–207.
- 1963 The distribution of conifer and taxad genera in time and space. *Acta Horti Bergiani* 20:121–312.
- Frenguelli J 1935 *Ptilophyllum hislopi* (Oldham) en los “Mayer river beds” del Lago San Martín. *Notas Mus La Plata Paleontol* 3:71–83.
- Gamarro JC 1982 Informe palinológico del perfil arroyo Caballo Muerto, Santa Cruz. Yacimientos Petrolíferos Fiscales, Buenos Aires.
- Gibson N, PCJ Barker, PJ Cullen, A Shapcott 1995 Conifers of southern Australia. Pages 223–251 in NJ Enright, RS Hill, eds. *Ecology of southern conifers*. Melbourne University Press, Melbourne.
- Guignard G, F Thévenard, JHA van Konijnenburg-van Cittert 1998 Cuticle ultrastructure of the cheirolepidiacean conifer *Hirmeriella muensteri* (Schenk) Jung. *Rev Palaeobot Palynol* 104:115–141.
- Guler MV, S Archangelsky 2006 Albian dinoflagellate cysts from the Kachaika Formation, Austral Basin, southwest Argentina. *Rev Mus Argent Cienc Nat, NS*, 8:179–184.
- Halle TG 1913 Some Mesozoic plant-bearing deposits in Patagonia and Tierra del Fuego and their floras. *K Sven Vetenskapsakad Handl* 51:1–58.
- Harris TM 1979 The Yorkshire Jurassic flora. V. Coniferales. British Museum of Natural History, London. 166 pp.
- Hill RS 1995 Conifer origin, evolution and diversification in the Southern Hemisphere. Pages 10–29 in NJ Enright, RS Hill, eds. *Ecology of southern conifers*. Melbourne University Press, Melbourne.
- 2001 The Cenozoic macrofossil record of the Cupressaceae in the Southern Hemisphere. *Acta Palaeobot* 42:123–132.
- Hill RS, TJ Brodribb 1999 Southern conifers in time and space. *Aust J Bot* 47:639–696.
- Hill RS, GJ Jordan, RJ Carpenter 1993 Taxodiaceous macrofossils from the Tertiary and Quaternary sediments in Tasmania. *Aust J Bot* 6:237–249.
- Hluštík A 1978 Frenelopsid plants (Pinopsida) from the Cretaceous of Czechoslovakia. Pages 129–141 in *Proceedings of Palaeontological Conference*, Charles University, Prague, February 10–11, 1977. Univerzita Karlova, Prague.
- Jordan GJ 1995 Extinct conifers and conifer diversity in the Early Pleistocene of western Tasmania. *Rev Palaeobot Palynol* 84:375–387.

- Jung W 1967 Eine neue Rekonstruktion des Fruchtzapfens von *Cheirolepis münsteri* (Schenk) Schimper. Neues Jahrb Geol Palaeontol Mon 2:11–114.
- 1968 *Hirmeriella münsteri* (Schenk) Jung nov. comb., eine bedeutsame Konifere des Mesozoikums. Palaeontographica B 122: 55–93.
- Krassilov VA 1982 On the ovuliferous organ of *Hirmeriella*. Phytol 1: 141–144.
- Kvaček J 2000 *Frenelopsis alata* and its microsporangiate and ovuliferous reproductive structures from the Cenomanian of Bohemia (Czech Republic, Central Europe). Rev Palaeobot Palynol 112: 51–78.
- Llorens M, GM Del Fueyo 2003 Coníferas fértiles de la Formación Kachaike, Cretácico Medio de la provincia de Santa Cruz, Argentina. Rev Mus Argent Cienc Nat, NS, 5:241–244.
- Longobucco MI, C Azcuy, B Aguirre-Urreta 1985 Plantas de la Formación Kachaike, Cretácico de la Provincia de Santa Cruz. Ameghiniana 21: 305–315.
- Looy CV 2007 Extending the range of derived Late Paleozoic conifers: *Lebouskia* gen. nov. (Majonicaceae). Int J Plant Sci 168:957–972.
- Lutz AI 2006 Estudio de la paleoflora de la Formación Carrizal (Triásico Superior) de la Cuenca de Marayes-Carrizal, provincia de San Juan, Argentina. PhD diss. Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes.
- Miller CN 1999 Implication of fossil conifers for the phylogenetic relationships of living families. Bot Rev 65:239–277.
- Miller CN, CA LaPasha 1983 Structure and affinities of *Atrothaxites berryi* Bell, an Early Cretaceous conifer. Am J Bot 70:772–779.
- Morel EM 1991 Estudio paleoflorístico y paleoambiental de la secuencia triásica en el área de Cacheuta (Provincia de Mendoza). PhD diss. Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Buenos Aires.
- Piatnitzky A 1938 Observaciones geológicas en el oeste de Santa Cruz (Patagonia). Bol Inf Petrol 165:45–95.
- Pole MS 1995 Late Cretaceous macrofloras of eastern Otago, New Zealand: gymnosperms. Aust Syst Bot 8:1067–1106.
- Rebasa M 1982 Análisis estratigráfico y paleoambiental de la Formación Kachaike, aflorante en la barranca epónima, provincia de Santa Cruz. MS diss. Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires.
- Retallack G 1981 Middle Triassic megafossil plants from Long Gully, near Otematata, north Otago, New Zealand. J R Soc N Z 11:167–200.
- Spegazzini C 1924a Coniferales fósiles patagónicas. An Soc Cient Argent 98:125–139.
- 1924b Sobre algunas impresiones vegetales Eocénicas de Patagonia. Com Mus Nac Hist Nat Buenos Aires 2:95–107.
- Sporne KR 1965 The morphology of gymnosperms. Hutchinson University Library, London.
- Srinivasan V 1995 Conifers from the Puddledock locality (Potomac Group, Early Cretaceous) in eastern North America. Rev Palaeobot Palynol 89:257–286.
- Stockey RA 1977 Reproductive biology of the Cerro Cuadrado (Jurassic) fossil conifers: *Pararaucaria patagonica*. Am J Bot 64:733–744.
- 1978 Reproductive biology of Cerro Cuadrado fossil conifers: ontogeny and reproductive strategies in *Araucaria mirabilis* (Spegazzini) Windhausen. Palaeontographica B 166:1–15.
- Thévenard F 1993 Les coniferales du Jurassique inférieur du gisement de Chaldecoste, bassin des Causses (Lozère, France). Rev Palaeobot Palynol 78:145–166.
- Townrow JA 1965 Notes on Tasmanian pines. II. *Athrotaxis* from the Lower Tertiary. Pap Proc R Soc Tasman 99:109–113.
- 1967 The *Brachyphyllum crassum* complex of fossil conifers. Pap Proc R Soc Tasman 101:149–172.
- Villar de Seoane L 1998 Comparative study of extant and fossil conifer leaves from the Baqueró Formation (Lower Cretaceous), Santa Cruz Province, Argentina. Rev Palaeobot Palynol 99:247–265.
- Watson J 1988 The Cheirolepidiaceae. Pages 382–447 in CB Beck, ed. Origin and evolution of gymnosperms. Columbia University Press, New York.
- Yao X, TN Taylor, EL Taylor 1993 The Triassic seed cone *Telemaichus* from Antarctica. Rev Palaeobot Palynol 78:269–276.