



Cheirolepidiaceae diversity: An anatomically preserved pollen cone from the Lower Jurassic of southern Victoria Land, Antarctica



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ABSTRACT

To date, the vast majority of fossils described for the extinct conifer family, the Cheirolepidiaceae, have been reported from compression/impressions primarily from Cretaceous rocks; there are fewer reports from permineralizations and the Jurassic. New specimens have recently been discovered in siliceous blocks composed of fusainized layers of plant remains that alternate with fine-grained sediments from the Carapace Nunatak (Lower Jurassic) locality of southern Victoria Land, Antarctica. Specimens were prepared using standard serial cellulose-acetate peel technique, transmitted-light microscopy, and SEM analysis. The cones are ellipsoidal, up to 5.5 mm long, and consist of helically arranged microsporophylls, each with a slender stalk containing a single vascular bundle; the distal lamina is peltate and most closely resembles those of the *Classostrobus*. Four to seven pollen sacs are arranged in an annular cluster abaxial to the sporophyll stalk. In situ *Classopollis* pollen ranges from 18 to 60 μm in equatorial diameter with an average diameter of 30 μm. In addition to these well-preserved pollen cones there is a large diversity of vegetative conifer remains within the Carapace Nunatak material including leaf and stem fragments. The discovery of the pollen cones in combination with vegetative remains provides additional information on the reproductive biology of the Cheirolepidiaceae and increases the probability of developing a whole-plant concept for this Jurassic permineralized conifer.

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1. Introduction

Jurassic floras are well known from the Antarctica Peninsula area. Members of the Swedish South Polar Expedition (1901–1903) collected some of the first plant specimens from Hope Bay on Trinity Peninsula (Halle, 1913; Cantrill and Poole, 2012), which has been variously dated as Lower Jurassic to Lower Cretaceous (Gee, 1987, 1989; Cantrill, 2000; Rees and Cleal, 2004). Petrographic and geochronological analyses by Hunter et al. (2005) indicated that the Botany Bay Group is Middle Jurassic. The floras are diverse, e.g., liverworts (*Schizolepidella* spp.), sphenophytes (*Equisetum* spp.), ferns (e.g., *Cladophlebis*, *Coniopteris*, *Dictyophyllum*, *Goepfertella*, *Hausmannia*, *Matonidium*, *Spesia*, *Sphenopteris*, *Todites*), seed ferns (e.g., *Archangelskya*, *Dicroidium*, *Komlopteris*, *Pachypteris*), Caytoniales (*Caytonanthus*), cycadophyte foliage (e.g., *Ctenis*, *Otozamites*, *Pseudoctenis*, *Taeniopteris*, *Weltrichia*, *Williamsonia*, *Zamites*), conifers (e.g., *Araucarites*, *Brachyphyllum*, *Elatocladus*, *Pagiophyllum*) (Gee, 1987, 1989; Rees and Cleal, 2004, and references therein; Ociepa, 2007; Ociepa and Barbacka, 2011).

In contrast to the Antarctic Peninsula, little is known about Jurassic plant life on the Antarctic continent. The Early Jurassic was the beginning of the break-up of Gondwana. Extensive volcanism at this time

led to the emplacement of the Ferrar Group, a large igneous province that is related to the continental flood basalts of South Africa (Karoo) and South America (Chon Aike) (Riley and Knight, 2001), along the central Transantarctic Mountains. Fossil plants of Jurassic age on the continent are found only in a few, exceptional sites where sedimentary interbeds occur within the volcanics. Compression and permineralized plant fossils have been described from the Lower Jurassic Shafer Peak Formation in northern Victoria Land (Bomfleur et al., 2007, 2011a,b; Schöner, et al., 2007; Bomfleur and Kerp, 2010). In addition, several examples of silicified conifers have been described from the Jurassic of Antarctica, including trees engulfed by lava flows from northern Victoria Land (Jefferson et al., 1983), silicified tree trunks from Brebbia and Ramírez Nunataks (Antarctic Peninsula; del Valle et al., 1997), a single tree stump from the Coombs Hills in southern Victoria Land (Garland et al., 2007), and permineralized woody axes from Suture Bench east of the Gair Mesa in northern Victoria Land (Bomfleur et al., 2011b; Harper et al., 2012). Permineralized peat deposits from Storm Peak in the central Transantarctic Mountains have yielded an anatomically preserved fern petiole, *Polyphacelus stormensis* (Yao et al., 1991). Of these rare Jurassic sites, to date, the most extensive and fossiliferous deposit is at Carapace Nunatak in southern Victoria Land (Townrow, 1967a; Ball et al., 1979; Babcock et al., 2006).

In addition to silicified Jurassic wood, there is evidence for reproductive remains of conifers from Antarctica (e.g., Plumstead,

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1962; Townrow, 1967a,b). Dispersed staminate cones belonging to *Classostrobus* Alvin, Spicer et Watson (Alvin et al., 1978) and containing in situ *Classopollis* pollen, and other cheirolepidiaceous cones have been found on other continents (see Van Konijnenburg-van Cittert (1987); Watson (1982, 1988); supplemental material); these are often attached to or associated with other macrofossils belonging to the family. Most of what is known about cheirolepidiaceous fossils is from compression-type preservation; discoveries and descriptions of permineralizations are rare. Only a single permineralized cheirolepidiaceous pollen cone has been described previously, *Classostrobus crossii* Rothwell et al. (2007), from Middle Jurassic calcareous nodules from southern England (Rothwell et al., 2007). Here we describe a new species of anatomically preserved conifer pollen cone based on five specimens, belonging to the Cheirolepidiaceae, that were discovered in Lower Jurassic sedimentary interbeds on Carapace Nunatak, southern Victoria Land, Antarctica. The specimens described in this report are the first examples of permineralized cheirolepidiaceous pollen cones from the Southern Hemisphere, and offer additional details about the anatomy and histology of the staminate cones of this extinct family.

2. Geological setting, materials, and methods

2.1. Geological setting

The collection site is located within the Ferrar Large Igneous Province (FLIP), which is a linear 3500 km belt of tholeiitic rocks (Elliot and Fleming, 2004) that contains occasional permineralizations. The cones are preserved in lake sediments within laminated chert. The Lower Jurassic chert blocks containing the fossils used in this study were collected from a moraine-debris field on the E-NE side of Carapace Nunatak

Nunatak, southern Victoria Land, central Transantarctic Mountains, Antarctica (76° 53' S, 159° 25' E, elevation 2149 m, Convoy Range Quadrangle) during the 1993–1994, 1997–1998, and 2011–2012 field seasons (Fig. 1, A–C). The rocks of the Kirkpatrick Basalt and Carapace Sandstone Member of the Mawson Formation at Carapace Nunatak are cross-cut by several faults (Bradshaw, 1987), but generally consist of subaerial basalt flows overlain by the volcanoclastic sandstone and breccia of the Carapace Sandstone. This is overlain by subaerial basaltic flows and columns of palagonite and basaltic pillows of the Kirkpatrick Basalt (Ballance and Watters, 1971). The fossil-bearing cherts occur as 2–6 m long pods or lenses set between palagonitic breccia and pillow basalts (Fig. 1, D). The cherts display several physical features (Fig. 1, E): millimeter-scale laminations, flame structures, diapirs, millimeter-scale normal faults that penetrate some laminae, rupturing of lamina sets, and intense folding of the lamina sets. A rough stratification of the chert and limestone lenses exists, but lateral continuity of the deposits does not occur due to the prevalence of subaqueous basaltic lava flows in this stratigraphic interval.

