

A voltzialean pollen cone from the Triassic of Antarctica

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Abstract

Leastrobus fallae gen. et sp. nov. is a morphotaxon representing structurally preserved microsporangiate strobili with *in situ* pollen from the Triassic of Antarctica. The small cone consists of a central axis with a region of helically arranged microsporophylls subtended by elongate, bilaterally symmetrical bracts. Each microsporophyll is differentiated into a pedicel and a laminar head; numerous (ca. 7) elongate microsporangia are attached to the inner surface of the laminar head. Pollen is protosaccate with two large sacchi, a corpus with reticulate ornamentation, and a well-defined distal aperture. *Leastrobus* represents the first documented microsporangiate conifer cone and the first evidence of “Voltziales” from the permineralized floras of the Triassic of Antarctica. The combination of polysporangiate microsporophylls, sporangia free of the sporophyll pedicel, and bisaccate, protosaccate pollen suggests that *Leastrobus* represents a member of the “Voltziales” most similar to the European genus *Ruehleostachys*.

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Keywords: Antarctica; Conifer; Fremouw Formation; Pollen; Triassic; Voltziales

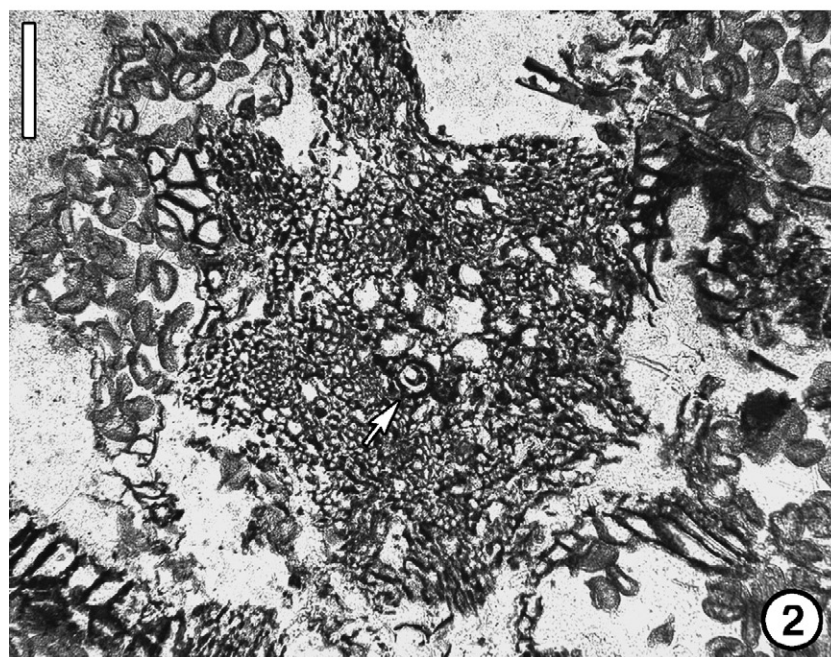
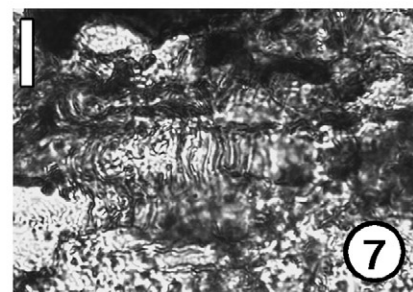
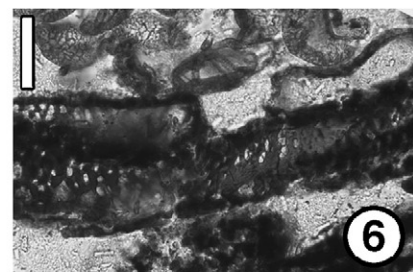
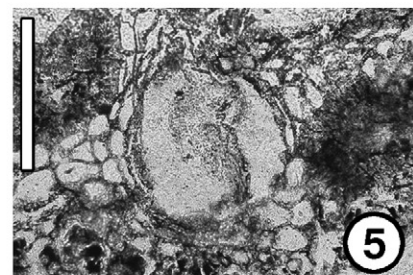
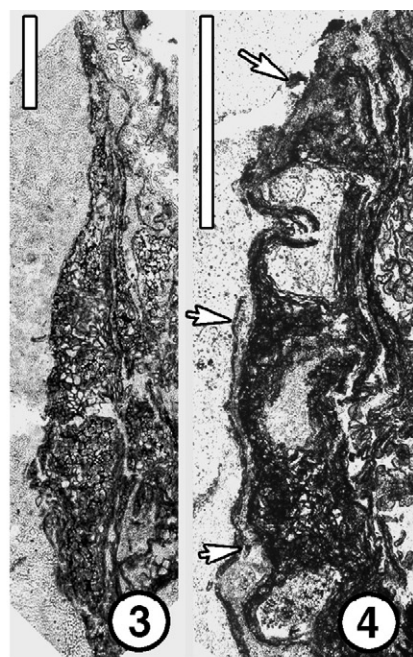
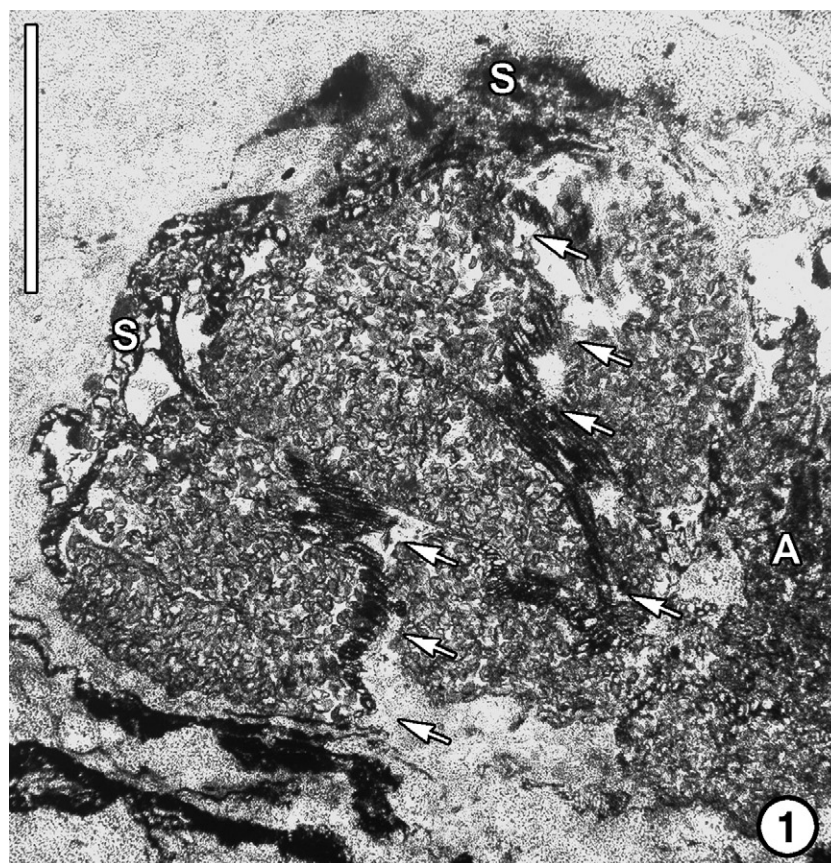
1. Introduction

