Antarctic Science 23(4), 379–385 (2011) © Antarctic Science Ltd 2011 doi:10.1017/S0954102011000241

The possible pollen cone of the Late Triassic conifer *Heidiphyllum*/*Telemachus* (Voltziales) from Antarctica

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Abstract: Fossil leaves of the Voltziales, an ancestral group of conifers, rank among the most common plant fossils in the Triassic of Gondwana. Even though the foliage taxon *Heidiphyllum* has been known for more than 150 years, our knowledge of the reproductive organs of these conifers still remains very incomplete. Seed cones assigned to *Telemachus* have become increasingly well understood in recent decades, but the pollen cones belonging to these Mesozoic conifers are rare. In this contribution we describe the first compression material of a voltzialean pollen cone from Upper Triassic strata of the Transantarctic Mountains. The cone can be assigned to *Switzianthus* Anderson & Anderson, a genus that was previously assumed to belong to an enigmatic group of pteridosperms from the Triassic Molteno Formation of South Africa. The similarities of cuticle and pollen morphology, together with co-occurrence at all known localities, indicate that *Switzianthus* most probably represents the pollen organ of the ubiquitous *Heidiphyllum/Telemachus* plant.

Received 9 December 2010, accepted 23 February 2011, first published online 5 April 2011

Key words: coniferophytes, Gondwana, *in situ* pollen, *Switzianthus*, systematic palaeobotany, Transantarctic Mountains

Introduction

The Voltziales encompasses a diverse array of extinct conifers that are believed to be transitional between the Palaeozoic conifers and the modern Coniferales (e.g. Florin 1938–45, Rothwell *et al*. 2005, Taylor *et al*. 2009). The majority of voltzialean taxa have been described from the upper Palaeozoic (e.g. Rothwell *et al*. 2005). There are, however, fossils of this ancient conifer group that occur in deposits as young as the Early Jurassic (Taylor *et al*. 2009), or possibly even Early Cretaceous (Miller 1977).

Several Northern Hemisphere representatives of Mesozoic voltzialean conifers have been intensely studied and are known in remarkable detail (e.g. Grauvogel-Stamm 1978). By contrast, knowledge about the Gondwanan Voltziales has remained very incomplete. This is remarkable, because voltzialean conifer leaves have been described from the Gondwanan Triassic since the first half of the 19th century (e.g. Morris 1845, Feistmantel 1889). These leaves have initially been assigned to a variety of morphogenera, including *Zeugophyllites* Brongniart, *Podozamites* Braun, *Phoenicopsis* Heer, *Desmiophyllum* Lesquereux, and *Noeggerathiopsis* Feistmantel, but the vast majority were later merged into a single species *Heidiphyllum elongatum* (Morris) Retallack (Retallack 1981). *Heidiphyllum* is currently recognized as the most widespread conifer leaf in the Triassic of the Southern Hemisphere. It is frequently found together with the supposedly affiliated seed cone *Telemachus* Escapa, Decombeix, Taylor & Taylor (Anderson 1978, Retallack 1981, Yao *et al*. 1993, Axsmith *et al*. 1998, Nielsen 2005, Escapa *et al*. 2010). Further evidence for Triassic transitional conifers from the Southern Hemisphere has come from permineralized deposits of the central Transantarctic Mountains, which have yielded various anatomically preserved conifer organs, including stems and leaves of *Notophytum krauselii* Meyer-Berthaud & Taylor (Meyer-Berthaud & Taylor 1991, Axsmith *et al*. 1998), seed cones of *Parasciadopitys aequata* Yao, Taylor & Taylor (Yao *et al*. 1997), and the pollen cone *Leastrobus fallae* Hermsen, Taylor & Taylor (Hermsen *et al*. 2007). The affinities and interrelationships of these fossils continue to remain largely obscure. At least some of these morphotaxa, however, are regarded as being the permineralized equivalents of the compression taxa *Heidiphyllum* and *Telemachus* (e.g. Axsmith *et al*. 1998, Escapa *et al*. 2010, Schwendemann *et al*. 2010).