The deformation features indicate that the material was initially soft and underwent a loss in volume prior to or concurrent with lithification. These lenses are interpreted as either rafts of lacustrine sediment during a single prolonged emplacement of a lava delta, or as rafts of material that was deposited in between two successive lava flows (Bradshaw, 1987). The fossil-bearing cherts are interpreted as freshwater (lacustrine) deposits that have been affected by various aspects of active volcanism (Ballance and Watters, 1971). Although our recognition of different scales of soft-sediment deformation and volume-loss features within the chert layers is consistent with Magadi-type chert (Eugster, 1967; Surdam et al., 1972; Krainer and Spötl, 1998), which forms from the early diagenetic conversion of the Na-rich phyllosilicate mineral

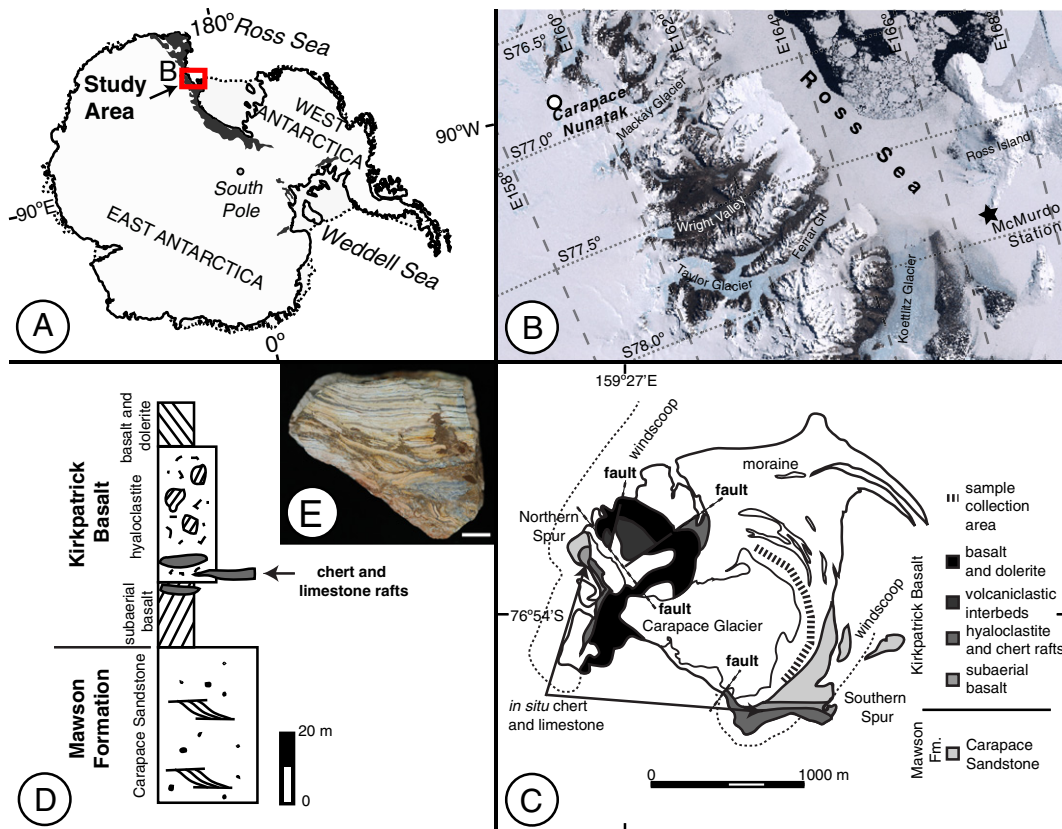


Fig. 1. Maps and stratigraphy of the study area. A. General map of Antarctica showing the study area in the Ross Sea region; red box highlighting the study site at Carapace Nunatak. B. Detailed map of red box area from A. Composite satellite image of the Ross Sea region, included in the Taylor Glacier USGS topographic map, highlighting the study site at Carapace Nunatak. C. Geologic map of Carapace Nunatak, modified from Bradshaw (1987); samples were collected from the ice-cored moraine on the E-NE side of Carapace Nunatak. D. Generalized stratigraphic column of the Mawson Formation and Kirkpatrick Basalt at Carapace Nunatak; fossiliferous chert and limestone occur as lenses within the basalt and hyaloclastite that overlie the Carapace Sandstone Member of the Mawson Formation. E. Rock sample of chert displaying soft sediment deformation and normal faults. Scale = 1 cm.

magadiite to chert in alkaline lakes or from alkaline groundwaters (Rooney et al., 1969). Magadi-type chert is unique among abiogenic cherts in that it preserves evidence of soft-sediment deformation and desiccation due to its formation from soft beds of magadiite (Krainer and Spötl, 1998). At the type locality, Lake Magadi in the Kenyan Rift Valley, magadiite is thought to form via a Na-rich influx of hydrothermal fluid and a high silicon concentration (Jones et al., 1967). The presence of Magadi-type chert in these lacustrine deposits would suggest that the Early Jurassic lake near Carapace Nunatak was likely alkaline, possibly fed by hydrothermal fluids. The presence of limestone lenses between palagonitic and basaltic pillows attests to lake water pH values near neutral, and likely indicates temporal variation, at an unknown scale, in the geochemistry of these lake waters.

2.2. Materials

The fossiliferous chert blocks from Carapace Nunatak were initially described by Gunn and Warren (1962), and preliminary studies describing and discussing the fossil floras and faunas have been investigated by multiple authors (e.g., Plumstead, 1962; Townrow, 1967a,b; Babcock et al., 2006; Ribecai, 2007). Within the chert blocks used in this study, we have observed an abundance of fusainized plant material and animal remains. The fine-grained matrix has preserved several layers that contain abundant plant fossils, including various taxa of fern pinnules, rachides and rhizomes, at least three conifer taxa represented by vegetative and reproductive structures, isolated ovules, and cycadophyte foliage. Intermixed within this flora are various arthropods—an abundance of shallow-water dwelling conchostracans and other ephemeral freshwater crustaceans (Ballance and Watters, 1971; Ball et al., 1979; Shen, 1994).