“Voltziales” is a primitive but nebulous conifer group with a temporal range that extends from the Late Paleozoic into the Mesozoic, and includes plants thought to be transitional between the Cordaitales and modern conifers; it is also thought to be the group from which the modern conifers originated (Taylor, 1988; Taylor and Grauvogel-Stamm, 1995). While the Paleozoic members of the “Voltziales,” and particularly the waltchian conifers, have received much recent attention (e.g., Mapes and Rothwell, 1998; Hernandez-Castillo et al., 2001; Rothwell et al., 2005), the Mesozoic voltzialean

taxa remain poorly understood (e.g., Yao et al., 1993). Voltzialean pollen organs in particular have received relatively little study because pollen-bearing microsporangiate cones are less often identified in the fossil record than ovulate cones or vegetative shoots, perhaps because they are ephemeral and non-woody, and thus less likely to be preserved (e.g., Taylor, 1988; Rothwell and Mapes, 2001). Microsporangiate cones of voltzialean conifers are more diverse than those of extant groups such as Pinaceae, and include cones with bisporangiate to polysporangiate microsporophylls and abaxially or adaxially attached pollen sacs (e.g., Grauvogel-Stamm and Schaarschmidt, 1979; Taylor, 1988). Pollen in the “Voltziales” is variable in both number and type of sacchi and details of fine structure (e.g., Taylor, 1988; Taylor and Grauvogel-Stamm, 1995; Rothwell et al., 2005).

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To date, few conifers and no voltzialean conifers have been described from the permineralized Triassic floras of Antarctica (Meyer-Berthaud and Taylor, 1991; Yao et al., 1997; Axsmith et al., 1998). In this paper, we describe and illustrate the first coniferophyte microsporangiate cone from the Triassic of Antarctica and elucidate its likely relationship to the Mesozoic voltzialean conifers.

2. Materials and methods

2.1. Preparation of fossil specimens

The specimens are preserved in permineralized peat collected from the Triassic of the Victoria Group at the base of Mt. Falla, in the Beardmore Glacier area, central Transantarctic Mountains, Antarctica (Barrett et al., 1986). It is probable that the blocks are from the Fremouw Formation; palynomorphs from peat blocks collected from the Fremouw Formation on Fremouw Peak yielded an age no younger than Anisian, or early Middle Triassic (Farabee et al., 1990). Peat blocks were cut into sections and the flat surfaces polished, then etched in 48–50% hydrofluoric acid (HF) for approximately 1.5–3 min. Acetate peels of the etched surfaces were prepared (Galtier and Phillips, 1999), and some were mounted on standard microscope slides for study using Eukitt™ as a mounting medium. Slides are housed in the Paleobotany Division of the Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, under accession numbers 22471–22482 and 22484–22494. Peels and slides were made from blocks 15454E and 15449C_{TOP}.