Even though voltzialean foliage and seed cones are common elements in Gondwanan Triassic floras and have (in part) been known for more than 150 years, information on the corresponding pollen cones has remained very limited. This may be due to the small size and ephemeral nature of these pollen cones (Rothwell & Mapes 2001, Hermsen *et al*. 2007). In this contribution we present the first record of voltzialean pollen cone compressions from the Triassic of Antarctica. The specimens are assigned to *Switzianthus* Anderson & Anderson, a morphogenus that was previously thought to belong to an enigmatic group of pteridosperms from the Molteno Formation of South Africa

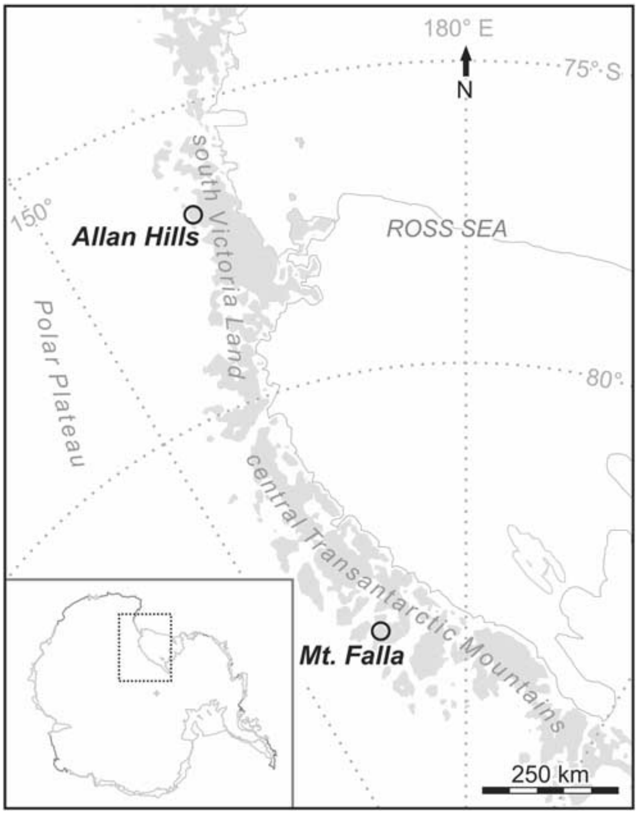

Fig. 1. Locality map showing the fossil sites in south Victoria Land and the central Transantarctic Mountains, East Antarctica. Light grey tones indicate areas of rock outcrop.

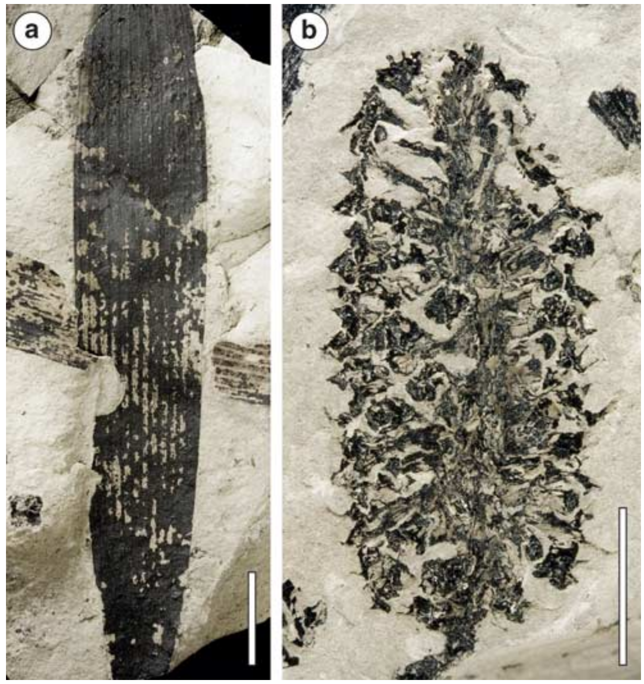

Fig. 2. Voltzialean foliage and seed cone from the Upper Triassic of the Allan Hills, south Victoria Land, East Antarctica. Scale bars = 1 cm. **a.** *Heidiphyllum elongatum* (Morris) Retallack. T11-582a. **b.** *Telemachus antarcticus* Escapa, Decombeix, Taylor & Taylor. T11-411.