2.3. Methods

Five permineralized pollen cones were analyzed in this study. The pollen cones are preserved in various planes of section and range from complete to fragmentary. Individual slabs containing two cones on the same surface are indicated as alpha and beta. Chert blocks were cut, polished, etched with 48% hydrofluoric acid, rinsed, and peeled using the standard acetate peel technique (Joy et al., 1956; Galtier and Phillips, 1999). A total of 177 serial peels were mounted on glass slides with Eukitt® mounting medium (O. Kindler, Freiburg, Germany). Pollen diameters were acquired using a Zeiss transmitted-light compound microscope. Scanning electron microscopy (SEM) images were acquired from peels mounted on SEM stubs with two-sided tape and were sputter-coated with gold (15 nm) using a Q150T Turbo-pumped Sputter Coater (Quorum Technologies). Images were captured by a Versa 3D dual beam Scanning Electron Microscope/Focused Ion Beam (FEI, Hillsboro, OR, USA). All SEM images were obtained at an acceleration voltage of 20 kV, spot size 4.0, and were acquired with an Everhart Thornley (ET) detector using built-in software (XT Microscope) of the FEI company. Digital images of surface peels were taken on a Leica MZ16 manual fluorescence stereomicroscope with an attached Leica DC500 digital camera. Images of slide-mounted peels were captured with a Leica DC500 digital camera on a Leica DM5000B compound microscope. Additional measurements were acquired using ImageJ 1.43u software (Abramoff et al., 2004) and edited (i.e., brightness, contrast, and color balance) using Adobe Photoshop CS4 version 11.0.2 (1990–2010, © Adobe Systems). Pollen terminology is in concordance with Punt et al. (2007); note that terms *sexine* 1, 2, 3 are in accordance with Punt et al. (2007) and differ from the same terms in Taylor and Alvin (1984). Specimens include accession numbers: 17570 G bot, 17607 A1 and B top, 17613 F top alpha and beta, 17654 F3 bot, peels, SEM stub: J 2138, and slides: 29,698–29,719, 29,744–29,856, and 29,910–29,951 and are housed in the Division of Paleobotany Collections, Natural History Museum and Biodiversity Institute, University of Kansas (KUPB).

3. Results

3.1. Systematic paleobotany

Division: Coniferophyta

Class: Coniferopsida

Order: Coniferales

Family: Cheirolepidiaceae Takhtajan

Genus: *Classostrobus* Alvin, Spicer et Watson

Species: *Classostrobus elliotii* Hieger, Serbet, Harper, Taylor, Taylor et Gulbranson, sp. nov.

Specific diagnosis: Cones ellipsoidal with bluntly pointed apex; microsporophylls stalked, peltate (laminae rhomboidal distally), and helically arranged on the main axis. Sporophyll stalks inflated at the base; comprised of a singular vascular strand and thick- and thin-walled parenchymatous cells with interspersed transfusion tracheids. Distal from main cone axis, sporophyll lamina with transfusion tracheids and some thick-walled parenchymatous cells. Pollen sacs abaxial, arranged in an annular cluster with a central vascular strand, attached to and hanging vertically from sporophyll stalk midway between cone axis and sporophyll lamina. Sporangia bear in situ *Classopollis* pollen; cryptopore on distal surface, prominent subequatorial rimula present, trilete on proximal surface, supracteal elements spinulose.

Etymology: The specific epithet is named in honor of Dr. David H. Elliot, for his numerous contributions over the past 40 years that enhance our understanding of the geology and stratigraphy of continental Antarctica, especially of Jurassic volcanic deposits.

Holotype (*hic designatus*): 17,654 F bot [Accession: slide nos. 29,910–29,951, SEM stub no. J 2138] (Plate I, 2, 4–7, Plate II, 1–12) this paper.

Paratypes: 17,613 F top alpha (Plate I, 3, 8, 9, 10) 17,613 F top beta (Plate I, 1)

Repository: Natural History Museum and Biodiversity Institute, Division of Paleobotany Collections (KUPB), University of Kansas, Lawrence, KS, USA

Type locality: Carapace Nunatak, southern Victoria Land, Transantarctic Mountains, Antarctica (76° 53' S, 159° 25' E, elevation 2149 m, Convoy Range Quadrangle)

Stratigraphic horizon: Carapace Sandstone Member, Mawson Formation, Ferrar Group

Age: Early Jurassic (Toarcian) (Elliot, 2013)

3.2. Description

The cones are ellipsoidal in longitudinal section, up to 5.5 mm in length with an average diameter of 2.8 mm (1.0–5.2 mm, $n = 5$), and the cone apex is bluntly pointed with helically arranged imbricate, peltate-shaped microsporophylls. The distal lamina is rhomboidal in face view with attenuate tips. The cone axis (Plate I, 1) is circular, approximately 0.5 mm in diameter and up to 4.4 mm long. Sporophylls (Plate I, 1, 2) diverge from the main axis at approximately 90°. Vascular tissue is poorly preserved in both longitudinal and transverse sections of the cone axis. Surrounding the vascular tissue are isodiametric parenchymatous cells 68 µm (60–76 µm) in diameter with several cells containing opaque contents. Vascular tissue in the sporophyll stalk (Plate I, 6) consists of a single bundle varying from 8 to 12 tracheids, each approximately 7 µm (5–10 µm) in diameter. The basal portion of stalk is about 0.7 mm in diameter narrowing to approximately 0.5 mm and flaring distally (Plate I, 1, 2). At this point, the vascular strand becomes diffuse and is gradually replaced by transfusion tracheids. Ultimately the transfusion tissue (Plate I, 7) comprises about half of the sporophyll lamina and terminates approximately halfway through the distal lamina. Transfusion cells are ovoid, range up to 51 µm in length

and up to 24 μm in diameter, and have scalariform wall thickenings (Plate I, 7). Resin ducts were not observed in any of the cones.

Microsporophylls consist of an expanded base, a circular stalk, and an expanded distal lamina. Distal laminae (Plate I, 4) are up to 2.7 mm long and 2.5 mm wide, and oriented perpendicular to the long axis of the stalk. The sporophyll epidermis (Plate I, 5) is divided into two parts on the outer distal lamina: an outer epidermis (Plate I, 5) made up of an uniseriate layer of thin-walled cells 17 μm (10–33 μm) in diameter and an inner hypodermal layer (Plate I, 5) constructed of thicker-walled columnar cells 21 μm (12–27 μm) long by 12 μm (8–15 μm) wide. In some sections, an amorphous layer covers the epidermis and is interpreted as the remains of cuticle and/or epicuticular wax. Transfusion tracheids appear clustered near the distal end of the stalk along the vascular trace and extend into the distal lamina in a fan-like configuration among the parenchymatous cells of the sporophyll head. Isodiametric parenchymatous cells of the sporophylls are typically empty but are occasionally filled with opaque contents (Plate I, 4). These cells vary from 40 to 116 μm in diameter.