Pollen was macerated from the cone preserved in block 15454E (the same cone represented in slides 22471–22479, 22482) and mounted on standard microscope slides. This was accomplished by making a wax well around the pollen cone and subsequently etching the cone with a ca. 15% HF solution. The solution was periodically decanted into a centrifuge tube.

The cone was etched in this way several times. After etching, the excess HF solution was decanted from the centrifuge tube and replaced with water and ultimately EtOH. Finally, the alcohol was decanted and replaced with xylene before the macerate was mounted on a glass slide using Eukitt™ as a mounting medium.

All specimens were photographed using a Leica DC 500 digital camera attachment on a Leica DM 5000B compound microscope, and digital images were processed using Adobe® Photoshop® CS Version 8.0 (©1999–2003, Adobe Systems Incorporated). Some images of pollen (Plate II, 2, 3, 4) were taken at high magnification under oil immersion.

2.2. Nomenclatural notes

Arndt (2002), upon reexamination and reinterpretation of the structure of *Ruehleostachys* Roselt, considered the taxon similar enough to *Willsiostrobus* Grauvogel-Stamm et Grauvogel that he suggested the latter be considered a synonym of the former (since the name *Ruehleostachys* has priority). Because the genera have identical diagnostic characters (Arndt, 2002), the generic name *Ruehleostachys* will hereafter be used for cones previously assigned to *Willsiostrobus*. *Ullmannia frumentaria* (Schlotheim) Göppert will not be included in *Ruehleostachys* following the comments by Grauvogel-Stamm and Schaarschmidt (1979) and contra Meyen (1997).

3. Systematics

Division Coniferophyta

Order “Voltziales”

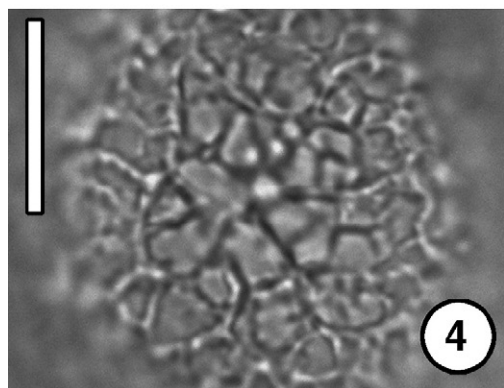
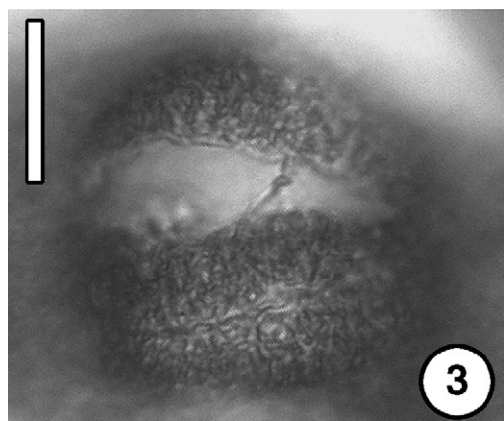
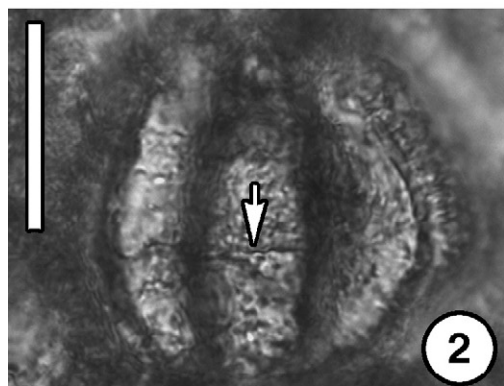
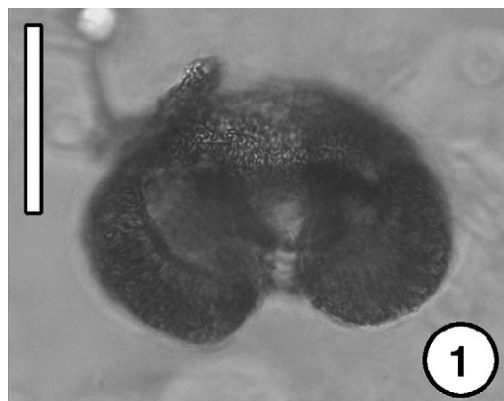
Genus *Leastrobus* Hermsen, T. N. Taylor et E. L. Taylor, gen. nov.

Type species: *Leastrobus fallae* Hermsen, T. N. Taylor et E. L. Taylor

Diagnosis: Simple microsporangiate cones with microsporophylls arranged helically around a central axis

Plate I. Anatomical characteristics of the *Leastrobus fallae* cone.