(Anderson & Anderson 2003). By contrast, the similarities in cuticle and pollen morphology, together with the co-occurrence at all known localities, lead us to the conclusion that *Switzianthus* probably represents the pollen cone of the ubiquitous *Heidiphyllum*/*Telemachus* plant.

Material and methods

Most specimens were collected from the type section of the Falla Formation on the northern flank of the western ridge of Mount Falla (Queen Alexandra Range, central Transantarctic Mountains; 84°22'S, 164°55'E) (Fig. 1). Plant fossils occur within a 16 m thick mudstone interval (Level 14, Profile 2 in Barrett 1969) with intercalated coaly layers and thin sheets of light-grey, very fine-grained sandstone. The Falla Formation is interpreted as deposits of a low-sinuosity braided-stream system with a high proportion of lacustrine and paludal overbank fines (e.g. Barrett *et al*. 1986). A single additional specimen comes from Member C of the Lashly Formation in the Allan Hills, south Victoria Land (Fig. 1). At both sites, the specimens co-occur with abundant *Heidiphyllum* leaves (Fig. 2a) and *Telemachus* seed cones (Fig. 2b). The age of the plant-bearing horizons is considered to be Carnian or Norian (early or middle Late Triassic) based on microfloras (Kyle & Schopf 1982, Farabee *et al*. 1989).

Hand specimens were photographed with a Nikon D100 digital camera. Macroimages were taken with a Leica DC500

Fig. 3. Gross morphology, cuticle features, and *in situ* pollen of the voltzialean pollen cone *Switzianthus* sp. from the Upper Triassic of the Transantarctic Mountains. **a.** Intact pollen cone. Note that the spiny aspect of some sporophyll apices along the cone margin is due to individual superpositioned sporophylls being cross-sectioned. Mount Falla, T7-185a. Scale bar = 5 mm. **b.** Counterpart of the same specimen. T7-185b. Scale bar = 5 mm. **c.** Partially disintegrated pollen cone. Mount Falla, T7-172b. Scale bar = 5 mm. **d.** Comparatively intact pollen cone. Allan Hills, T8-229b. Scale bar = 5 mm. **e & f.** Details of individual ovate distal microsporophyll laminae with a slightly displaced central pedicel scar, a surrounding rugose area, and a distal portion with fine radiating striations. Scale bar = 1 mm. **g.** Cuticle of the presumably outer (i.e. abaxial) surface of the distal microsporophyll lamina from a partially disintegrated pollen cone from Mount Falla (T5-111), showing the outlines of more or less longitudinally aligned, elongated rectangular to polygonal cells. Slide #24033. Scale bar = 50 μm. **h.** Large cluster of *Alisporites* Daugherty type pollen grains isolated from a partially disintegrated cone from Mount Falla (T5-111). Slide #24034. Scale bar = 100 μm. **i–k.** Individual pollen grains in polar (i & j) and lateral (k) view. Slides #24033 (j & k) and #24037 (i). Scale bars = 25 μm.