Multiple sequences of serial peels indicate that a cluster of 4 to 7 ellipsoidal microsporangia in an annular arrangement (Plate I, 2, 3) is attached to the abaxial surface of the sporophyll stalk, equidistantly positioned between the distal lamina and the cone central axis (Fig. 2). Microsporangia average 0.5 mm long and 0.3 mm in diameter. Vascular tissue is found in the center of the ring of sporangia (Plate I, 3 and 8). Some pollen sacs are devoid of pollen while others contain densely packed well-preserved or degraded grains. Sporangial wall cells are columnar and approximately 34 μm (20–45 μm) long by 9 μm (5–13 μm) wide. These cells are primarily filled with opaque contents (Plate I, 3) or may occasionally be empty (Plate I, 9). Some sporangial walls are intact while others are ruptured possibly indicating pollen dispersal or damage to the sporangial wall. Bordering the microsporangial walls are numerous spheroidal tapetal orbicules (Plate II, 8, 12) that range from 0.8 μm to 1.9 μm in diameter.

Pollen sacs of *Classostrobus elliotii* are densely packed with pollen grains; identical pollen is (Plate II, 1) often found dispersed in other areas of the pollen cone, e.g., along the cone axis, outer sporangial walls, sporophyll stalks, and the abaxial surfaces of the sporophyll laminae. Some of the grains are in tetrads (Plate II, 2), but most occur as

individual grains. In equatorial view, the pollen is globose and shows a size difference from the proximal to the distal (or vice-versa) poles; equatorial diameters of the individual grains are approximately 30 μm (18–60 μm ; $n = 123$). Examination of these grains indicates features that are consistent with *Classopollis* pollen, including a distal cryptopore (Plate II, 3, 4, 5), subequatorial furrow or rimula (Plate II, 3, 6, 7), internal equatorial striae (Plate II, 6, 7, 9), and a proximal trilete (Plate II, 8, 9). The cryptopore is 3.5–4.4 μm in diameter. The rimula extends around the pollen grain and is approximately 1.5 μm (1.0–1.8 μm) wide. In proximal view, laesurae of the trilete (Plate II, 8) are 6.6–12.8 μm long. Anastomosing bands of striae (Plate II, 6) are rarely seen in external view; however, internal views from SEM images reveal linear arrangements of infratectal columellae indicative of striations.

Details of the pollen wall are well preserved and consist of an outer sexine and inner nexine layer, and the infrastructure of the grains is reticulate to pseudoreticulate. Layers 1–3 of the sexine (Plate II, 10) are approximately 1.9 μm (1.7–2.1 μm) thick all together and are represented by infratectal columellae (sexine 1), an inner tectum (sexine 2), and supracteal spinules (sexine 3) in a discordant pattern. Supracteal spinules are conical, wide at the base and thinly tapered toward the tip. These wall structures average approximately 320 nm (240–530 nm) long. The distal and proximal surfaces have numerous columellae (sexine 1) that protrude inwards toward the nexine and are about 890 nm (740–1000 nm) long by 450 nm (260–740 nm) wide. The tectum (sexine 2) between the spinules and columns of the sexine is approximately 330 nm (210–440 nm) thick. In some grains, the nexine (Plate II, 5, 11) is around 280 nm (210–330 nm) thick. Broken grains allow for the internal examination of structures such as the proximal trilete (Plate II, 9). This triangular structure has equidistant arms that are about 12 μm long. Internal views of the grains reveal 3–5 linear arrangements (Plate II, 7, 9) of the infratectal columellae indicative of striae below the rimula.

Up to five *Brachyphyllum*-type leaves are in close association with these cones (Plate I, 2, 10). There was no direct anatomical connection between the leaves and the pollen cones used in this study. These leaves appear near the basal region of the cone and attenuate before extending the entire length of the cones; the leaves are incomplete but include some morphological and anatomical features. Leaves are 0.4–0.5 mm

Plate I. Components of *Classostrobus elliotii* pollen cones from permineralizations, Early Jurassic of Antarctica. (See on page 82)

- Fig. 1. Apical portion of a longitudinal section of pollen cone. Note helical arrangement of microsporophylls (S = microsporophyll, C = cone axis). Scale = 1.0 mm. Slide no. 29,833.
 Fig. 2. Transverse section of pollen cone about halfway through specimen. Note masses of pollen grains (amber in color) within microsporangia, and annular arrangement of pollen sacs. Image taken of a peel still attached to the surface of the specimen (S = microsporophyll, L = associated leaf). Scale = 2.0 mm. 17654 F3 bot peel no. 35. Slide no. 29,944.
 Fig. 3. Annular cluster of 5 microsporangia with presumed remnants of abaxial microsporophyll stalk in the center (arrow), recognized by the presence of tracheids (see enlargement in Fig. 8). Scale = 0.3 mm. 17613 F top alpha slide no. 22.
 Fig. 4. Transverse section of a microsporophyll with rhomboidal head at the top left. Note epidermis (arrow) and opaque parenchymatous cells; cells below these are transfusion tissue (T). Scale = 0.5 mm. Slide no. 29,912.
 Fig. 5. Dermal layers of microsporophyll (E = epidermis, H = hypodermis). Scale = 25 μm . Slide no. 29,912.
 Fig. 6. Single vascular trace from approximately the middle of microsporophyll stalk, showing metaxylem tracheids with scalariform thickenings and possible protoxylem tracheids with helical-annual thickenings (arrow). Scale = 50 μm . Slide no. 29,915.
 Fig. 7. Transfusion tracheids of the microsporophyll. Note scalariform pitting (arrow). Scale = 50 μm . Slide no. 29,913.
 Fig. 8. Higher magnification of central area indicated by arrow in Fig. 3, showing part of a tracheid with scalariform thickenings (arrow). Scale = 30 μm . Slide no. 29,822.
 Fig. 9. Uniseriate wall of pollen sac showing sporangial walls lacking opaque contents. Scale = 50 μm . Slide no. 29,813.
 Fig. 10. Detail of vascular bundle of one of the associated *Brachyphyllum*-type leaves. Surrounding the vascular tissue are round cells (indicated by *) of unknown affinities that may represent some type of secretory cell, form of transfusion tissue, or some type of thick-walled fungal hyphae. Scale = 50 μm . Slide no. 29,812.