1. Transverse section of microsporangiate cone showing peltate microsporophylls and pollen sacs; arrows indicate positions of seven microsporangia attached to the inner face of the microsporophyll. Abbreviations: A=central axis of the pollen cone; S=sporophyll. Slide no. 22473 (holotype); scale bar=0.9 mm.
2. Transverse section of central axis of pollen cone showing thick-walled cell possibly representing a pitted tracheid (arrow). Slide no. 22482 (holotype); scale bar=0.1 mm.
3. Surface view of bract subtending the region of the sporophylls. Slide no. 22493 (paratype); scale bar=0.45 mm.
4. Longitudinal section of microsporangiate cone showing peltate microsporophylls (arrows). Slide no. 22485 (paratype); scale bar=0.63 mm.
5. Section of resin canal in possible bract or leaf subtending the region of the sporophylls. Note delicate epithelium. Slide no. 22491 (paratype); scale bar=0.19 mm.
6. Tracheids in sporophyll pedicel showing circular pitting. Slide no. 22473 (holotype); scale bar=35 µm.
7. Tracheids in sporophyll pedicel showing helical thickenings. Slide no. 22475 (holotype); scale bar=10 µm.



above a region of bilaterally symmetrical bracts; each microsporophyll differentiated into a pedicel and laminar head; microsporangia attached to inner surface of laminar portion of microsporophyll, long axes of the sporangia oriented parallel with the sporophyll pedicel. Resin canals present. Tracheids with helical thickenings or circular pitting, pollen bisaccate with distal aperture, protosaccate; corpus reticulate.

Derivatio nominis: The generic name *Leastrobus* is proposed in honor of Léa Grauvogel-Stamm, in recognition of her many significant contributions to our understanding of Mesozoic coniferophytes.

Leastrobus fallae Hermsen, T. N. Taylor et E. L. Taylor, sp. nov.

Diagnosis: As for the genus.

Derivatio nominis: The specific epithet *fallae* is proposed for Mt. Falla, the locality where specimens of this species were found.

Holotype: Ten slides of the specimen from block 15454E and macerated pollen (slide nos. 22471–22482) and peels of the same cone (nos. 1–36, excluding those mounted on slides) from block 15454E, [Plate I](#), 1, 2, 6, 7, and [Plate II](#), 1, 2, 3, 4, here designated.

Paratype: Eleven slides of specimen 15449C_{TOP} (slide nos. 22484–22494) and peels of the same cone (nos. 1–128, excluding those mounted on slides) from block 15449C_{TOP}, [Plate I](#), 3, 4, 5, here designated.

Locality: Base of Mt. Falla in the Beardmore Glacier area, Queen Alexandra Range, central Transantarctic Mountains, Antarctica ([Barrett et al., 1986](#)).

Stratigraphy: Beacon Supergroup, Victoria Group ([Barrett et al., 1986](#)); probably Fremouw Formation.

Age: Triassic, possibly Middle Triassic ([Farabee et al., 1990](#)).

Description: *Leastrobus fallae* is a small simple microsporangiate cone, overall greater than ca. 6 mm in longitudinal section (the apex of the cone is missing) and ca. 3.8 mm in transverse section with microsporophylls arranged helically around a tapering central axis ca.

Plate II. Palynological characteristics of *Leastrobus fallae*.

1. Pollen grain macerated from cone showing two invaginated sacci. Slide no. 22480 (pollen macerated from holotype); scale bar=31 μ m.
2. Detail of *in situ* pollen grain showing the distal aperture between sacci (arrow). Slide no. 22474 (holotype); scale bar=20 μ m.
3. Proximal view of surface of corpus (split laterally) of pollen grain showing reticulate ornamentation. Slide no. 22480 (pollen macerated from holotype); scale bar=20 μ m.
4. Detail of protosaccus of pollen grain. Slide no. 22481 (pollen macerated from holotype); Scale bar=10 μ m.

0.41 mm in diameter at its widest (Plate I, 1, 2). Elongate, bilaterally symmetrical bracts up to ca. 2.9 mm long and 0.45 mm wide subtend the region of the sporophylls (Plate I, 3). Each microsporophyll consists of an elongate axis or pedicel (shank of Rothwell et al., 2005) that bears an expanded laminar portion attached to its distal end (Plate I, 1, 4). The pedicel of each microsporophyll is up to ca. 1.7 mm long with the laminar portion up to ca. 1.2 mm wide in transverse section. Margins of the laminar heads are slightly recurved in longitudinal section and up to 0.81 mm high (Plate I, 4). Multiple elongate microsporangia (ca. 7) are attached to the proximal surface of the microsporophyll head, with the long axes of the microsporangia parallel to the long axis of the microsporophyll pedicel; based on their size and number, they are probably free of the pedicel (Plate I, 1). Microsporangia are up to ca. 1.2 mm long and 0.32 mm wide in transverse section. In the paratype, a resin canal ca. 0.19 mm in diameter lined with epithelial tissue occurs in a structure possibly representing a bract or leaf on the cone axis below the region of attachment of the microsporophylls (Plate I, 5). Tracheids have either circular pitting or helical thickenings (Plate I, 6, 7). At least one thick-walled structure ca. 32 μ m in diameter occurs within a transverse section of the central axis of the holotype (Plate I, 2) with a group of other, more degraded cavities ca. 16–30 μ m in diameter (Plate I, 2); these structures are similar in width to the pitted tracheids observed in longitudinal section in the sporophylls (Plate I, 6), and at least some may represent similar tracheids in the cone axis. Most cells external to these cavities are poorly preserved (Plate I, 2).