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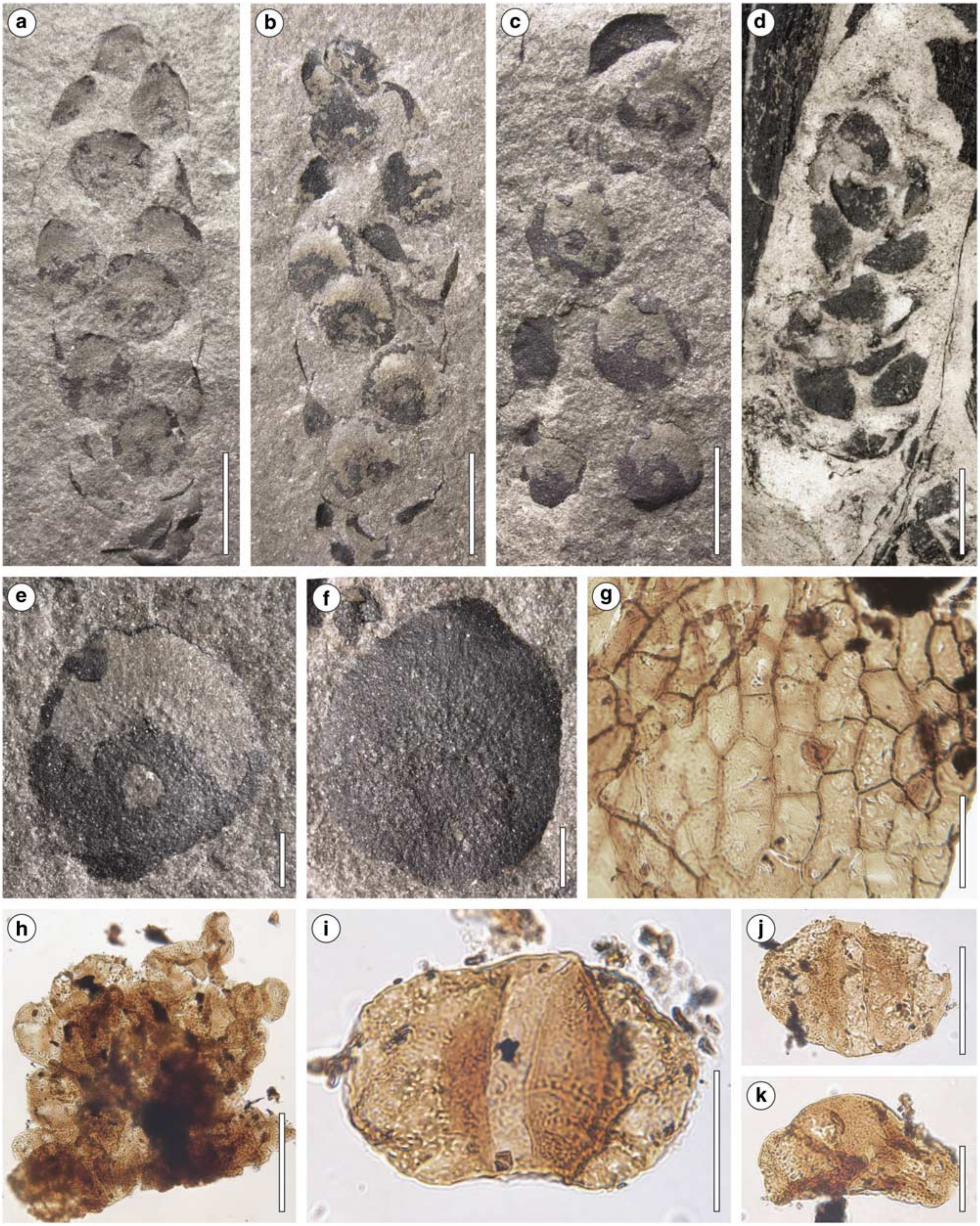

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digital camera mounted on a Leica MZ16 stereo dissecting microscope. Cuticle and *in situ* pollen samples were freed from the matrix using 48% hydrofluoric acid (HF) for several days, and then carefully neutralized by repeated washing with distilled water. Organic residues were further macerated using Schulze's reagent (40% nitric acid (HNO_3) with a few crystals of potassium chlorate ($KClO_3$)) for several hours, and subsequently cleaned and bleached using a 4% potassium hydroxide solution (KOH_{aq}) for a few seconds. Cuticle and pollen were finally dehydrated in glycerol and mounted on permanent slides using glycerol jelly.