Plate II. Pollen of *Classostrobus elliotii*. All SEM images from SEM stub no. J 2138. (See on page 83)

- Fig. 1. Light micrograph (LM) of numerous pollen grains within a microsporangium. Scale = 50 μm . Slide no. 29,940.
 Fig. 2. LM of pollen grains still within a tetrad. Scale = 10 μm . Slide no. 29,937.
 Fig. 3. Scanning electron micrograph (SEM) of distal view of pollen grain. Note cryptopore (C) and furrow (F). Scale = 5 μm .
 Fig. 4. LM of side view displaying distal cryptopore (arrow). Scale = 10 μm . Slide no. 29,937.
 Fig. 5. SEM of distal view of pollen grain. Sexine (S) is partially separated revealing preserved nexine (N) layer displaying the distal cryptopore (C). Note perforations on nexine from contact with columellae of the sexine. Scale = 10 μm .
 Fig. 6. LM of side view of pollen grain showing rimula (arrow) and striae in equatorial region. Scale = 10 μm . Slide no. 29,937.
 Fig. 7. SEM of internal view of pollen grain showing rimula (arrow) and equatorial striae. Scale = 10 μm .
 Fig. 8. LM of proximal view of trilete. Orbicules are indicated at arrow. Scale = 10 μm . Slide no. 29,939.
 Fig. 9. SEM of internal view of pollen grain showing trilete mark. Note linear striation patterns (arrow) of sexine columellae. Scale = 10 μm .
 Fig. 10. Section of sexine layer displaying internal columellae on the left and external protruding spinules on the right. Scale = 2 μm .
 Fig. 11. Internal view of smooth surface of nexine layer. Scale = 2 μm .
 Fig. 12. Orbicules with spinules. Scale = 2 μm .

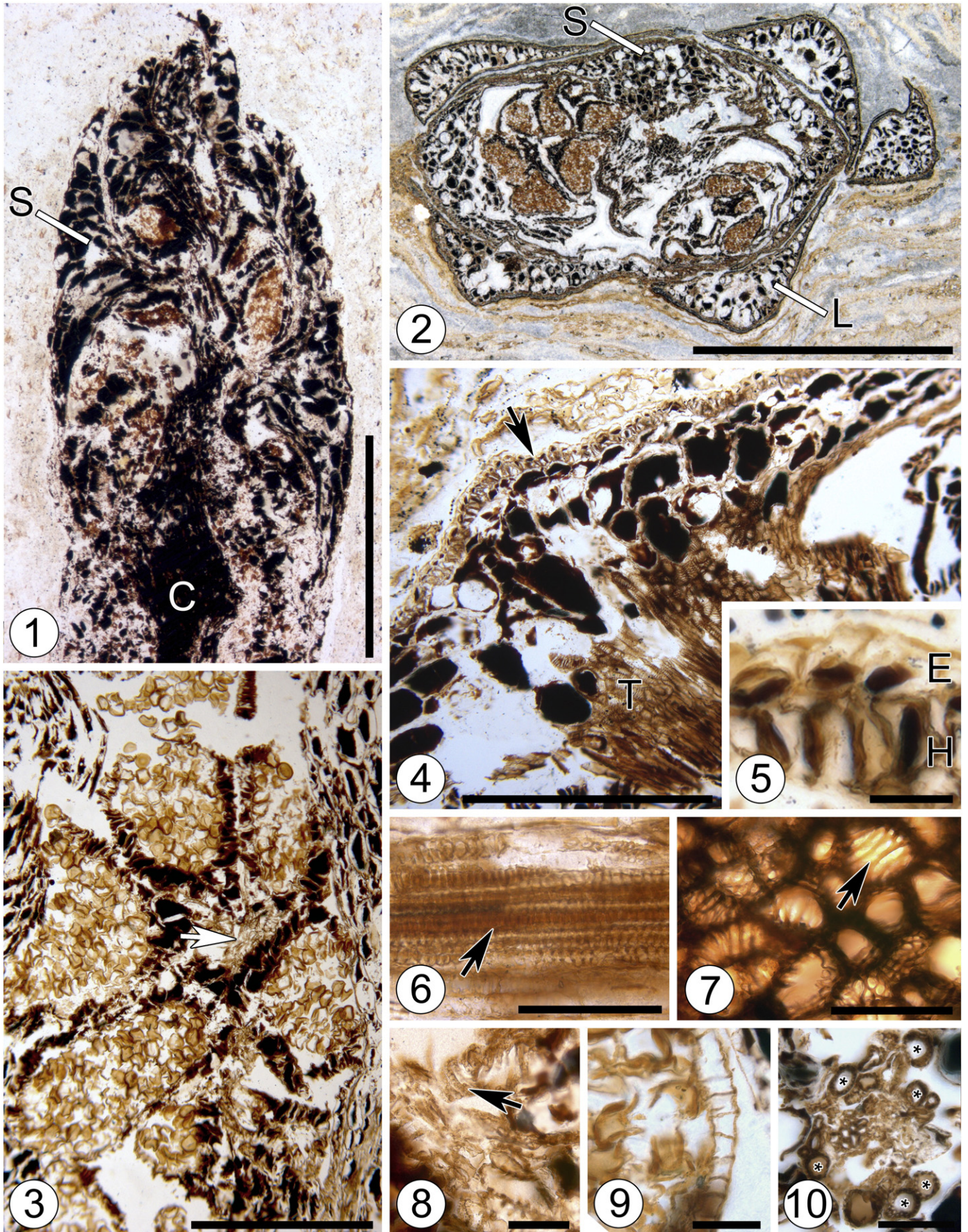


Plate I. (caption on page 81).