Pollen grains are small and protosaccate (Plate II, 1–4), overall ca. 42–73 μ m in length, with two relatively large sacchi each ca. 15–35 μ m in length in distal view. Each saccus is slightly constricted where it attaches to the corpus (Plate II, 1, 2), which may represent an artifact of dehydration during preservation and is likely not a feature of pollen morphology. Each grain has a well-defined distal aperture between the sacchi (Plate II, 2). The corpus is reticulate with relatively thick muri and small and irregular lumina (Plate II, 3).

The holotype and paratype specimens are considered conspecific based on their small size and the similar pollen grains preserved in each specimen.

4. Discussion

4.1. Comparison with other permineralized Triassic conifers of Antarctica

Several groups of coniferophytes are known from the early Mesozoic, with two families, Taxodiaceae

(Cupressaceae *sensu lato*) and Podocarpaceae, having been previously documented from the Middle Triassic floras of the Transantarctic Mountains. Two taxa, *Notophytum krausellii* Meyer-Berthaud et Taylor, and *Parasciadopitys aequata* Yao, T.N. Taylor et E.L. Taylor, have been described from the structurally preserved flora from Fremouw Peak (Meyer-Berthaud and Taylor, 1991; Yao et al., 1997; Axsmith et al., 1998); an additional two taxa possibly linked to *Notophytum* Meyer-Berthaud et Taylor, *Telemachus elongatus* Anderson and *Heidiphyllum elongatum* (Morris) Retallack, represent the only conifers reported from the Upper Triassic compression floras of the Lashly Formation in the Allan Hills and the Falla Formation in the Shackleton Glacier area of Antarctica (Yao et al., 1993; Axsmith et al., 1998). *Notophytum* encompasses stems and leaves; *Parasciadopitys* Yao, T.N. Taylor et E.L. Taylor and *Telemachus* Anderson are megastrobili, and *Heidiphyllum* Retallack, leaves. Axsmith et al. (1998) argued that *Notophytum* and *Heidiphyllum* may represent the same or closely related leaf species in different modes of preservation on the basis of similarities in morphology (apetiolate base, number and spacing of veins), epidermal features, and inferred mode of abscission; they then linked *Telemachus* with *Heidiphyllum* (and thus, by extension, possibly with *Notophytum*) on the basis of cuticular similarities and co-occurrence between the two taxa at 14 localities worldwide. *Leastrobus* and each of the compression genera cannot be meaningfully compared at this time because the compression genera represent different organs from *Leastrobus* and lack histological features (other than cuticular features).

Of the permineralized genera, *Parasciadopitys* is similar to *Leastrobus* in having primary xylem tracheids with annual-helical thickenings (radially aligned tracheids extending from the metaxylem in *Parasciadopitys* have circular-elliptical pitting) but different in lacking resin canals (Yao et al., 1997; Axsmith et al., 1998). *Notophytum* is similar to *Leastrobus* in that it has resin canals and primary xylem tracheids characterized by helical thickenings, among other types (Meyer-Berthaud and Taylor, 1991). Some primary xylem tracheids in *Notophytum* have pitted wall thickenings, and secondary xylem in *Notophytum* is characterized by opposite to alternate bordered pits (Meyer-Berthaud and Taylor, 1991; Axsmith et al., 1998); the pits in tracheids of *Leastrobus* show no clear evidence of borders (Plate I, 6) and the cone axis shows no sign of secondary growth (Plate I, 2). The organization of the axis in *Leastrobus* is simpler than the cone axis of *Parasciadopitys* and the stem of *Notophytum* (Meyer-Berthaud and Taylor, 1991; Yao et al., 1997).

However, this may not be significant in the context of conifer anatomy. Rothwell and Basinger (1979), for instance, found that the fertile portion of the male cone in *Metasequoia milleri* Rothwell et Basinger was poorly preserved with no apparent vascular tissue, whereas the axis in the vegetative region had a pith and primary and secondary growth; similarly, Sterling (1949) noted that the vascularization of male cones of *Metasequoia glyptostroboides* Hu et Chang was poorly developed. Unfortunately, these are the few points of comparison that can be made directly between the other permineralized genera and the microstrobilus *Leastrobus*, and, thus, the possibility that *Leastrobus* and one of the other two taxa were produced by the same plant cannot be completely excluded on anatomical grounds (Axsmith et al., 1998, considered the possibility that *Parasciadopitys* and *Notophytum* were produced by the same plant unlikely on the basis of comparative anatomy and assessment of taxonomically informative characters, which suggest they have affinities to different families), although the lack of resin canals in *Parasciadopitys* casts more doubt on a relationship between *Leastrobus* and *Parasciadopitys* than *Leastrobus* and *Notophytum*. It is also notable that *Leastrobus* and the other two genera do not derive from the same localities, the former being from the base of Mt. Falla, and the latter two from Fremouw Peak.