Hand specimens and slides are stored in the Paleobotanical Collections of the Department of Ecology and Evolutionary Biology, and Natural History Museum and Biodiversity Institute, University of Kansas, Lawrence (KS), USA.

Systematics

Phylum CONIFEROPHYTA
Class CONIFEROPSIDA
Order VOLTZIALES
Family *incertae sedis*
Genus *Switzianthus* Anderson & Anderson

Type species. Switzianthus moriformis Anderson & Anderson, 2003

Switzianthus sp.
(Fig. 3a–k)

Material: Eight specimens from Mount Falla on the following seven slabs: T5-69, 79, 86, 111, T7-161, 172, 185 (Upper Triassic, Falla Formation, Mount Falla, Queen Alexandra Range; 84°22'S, 164°55'E); one additional specimen T8-229 from the Allan Hills (Upper Triassic, Member C, Lashly Formation, Allan Hills, south Victoria Land). Cuticle and pollen preparations of specimen T5-111 on slides #24026–24038.

Description: Cylindrical pollen cones, 2.7–*c.* 4 cm long and 0.8–1.5 cm in diameter, more or less compact, composed of helically arranged microsporophylls with each helix comprising *c.* 6–10 scales (Fig. 3a–d). Scales robust, peltate, each with a delicate pedicel and an ovate distal portion with an obtuse to acuminate apex (Fig. 3a–c, e & f); distal microsporophyll portions *c.* 4–6 mm long and 3–5 mm wide; adaxial surface with a circular pedicel scar of *c.* 1 mm diameter positioned slightly below the centre, a surrounding thickened area with a granulose surface, and a thin, woody distal portion with radiating striations (Fig. 3e & f). Cuticle fragments thin, showing a pattern of more or less longitudinally aligned, elongated rectangular to polygonal cells 30–40 μm long and 20–30 μm wide (Fig. 3g).

Pollen grains bisaccate, measuring between 60 x 38 μm and 100 x 60 μm (Fig. 3h–k). Sacci narrow-elliptical in polar view (Fig. 3h–j), proximally attached in equatorial region, distally inclined (Fig. 3k). Corpus outline circular to narrow-elliptic in polar view, approximately half as wide as the entire grain; cappa generally thickened, with smooth or finely reticulated to rugose surface; distal surface with a sharply defined, narrow-rectangular longitudinal sulcus of *c.* 10–12 μm width (Fig. 3i & j).

Remarks: The material agrees in all comparable features with the pollen cone genus *Switzianthus* from the Upper Triassic Molteno Formation of South Africa, including: 1) organization of a more or less compact cone, 2) the size range (2.8–4.5 cm long), 3) number of scales per helix, 4) dimension, morphology and texture of the sporophylls, and 5) the *in situ* pollen grains. Compared to the South African specimens, the cuticle fragments probably derive from the distal microsporophyll portion (see Anderson & Anderson 2003 pl. 56, fig. 1).

Two species have been described in the South African material, i.e. *S. moriformis* Anderson & Anderson and *S. crispiformis* Anderson & Anderson. The present material more closely resembles *S. crispiformis* due to its relatively small size and well-defined pedicel scar. However, as both species lack well-defined diagnostic criteria and remain poorly understood, we refrain from attempting a species determination until additional and better preserved material becomes available.

Essential details on pollen-sac morphology and attachment in *Switzianthus* remain uncertain. Following Anderson & Anderson (2003), we suggest that the pitted area around the pedicel scar on the adaxial microsporophyll surface may be the area of former pollen-sac attachment. In none of the specimens so far described, however, are the actual pollen sacs preserved. This may indicate that the pollen-sac material was very delicate and already withered away when the cones became buried.

In situ palynological samples were taken by carefully removing organic material from the microsporophylls of a disintegrated cone. The recovered palynomorphs consist exclusively of microsporophyll cuticle fragments and the above described bisaccate pollen grains, many of the latter occurring in distinct clusters (Fig. 3h).