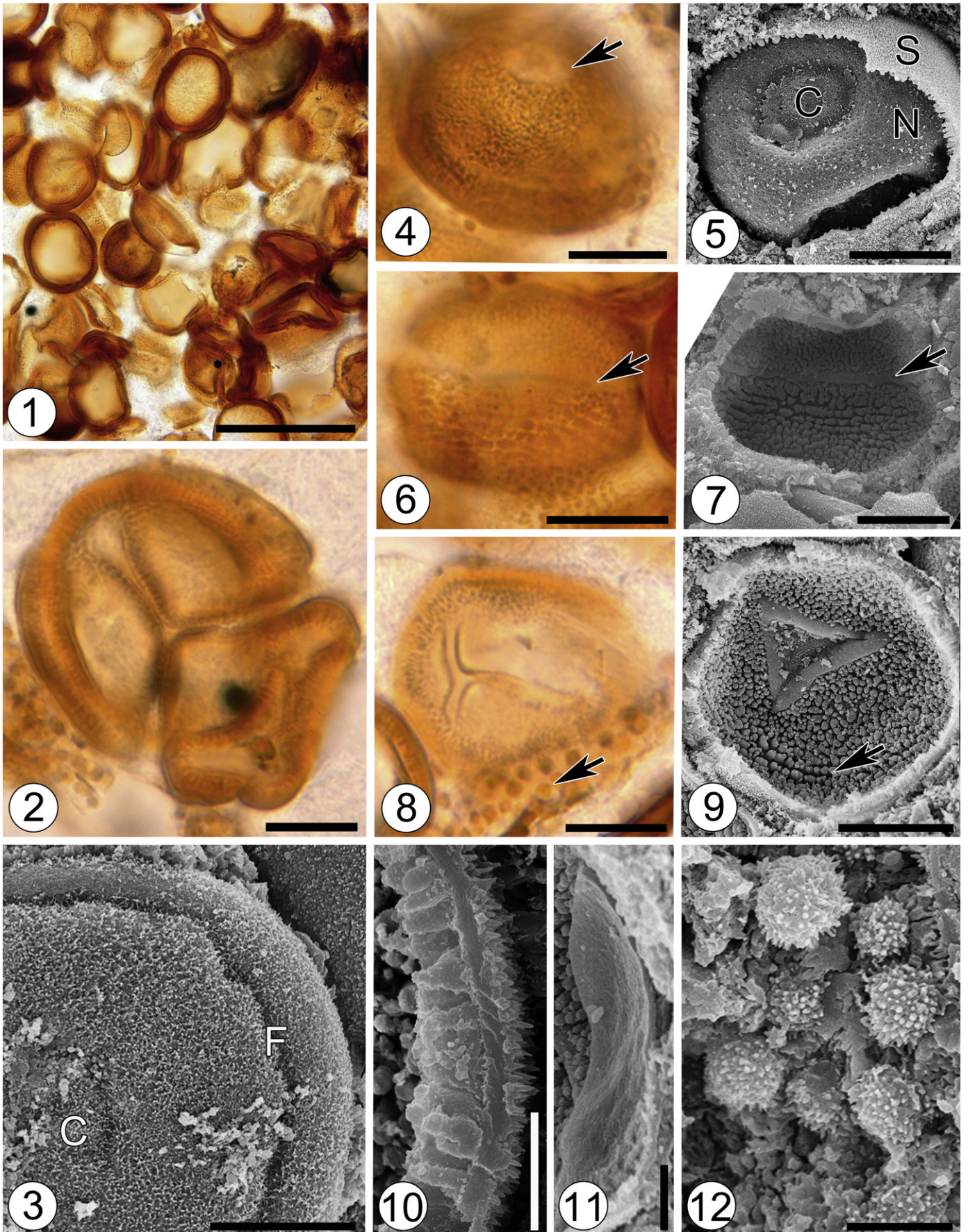


Plate II. (caption on page 81).

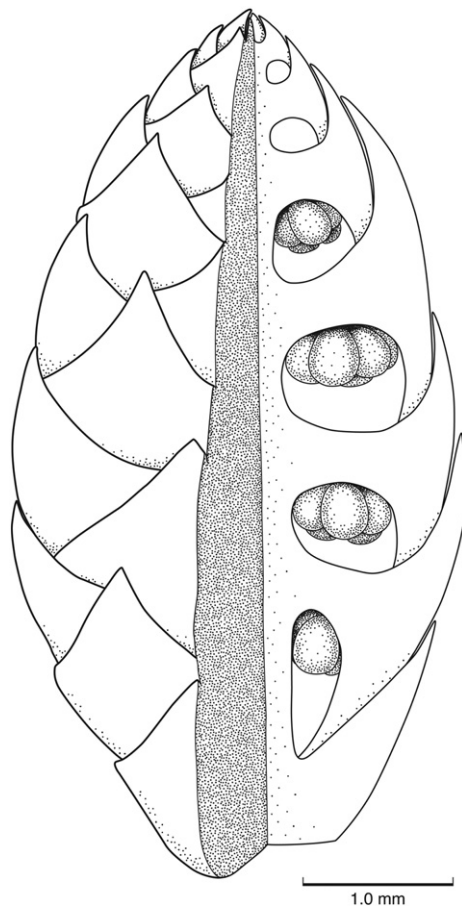


Fig. 2. Suggested reconstruction of *Classostrobus elliotii*. The left side is an external view, and the right side is a cutaway that displays internal details such as the position and arrangement of the microsporangia. Illustration by Sara L. Taliaferro.

thick and 1.3–1.9 mm wide. Ground tissue is of isodiametric cells, 66 μm (30–123 μm) in diameter, which are primarily filled with opaque contents. Each leaf contains a single vascular strand (Plate I, 10), consisting of about nine metaxylem tracheids 5–6 μm in diameter together with a few protoxylem tracheids. There is a space next to the xylem tissue that presumably represented the position of the phloem. Surrounding the vascular tissue of several associated leaves are round cells (Plate I, 10) of unknown affinities that may represent some type of secretory cell or a form of transfusion tissue. Such cells contain contents which may also represent some type of thick-walled fungal hyphae. These cells are 10–25 μm in diameter with walls that are 2–5 μm thick.

4. Discussion

4.1. The Cheirolepidiaceae

The Cheirolepidiaceae is a large family of important extinct Mesozoic conifers (Alvin, 1982; Watson, 1988; Axsmith and Jacobs, 2005; Escapa et al., 2012; Stockey and Rothwell, 2013), which produce a diverse range of growth habits (Watson, 1988; Taylor et al., 2009). Spanning the Late Triassic to the Cretaceous, cheirolepidiaceous plants were components of coastal environments inundated by tides (Upchurch and Doyle, 1981) and one of the dominant components of forests on several continents (Vakhrameev, 1970; Alvin, 1982; Watson, 1988; Taylor et al., 2009; Stockey and Rothwell, 2013). Cheirolepidiaceous plants were widely distributed geographically with most examples at low paleolatitudes (Alvin et al., 1978; Alvin, 1982). To date, the majority of

reports of cheirolepidiaceous macrofossils are from the Northern Hemisphere with fewer examples from the Southern Hemisphere (Alvin, 1982; Francis, 1983; Watson, 1988; Taylor et al., 2009; Escapa et al., 2012). *Classopollis* pollen is distributed worldwide, but is rare at higher paleolatitudes (Vakhrameev, 1970; Brenner, 1976; Alvin, 1983). The pollen type of the Cheirolepidiaceae (*Classopollis*) is present on all Gondwana continents during the Early Jurassic (Grant-Mackie et al., 2000). Therefore, the discovery of the permineralized cheirolepidiaceous pollen cones provides evidence of their presence in Antarctica during the Jurassic.

4.2. General comparisons

Previous to this study, there was a single coniferous pollen cone, *Masculostrobus warrenii* Townrow, described from the Carapace Nunatak locality (Townrow, 1967b). This cone is 8 mm long and 5 mm wide with rhomboidal microsporophyll distal laminae, but it contains saccate pollen. Since one of the unifying characters of the Cheirolepidiaceae is *Classopollis*-type pollen (Alvin et al., 1978), *M. warrenii* clearly cannot be assigned to the Cheirolepidiaceae and was suggested by Townrow (1967b) to share affinities with the Podocarpaceae.