Considering the characters of the microstrobili of Cupressaceae and Podocarpaceae in general, microsporangiate cones of Podocarpaceae are characterized by bisporangiate microsporophylls, and, while taxodiaceous/cupressaceous cones have bi- to polysporangiate microsporophylls, pollen in this group is not saccate (Taylor, 1988; Taylor and Taylor, 1993; Judd et al., 1999). While the possibility that *Leastrobus* represents an extinct morphology within one of these groups cannot be absolutely eliminated, the differences in the characteristics of their cones and *Leastrobus* indicate that *Leastrobus* may represent a pollen cone attributable to another coniferophyte group. However, it should be noted that Axsmith et al. (1998) have suggested a possible relationship between a group of early Mesozoic conifer taxa united by similar ovulate cones and multiveined leaves—including the *Aethophyllum* Brongniart plant, *Cycadocarpidium* Nathorst seed cones (sometimes with attached leaf-bearing stems), selected other Northern Hemisphere conifers, and the *Telemachus/Heidiphyllum* plant—and Podocarpaceae based on the possible conspecificity of *Notophytum* and *Heidiphyllum*. At least one of the taxa in this group, *Aethophyllum*, has a pollen cone similar in structure to *Leastrobus* and one species of another, *Cycadocarpidium*, has been found associated with pollen cones

similar to *Leastrobus* (Grauvogel-Stamm, 1978; both mentioned below), thus at least very speculatively suggesting the possibility that *Leastrobus* and *Notophytum* could be linked, and/or that *Leastrobus* could be within or near Podocarpaceae.

4.2. Comparison with other Triassic conifer microstrobili

Meyen (1997) characterized Late Palaeozoic to Triassic conifer microstrobili as generally possessing microsporophylls of one of three types: 1) with sporangia attached to the shield; 2) with sporangia adnate to the stalk their entire length; 3) with sporangia attached to the adaxial side of the stalk by thin sporangiophores. Grauvogel-Stamm and Galtier (1998) argued that cones of the third type should be interpreted as compound microstrobili where the lateral appendages represent bract-scale complexes homologous to the bract-scale complexes in conifer seed cones (i.e., *Darneya* Schaarschmidt et Maubeuge). Evidence for the compound nature of *Darneya*-type lateral appendages includes the adaxial attachment of the pollen sacs at regular intervals to the stalk by means of sporangiophores (thus suggesting a fertile shoot), the lines of junction in the lateral appendages delimiting adaxial and abaxial sides (representing the fertile shoot and subtending bract, respectively), and the distribution of stomata. Provided one accepts the interpretation of the lateral appendages on cones of the *Darneya* type as compound, then *Leastrobus* would appear to have simple lateral appendages (microsporophylls) because its sporangia lack sporangiophores that are attached to the stalk at regular intervals and because there are no evident lines of juncture in the sporophylls (Plate I, 1, 4). Thus, *Leastrobus* does not belong within Meyen's third group. The sporangia of *Leastrobus* are clearly attached to the sporophyll shield (Plate I, 1), suggesting that, of Meyen's two remaining groups, *Leastrobus* belongs with the first, among taxa with sporangia attached to the shield.

Meyen subdivided this major group into three additional types: a) with sporangia paired and free; b) with sporangia paired and adnate to the stalk; c) with sporangia numerous and free. Of this division, *Leastrobus* appears to belong with the final group, which also includes *Ruehleostachys* Roselt from the Triassic of England, France, Spain, and Germany (Grauvogel-Stamm, 1978; Grauvogel-Stamm and Álvarez-Ramis, 1996; Arndt, 2002), and "microstrobili associated with *Ullmannia*." (Meyen, 1997, p. 425), particularly *U. frumentaria* (Schweitzer, 1960). *Leastrobus* is interpreted as differing from *U. frumentaria* in the morphology of its pollen; *U. frumentaria* has operculate pollen that can be monosaccate or bisaccate (Potonié and

Schweitzer, 1969; Foster, 1983), whereas the pollen of *Leastrobus* shows no evidence of a proximal operculum and is bisaccate (Plate II, 1, 2, 3). *Leastrobus* instead appears similar to at least some species of *Ruehleostachys*, with which it shares a similar overall cone structure, and, in most cases, pollen type. Species of *Ruehleostachys* are pollen cones with “helically arranged peltate microsporophylls with numerous pollen sacs attached to the keel of the sporophyll with each pollen sac approximately as long as the sporophyll pedicel, but free from it” (Taylor and Grauvogel-Stamm, 1995, p. 282). Tracheids macerated from *R. pseudarticulatus* Roselt (Roselt, 1955/56, pl. 7, Fig. 4) appear to have annular or helical thickenings. Generally, *Ruehleostachys* cones bear bisaccate, protosaccate pollen with a distal aperture that may have been the point of germination of the pollen grain (Taylor and Grauvogel-Stamm, 1995). However, at least one species, *R. acuminatus* (Grauvogel-Stamm et al. Grauvogel) Arndt, the pollen cone of the *Aethophyllum stipulare* Brongniart plant, is different in having eusaccate pollen and a proximal tetrad mark in addition to a distal aperture (Grauvogel-