Discussion

Switzianthus has previously been affiliated with the enigmatic and poorly defined pteridosperm leaf *Dejerseya* Herbst, based on what have been described as similar cuticle features and co-occurrence at some localities. By contrast, we interpret *Switzianthus* as a voltzialean pollen cone that probably belongs to the Antarctic *Heidiphyllum*/*Telemachus* conifer. This determination is based on: 1) structural correspondence to other voltzialean pollen cones, 2) similarities in cuticle and pollen morphology, and 3) co-occurrence at all known localities.

Structural correspondence

The morphology of *Switzianthus* is unlike that of any known pteridosperm pollen organ. By contrast, the helical

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arrangement of peltate microsporophylls with ovate, bilaterally symmetrical distal portions indicates affinities with either conifers or cycads (e.g. Taylor *et al*. 2009). A cycadalean affinity of *Switzianthus* can be excluded because fossil cycads are known to have produced simple, monocolpate *Cycadopites* Wodehouse pollen, whereas *in situ* pollen of *Switzianthus* is bisaccate non-taeniate, and of the *Alisporites* Daugherty type (= *Alisporites sensu lato*; see Balme 1995, Anderson & Anderson 2003).

Structurally, *Switzianthus* agrees with many of the well-known Triassic pollen-cone compressions from the Northern Hemisphere, including *Ruehleostachys* Roselt emend. Arndt (= *Willsiostrobus* Grauvogel-Stamm & Grauvogel), *Darneya* Schaarschmidt & Maubeuge emend. Grauvogel-Stamm, and *Sertostrobus* Grauvogel-Stamm (see Grauvogel-Stamm 1978, Arndt 2002). These taxa are distinguished primarily by the morphology and mode of attachment of the pollen sacs (e.g. Grauvogel-Stamm & Schaarschmidt 1979). Because evidence for pollen-sac morphology and attachment in *Switzianthus* is still lacking, more detailed comparisons cannot be made. Several types of voltzialean pollen cones have recently also been described from the Molteno Formation of South Africa (Anderson & Anderson 2003). These differ from *Switzianthus* primarily in the larger size and the more complex cone structure, some with up to 30 variably ornamented microsporophyll scales per helix (Anderson & Anderson 2003).

Until now only two conifer pollen cones are known from the Triassic of Antarctica. The voltzialean pollen cone *Leastrobus fallae* is based on anatomically preserved material from an outcrop at the base of Mount Falla (Hermsen *et al*. 2007). The cone structure of *Switzianthus* corresponds well with that of *Leastrobus*, although the latter appears to be much smaller, with microsporophyll laminae measuring only up to 1.2 mm wide (Hermsen *et al*. 2007). Cantrill *et al*. (1995) described charcoalified remains of an undetermined conifer cone from the Upper Triassic of the Amery Group, Prince Charles Mountains. This cone is characterized by helically arranged, peltate scales with obovate distal portions that are superficially similar to those of *Switzianthus*. The size range of the microsporophylls, with distal portions being 0.6–3.2 mm long by 0.5–2.3 mm wide, appears to be somewhat intermediate between those of *Leastrobus* and the specimens described here. Hence, these three Antarctic taxa may be interpreted as forming an intergrading series within a group of structurally similar conifer pollen cones.

Similarities in cuticle and pollen morphology

The cuticles recovered from the Antarctic cones are poorly preserved and demonstrate only few diagnostically relevant details. Well-preserved cuticles of microsporophylls of *Switzianthus* have been described from South Africa (Anderson & Anderson 2003). The sporophyll laminae are hypostomatic, and the stomata are surrounded by a ring of five to six strongly cutinized subsidiary cells. Guard cell cutinizations are not preserved. The cuticle of regular epidermal cells and subsidiary cells has been described to be nonpapillate. Judging from the illustrations, however, papillae occur on the lower sporophyll surface of at least some of the specimens (Anderson & Anderson 2003 pl. 56, fig. 1).