Classostrobus elliotii cones contain many unique characters that provide the basis for a new species, such as helically arranged microsporophylls, and a cluster of four to seven pollen sacs that are attached approximately midway on the abaxial microsporophyll stalk in an annular arrangement. The specimens used in this study are also similar in some characters to other cheirolepidiaceous pollen cones from different localities (see Van Konijnenburg-van Cittert (1987)), i.e., cones are small and simple, have helically arranged peltate microsporophylls with rhomboidal laminar heads situated around a central axis, and contain *Classopollis* pollen (Alvin, 1983; Rothwell et al., 2007). Cheirolepidiaceous cones have been found at other localities attached to or associated with vegetative remains (e.g., Barnard, 1968; Lorch, 1968; Barnard and Miller, 1976; Alvin et al., 1978, 1994; Watson, 1982; 1988; Francis, 1983; Van Konijnenburg-van Cittert, 1987; Thévenard, 1993; Gomez et al., 2002; Axsmith et al., 2004; Barbacka et al., 2007; Yang, 2008; Kim et al., 2012; see supplemental material). Isolated pollen cones that contain *Classopollis* pollen are placed within the genus *Classostrobus* (Alvin et al., 1978). Comparison is difficult with other cheirolepidiaceous cones due to the lack of stomatal information or compressional views of the cones, since most cones have been described from compression/impressions (Rothwell et al., 2007; Archangelsky and Del Fueyo, 2010).

There has been a single report of a permineralized cheirolepidiaceous cone, *Classostrobus crossii*, of southern England (Rothwell et al., 2007), which is from the Middle Jurassic. *C. crossii* is larger than *C. elliotii*, with a length of 20 mm and width of 18 mm; microsporophyll laminae are up to 11 mm long (Rothwell et al., 2007), whereas microsporophyll laminae of *C. elliotii* are up to 2.7 mm long and the cones have a maximum diameter of 5.2 mm and length of 5.5 mm. The number of pollen sacs in *C. crossii* is described as several and the microsporangia are situated abaxially at the juncture of the stalk and basal heel of the distal lamina. The pollen sacs of *C. elliotii* occur approximately midway between the microsporophyll head and cone axis and are attached to and the abaxial surface of the microsporophyll stalk.

Characters available for comparison with previously described cones lacking internal anatomy are cone shape and size, shape of the sporophyll head, pollen sac arrangement and position, and pollen features (Rothwell et al., 2007). The largest pollen cone, *Classostrobus cathayanus* Zhou (Zhou, 1983), is 23 mm in diameter and more than 20 mm long. Cones of *Tomaxiella biforme* Archangelsky (Archangelsky and Gamarro, 1967) are the smallest, 2–3 mm long and 1 mm wide. *C. elliotii* is up to 5.5 mm long and 5.2 mm wide with an average diameter of 2.8 mm. The overall shape of the microsporophylls is peltate, and the microsporophyll heads are rhomboidal in face view like most other cheirolepidiaceous cones. For further comparisons of all cheirolepidiaceous cones, see supplemental material.

4.3. Microsporangia

The pollen sacs of the Cheirolepidiaceae are typically situated on the abaxial surface of the microsporophyll attached near the microsporophyll head. For the type species, *Classostrobus rishra* (Barnard) Alvin, Spicer et Watson (Alvin et al., 1978), six to eight pollen sacs are layered on the abaxial surface of the microsporophyll stalk. The microsporangia of *C. arkansensis* Axsmith, Krings et Waselkov (Axsmith et al., 2004) are located on the abaxial side of the sporophyll stalk near the basal inner region of the microsporophyll head. Abaxial positioning of pollen sacs is also present in cones associated with the foliage taxa *Hirmeriella airelensis* Muir et Van Konijnenburg-van Cittert (Muir and Van Konijnenburg-van Cittert, 1970), and *Frenelopsis* (Schenk) sp. (Barale et al., 1988).

The number of pollen sacs per microsporophyll is variable within *Classostrobus elliotii* cones, i.e., four to seven pollen sacs, which occur in an annular cluster attached to the abaxial sporophyll stalk. When compared to other cheirolepidiaceous cones, the annular arrangement of the pollen sacs is a unique character of *C. elliotii*. Where observed, most other staminate cones of the Cheirolepidiaceae have two to three pollen sacs per microsporophyll or the number is unknown (Van Konijnenburg-van Cittert, 1987). Up to four pollen sacs are observed in *C. dalatzensis* Yang (Yang, 2008), and cones belonging to *Hirmeriella muensteri* (Schenk) Jung (Jung, 1968) have up to twelve microsporangia per microsporophyll. However, Van Konijnenburg-van Cittert (1987) observed six microsporangia per microsporophyll in *H. muensteri*.

In general, Jurassic cheirolepidiaceous pollen cones contain more pollen sacs per microsporophyll relative to Cretaceous pollen cones (see supplemental material and references therein). To date, evolutionary inferences and trends on the number and positioning of microsporangia in the Cheirolepidiaceae are based on limited reports. Increased datasets on pollen cones from permineralized material such as specimens from Carapace Nunatak may shed additional light on this aspect of pollen cone evolution within this conifer family.

4.4. Pollen

Classopollis pollen is known from the Early Triassic through the Late Cretaceous and is numerous in deposits worldwide (Taylor et al., 2009; Zavalova et al., 2010a,b). Previous studies of palynofloras from Carapace Nunatak have been interpreted as late Middle Jurassic (Shang, 1997; Ribecai, 2007), which conflicts with Early Jurassic radiometric age constraints on the timing of lava emplacement (Elliot, 2013). A more recent revision of the palynoflora of Carapace Nunatak indicates that it is dominated by *Classopollis* pollen, which suggests that members of the Cheirolepidiaceae were present (Bomfleur et al., 2014). *Classopollis* is said to be the one reliable characteristic that allows assignment to the Cheirolepidiaceae, including pollen cones (Watson, 1988), and the presence of in situ pollen of this type is a consistent characteristic of *Classostrobus* cones (Alvin et al., 1978). *Classostrobus elliotii* contains numerous in situ pollen grains that would be assigned to *Classopollis*, as they exhibit a distal cryptopore, subequatorial furrow (rimula), equatorial striae, and a proximal trilete (Plate II). Striations are rarely seen in light transmitted light microscopy, but are revealed as patterns in infratectal columellae under SEM.

The average pollen diameter (30 µm) of the Antarctic grains is comparable to that of most other cheirolepidiaceous cones that contain *Classopollis* along with those from dispersed pollen assemblages. Pollen grains associated with *Classostrobus dalatzensis* are reported to be as small as 13 µm (Axsmith et al., 2004). The largest pollen grains associated with cheirolepidiaceous cones reported to date is 65 µm from cones associated with *Frenelopsis alata* (Hlušík and Konzalová, 1976). Equatorial diameters of the solitary, mature pollen within *C. elliotii* are as small as 18 µm and can be as large as 60 µm. Smaller, dispersed pollen grains associated with *C. elliotii* may be interpreted as aborted, but larger grains

may be interpreted as possible forms of polyploid pollen (see Kürschner et al. (2013)).