Stamm and Grauvogel, 1973; Grauvogel-Stamm, 1978); this pollen has been compared to the dispersed pollen genus *Illinites* Kosanke (Grauvogel-Stamm and Grauvogel, 1973; Grauvogel-Stamm, 1978). Grauvogel-Stamm (1978) suggested that the pollen of *R. acuminatus* might be more similar to the pollen of *U. frumentaria* (at least some of which is of the *Jugasporites* Leschik-type) than other species of *Ruehleostachys* (Table 1). In light of the difference in the pollen of *R. acuminatus* from the remainder of *Ruehleostachys* and its incorporation into the *Aethophyllum* plant, consideration should be given to removing *R. acuminatus* to a new organ genus. Another species, *R. hexasacciphorus* Grauvogel-Stamm et al. Álvarez-Ramis, differs from the remainder of *Ruehleostachys* in having hexasaccate pollen and a distinctive cone structure (Grauvogel-Stamm and Álvarez-Ramis, 1996). Reference to *Ruehleostachys* below will exclude these two species.

The remaining seven species of *Ruehleostachys* are differentiated from one another on the basis of overall size, shape of the microsporophylls, and characteristics of the pollen (Grauvogel-Stamm, 1969, 1972, 1978; Taylor and

Table 1

Comparison of basic features of *Leastrobus* to selected Late Paleozoic to Triassic pollen cones with polysporangiate microsporophylls, bisaccate pollen, and similar overall structure

	<i>Leastrobus</i>	<i>Ruehleostachys</i> (except <i>R. acuminatus</i> and <i>R. hexasacciphorus</i>)	<i>Aethophyllum stipulare</i> plant (male cone <i>R. acuminatus</i>)	<i>Ullmannia frumentaria</i> ¹ (cones and leafy shoots)
Preservation type	Permineralization in silica	Compression, some pyritization	Compression and permineralization	Compression and permineralization
Length	ca. 0.6 cm	ca. 0.7–13 cm	ca. 3.5–5 cm	ca. 2–2.5 cm
Pollen sac position	Unknown	Abaxial	Abaxial	Abaxial
No. of pollen sacs per sporophyll	ca. 7	Polysporangiate (4–12 where enumerated by Grauvogel-Stamm, 1969)	4–6	8
No. of sacchi	Bisaccate	Bisaccate	Bisaccate	Monosaccate and bisaccate
Sacchi type	Protosaccate	Protosaccate (not confirmed in all species)	Eusaccate	Protosaccate
Aperture/point of germination	Distal aperture (no proximal tetrad mark?)	Distal aperture	Distal aperture with perpendicular equatorial to subequatorial tenuitates, proximal laesura	Distal tenuitates, proximal operculum and laesura of intexinal layer
Temporal occurrence	Triassic	Triassic	Triassic	Permian
Geographic occurrence	Antarctica	England, France, Germany, Spain	France	Germany (pollen cones)
References	This paper	Roselt (1955/56), Grauvogel-Stamm (1969, 1972, 1978), Grauvogel-Stamm and Schaarschmidt (1978, 1979), Taylor and Grauvogel-Stamm (1995), Grauvogel-Stamm and Álvarez-Ramis (1996) Grauvogel-Stamm and Galtier (1998), Arndt (2002)	Grauvogel-Stamm and Grauvogel (1973), Grauvogel-Stamm (1978), Grauvogel-Stamm and Schaarschmidt (1978, 1979), Rothwell et al. (2000)	Schweitzer (1960), Potonié and Schweitzer (1969), Grauvogel-Stamm and Schaarschmidt (1979), Foster (1983), Meyen (1987), Grauvogel-Stamm and Galtier (1998)

¹Clement-Westerhof (1974) reported cones similar in structure to *U. frumentaria* from the Permian of Italy; these cones have 6–8 pollen sacs, average 3 cm in length, and have similar pollen.

Grauvogel-Stamm, 1995). *Leastrobus* is most similar in size to *R. denticulatus* (Grauvogel-Stamm) Arndt (the pollen cone associated with *Cycadocarpidium pilosum* Grauvogel-Stamm), which is ca. 0.7–2 cm in length and 0.5–1.1 cm in width; cones of other species range from ca. 3.5–13 cm long and ca. 1.0–3.0 cm in width (Grauvogel-Stamm, 1978). The shape of the microsporophylls in *Leastrobus* is unknown. Like *R. denticulatus*, *Leastrobus* is also interpreted as having a region of bracts that subtends the region of the microsporophylls on the cone axis (Grauvogel-Stamm, 1969).