The infrastructure of *Classostrobus elliotii* in situ pollen grains is reticulate to pseudoreticulate making the striae appear to be absent or vague, which is similar to other cheirolepidiaceous pollen grains from the Early Jurassic. The pollen striae of *C. elliotii* are similar to the *sporae dispersae* species *Classopollis chateauovi* and *C. kieseri* Reyre (Reyre, 1970) that lack or have vague striations. The combination of no striations to vague striations and possession of reticulate infratectal patterns among species with similar supracteal elements is common among Early Jurassic *Classopollis* species (Reyre, 1970). Similar to these Early Jurassic species of *Classopollis*, the striae of *C. elliotii* pollen grains are difficult to discern under light microscopy and are revealed as sinuous linear arrangements of infratectal columellae under SEM. When compared to the Middle Jurassic *Classopollis* pollen of southern England, supracteal elements of *Classostrobus crossii* grains described as spines (Rothwell et al., 2007) are similar in shape to the surface ornaments of *C. elliotii* pollen, but the infratectal columellae of *C. crossii* is differentiated so that anastomosing striae are distinct. In situ mature pollen grains of *C. comptonensis* from the Lower Cretaceous Wealden beds provided the opportunity of ultrastructural studies by Taylor and Alvin (1984), and revealed that the grains exhibit distinct striae with supracteal spinules. Pollen of *Classostrobus arkansensis* Axsmith et al. (2004) of the United States shares these characteristics with *C. comptonensis* in situ grains (Axsmith et al., 2004). The pollen of *C. comptonensis* is similar to the pollen of the Early Cretaceous pollen cones of Spain, *C. turoloensis* and *C. ugnensis* Gomez et al. (2002), in possessing distinct striae and microechinate supracteal ornaments, which were described based on in situ and dispersed pollen from the same locality (Gomez et al., 2002).

Infrastructure, supracteal ornamentation, and striations have recently been used in Argentina to assign taxonomic value to *Classopollis sporae dispersae* discussed by Reyre (1970) and to introduce new species (Villar de Seoane, 2014), and the differentiation of infrastructure among species of *Classopollis* has been discussed by Zavalova et al. (2010a, 2010b). One concern about taxonomic placement into dispersed species based on these pollen characters is that they may represent different stages in pollen development, but the pollen characters of *Classostrobus comptonensis* discussed by Taylor and Alvin (1984) were based on samples from interpreted mature and immature cones, which helped to clarify differences between developmental morphologies of the pollen wall. Therefore, the pollen cones of *C. elliotii* (Early Jurassic), *C. crossii* (Middle Jurassic), *C. comptonensis* (Early Cretaceous) may all be interpreted as mature (i.e., complete tetrad development) with developed pollen walls, thus providing insight into ultrastructural differences of in situ pollen. Through comparisons with ultrastructure of pollen from other cheirolepidiaceous cones, the pollen characters of *C. elliotii* assist in supporting the hypothesis of Reyre (1970) that in the early evolution of the Cheirolepidiaceae (Late Triassic–Early Jurassic), the pollen cones produced pollen having a less differentiated arrangement of infratectal columellae than in more evolved (i.e., later) forms (Middle Jurassic–Cretaceous) yet similar supracteal elements, in this case, echinate features. If factors other than grain maturity, i.e., taphonomy, preservation, and preparation, have little effect on these aspects of *Classopollis* ultrastructure, this adds further support for the numerous different species of identified *Classopollis* pollen by advancement of morphological traits and strengthens the morphological diversity known for this extinct conifer family.

4.5. Paleobiogeography and paleoenvironment

Classostrobus elliotii extends the biogeographical distribution of macrofossils of the Cheirolepidiaceae to the southernmost Lower Jurassic paleolatitude to date. During the Lower Jurassic, Carapace Nunatak was located at ~60°S paleolatitude. Other occurrences have been noted as far south as Patagonia, Argentina (e.g., Archangelsky and Gamarro, 1967; Archangelsky, 1968; Escapa et al., 2012, 2013) and

Australia (e.g., Pole, 2000; Tosolini et al., 2015). This is also the first report of macrofossil evidence of the Cheirolepidiaceae from Antarctica; therefore, the specimens used in this study extend the biogeographical distribution of this family to all present-day continents.

A number of cheirolepidiacean plants are considered to have been halophytes and were clearly thermophilous (Alvin, 1982), although the family was also successful in temperate climates (Watson, 1988). Crustaceans, insects, and plants collected from Carapace Nunatak suggest a non-arid, temperate or possibly warmer climate, based on comparisons to extant representatives (Ball et al., 1979). Deposits represent freshwater, ephemeral pond, and deep-lake environments (Stigall et al., 2008). Plants have been used as proxies for paleoclimate and as paleoenvironmental indicators (Rees et al., 2000; Taylor and Ryberg, 2007). The Cheirolepidiaceae can also be used as a proxy for the Carapace Nunatak locality during the Early Jurassic, which suggests that it may have been a xeric or halophytic habitat based on specific characters of this Mesozoic conifer family. The Cheirolepidiaceae typically show xeromorphic characters, such as thick, succulent shoots, and reduced scale-like leaves, and this may explain how this plant was able to grow in a warm environment close to active volcanism. Although more paleobotanical data, e.g., cuticle and stomatal information, are needed to further understand the paleoenvironment of the locality, this discovery adds to the wide range of habitats occupied by this important Mesozoic conifer family.

5. Conclusions

The presence of a cheirolepidiacean pollen cone in Lower Jurassic rocks from Carapace Nunatak, Antarctica bridges the gap between southern and northern Gondwanan continents and provides evolutionary insight into this biogeographically important extinct conifer group. This discovery extends the biogeographical range of macrofossils of the Cheirolepidiaceae during the Early Jurassic to its southernmost point and is the highest paleolatitude, i.e., ~60°S paleolatitude, occurrence. *Classostrobus elliotii* is the first anatomically preserved cheirolepidiacean cone discovered in the Southern Hemisphere. The cones are small and simple, similar to other cones of the Cheirolepidiaceae. In situ pollen of Early Jurassic cheirolepidiacean pollen cones like that of *C. elliotii* provides additional data for preexisting hypotheses of *Classopollis* ultrastructural evolution. The number and position of pollen sacs are considered taxonomically important for understanding the evolution of pollen cones in conifers, and this study provides new information on key taxonomic characters for a group of conifers, which is phylogenetically poorly resolved, in order to better understand the evolution on the morphology of pollen cones belonging to the Cheirolepidiaceae.

Plumstead (1962) described a small shoot belonging to *Brachyphyllum* cf. *expansum* Sternberg from the Carapace Nunatak locality (Townrow, 1967a). The associated leaves of *Classostrobus elliotii* resemble those of *Brachyphyllum* and appear to be thick, fleshy, and triangulate. Whether *C. elliotii* may have been produced by a shoot that bears this type of leaf merits further investigation. Additionally, isolated ovules have been observed in cherts from the Carapace Nunatak locality, which increases the likelihood of finding ovulate cones or the seed-bearing reproductive organs of these plants. We are hopeful that additional studies in progress will likely provide the opportunity of developing a whole-plant concept for this extinct conifer.

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Appendix A. Supplementary data

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