In overall pollen form, *Leastrobus* agrees well with multiple species of *Ruehleostachys*. In addition to being bisaccate with protosacci and a distal aperture, the overall size of the pollen in *Leastrobus* and many species of *Ruehleostachys* is comparable; length or diameter of pollen grains, for instance, of selected taxa is as follows: 60–99 µm in *Ruehleostachys ligulatus* (Grauvogel-Stamm) Arndt, 46–101 µm in *R. rhomboidalis* (Grauvogel-Stamm) Arndt, 46–85 µm in *R. denticulatus*, 55–100 µm in *R. willsii* (Townrow) Arndt, 50–182 µm in *R. cordiformis* (Grauvogel-Stamm) Arndt, 70–80 µm in *R. pseudarticulatus*, and 42–73 µm in *Leastrobus* (Taylor and Grauvogel-Stamm, 1995; Arndt, 2002). According to Taylor and Grauvogel-Stamm (1995), a feature that may unite many voltzialean pollen grains is the size of the sacchi, which are about one quarter the grain diameter in transmitted light micrographs. The sacchi of *Leastrobus* grains may seem relatively large by comparison (Plate II, 1, 2). However, Taylor and Grauvogel-Stamm (1995) may have been referring to the offset of the saccus from the corpus in proximal view and not the full length of saccus in distal view (e.g., Grauvogel-Stamm, 1972, fig. 2), in which case the sacchi of *Leastrobus* do not appear to be unusually large (Plate II, 1). In lateral view, the pollen of *Leastrobus* resembles pollen of *R. pseudarticulatus* figured by Roselt (Roselt, 1955/56, pl. 11, figs. 1–3, 11).

While *Leastrobus* is similar to *Ruehleostachys* in cone structure and pollen type (at least in features that can be compared between the taxa), there are several characters that can be used to differentiate between the Antarctic and European taxa. *Leastrobus* can be differentiated from selected species of *Ruehleostachys* by the small overall size of the pollen cone (Table 1) and the presence of a region of bracts subtending the sporophylls. If *Leastrobus* cones were preserved as compressions, these differences might be recognized as specific rather than generic-level distinctions. Significantly, however, specimens of *Leastrobus* are permineralized, whereas *Ruehleostachys* is based primarily on compression fossils (Table 1). Unfortunately, cuticular characters, known from *Ruehleostachys*, are unknown in

Leastrobus, and most anatomical characters are unknown for *Ruehleostachys*. Some details of the structure of the *Leastrobus* cone (e.g., adaxial or abaxial position of the pollen sacs) also cannot be confirmed. Thus, *Leastrobus* is here recognized as a separate genus based primarily on its preservation type, which is different from the preservation types of *Ruehleostachys* cones (Table 1). Perhaps, when more anatomical details of *Ruehleostachys* or structural details of *Leastrobus* are known, the taxonomy of these two genera will be revisited.

4.3. Systematic position

Ruehleostachys and *Leastrobus* might be considered among the Mesozoic conifer taxa that have a “voltzialean” morphology. The voltzialean conifers are likely an artificial group with a diversity of pollen cone structures, including cones with abaxially or adaxially attached pollen sacs, sporangia that are sessile or attached to the cone by a sporangiophore, and cones that may have simple sporophylls or possibly compound lateral appendages (e.g., Grauvogel-Stamm and Schaarschmidt, 1979; Grauvogel-Stamm and Galtier, 1998). Traditionally considered to be intermediate between the Cordaitales and the modern conifers, the precise relationship of the voltzialean conifers to these groups remains unclear (Taylor and Grauvogel-Stamm, 1995). However, a recent cladistic analysis by Rothwell et al. (2005) based primarily on reconstructed Paleozoic voltzialean taxa suggests that the “Voltziales” includes a basal grade encompassing an early-diverging Gondwanan clade (*Ferugliocladus* Archangelsky et Cuneo and *Genoites* Feruglio), the “Angaran Voltziales” (*Concholepis* Meyen, *Timanostrobus* Meyen, and *Kungurodendron* Meyen), and some of the walachian conifers, as well as two derived sister clades, the “lebachoid walachians” and the “voltzian Voltziales.” While the Rothwell et al. (2005) analysis did include members of the Cordaitales, no non-voltzialean conifer groups were included, so the hypothesis that the “Voltziales” are intermediate between the conifers and cordaitaleans was not tested in that study. However, recent seed plant analyses including a broader sampling of conifers and cordaitaleans with one or two terminals representing voltzialeans, suggest that Cordaitales and conifers may form separate clades sister to one another (Hilton and Bateman, 2006, fig. 4) or may comprise separate lineages that are not particularly closely related (Doyle, 2006, fig. 6), with “Voltziales” possibly representing a paraphyletic basal grade of conifers (Hilton and Bateman, 2006, fig. 4).

While the position of *Leastrobus* cannot yet be evaluated in a phylogenetic context, *Leastrobus* differs

from *Ferugliocladus* in having bisaccate and proto-saccate rather than monosaccate and eusaccate pollen, microsporangia free of the pedicel, and microsporphylls differentiated into a stalk and distal lamina (Archangelsky and Cuneo, 1987; Rothwell et al., 2005), suggesting the new genus may not belong within the “Gondwanan voltziales” (the male cone of *Genoites* is unknown). As additional voltzialean reproductive organs are described and placed within a phylogenetic context with both extinct and extant conifer taxa, the evolutionary relationships of these unique plants may be better understood.

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