Although these features agree to some extent with the cuticle morphology of *Dejerseya* (Anderson & Anderson 1989), as suggested by Anderson & Anderson (2003), they are also well in accordance with those of *Heidiphyllum* and *Telemachus*. *Heidiphyllum* leaves are hypostomatic to weakly amphistomatic (Anderson 1978, Anderson & Anderson 1989, Axsmith *et al*. 1998). In *Heidiphyllum* and *Telemachus*, the stomata are surrounded by a ring of five to six variably thickened subsidiary cells (Anderson 1978, Anderson & Anderson 1989, Yao *et al*. 1993, Axsmith *et al*. 1998). The development of papillae on regular epidermal cells and subsidiary cells is variable in *Heidiphyllum*, with papillae on the lower leaf surface being strongly developed (e.g. Axsmith *et al*. 1998), weakly developed (e.g. Anderson 1978 pl. 9, fig. 5), or absent (Anderson & Anderson 1989 pl. 251, figs 6 & 7). Papillae are also absent in *Telemachus* (Yao *et al*. 1993). Hence, the cuticle features of *Switzianthus*, which were suggested as indicating affinities with the pteridosperm *Dejerseya*, are at least as close to those of the Voltziales.

The bisaccate, non-taeniate, sulcate pollen of *Switzianthus* corresponds to the dispersed pollen genus *Alisporites* (e.g. Balme 1995). Yao *et al*. (1993) reported large numbers of similar grains attached to the cuticles of *Telemachus* cones, which led these authors to suggest that the parent plant of *Telemachus* may have produced *Alisporites*-type pollen (Yao *et al*. 1993). This interpretation is further supported by the fact that several voltzialean pollen cones from the Triassic of the Northern Hemisphere, e.g. *Ruehleostachys bromsgrovensis* (Grauvogel-Stamm) Roselt emend. Arndt, *R. rhomboidalis* (Grauvogel-Stamm) Roselt emend. Arndt, and *R. willsii* (Townrow) Roselt emend. Arndt, produced *Alisporites*-type pollen as well (see Grauvogel-Stamm 1978, Balme 1995, Arndt 2002). Also the Antarctic cone *Leastrobus fallae* contains morphologically similar pollen. The grains differ mainly in the smaller size and in the more clearly developed, fine corpus reticulation (Hermsen *et al*. 2007).

Co-occurrence

Switzianthus has been affiliated with *Dejerseya* foliage in part because of the co-occurrence at some localities in South Africa (Anderson & Anderson 2003). A particular reference for this hypothesis is supposed to be a large collection of plant fossils from the Lit111 site, where *Dejerseya* leaves account for *c*. 20% of the foliage taxa and *Switzianthus* is the most common pollen organ (Anderson & Anderson 2003). However, nineteen other gymnosperm

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Table I. Comparison of localities where *Switzianthus* Anderson & Anderson has been found (data for South Africa are taken from Anderson & Anderson 2003).

Region	Locality	Sample size (no. of slabs)	*Dejerseya* Herbst	*Heidiphyllum* Retallack
Antarctica	Mount Falla, Level 14	~ 150	+	+
	Allan Hills	~ 900	–	+
South Africa	Little Switzerland, 111	2173	+	+
	Aasvoëlberg, 411	2176	–	+
	Matatiele, 111	1082	–	+
	Winnaarspruit, 111	64	+	+

foliage genera and not less than six other pollen organ genera occur at the Lit111 site. An affiliation based on the quantitative occurrences of individual taxa in this assemblage must therefore remain questionable. Moreover, *Switzianthus* is now known from several extensively sampled plant fossil localities in which *Dejerseya* is absent (Table I). This is remarkable, as it can be assumed that the pollen organs of an individual plant are far less likely to become preserved in a fossil assemblage than the affiliated foliage (e.g. Rothwell & Mapes 2001).

By contrast, *Switzianthus* is associated with *Heidiphyllum* leaves at all known localities (Table I). In the present collections from Allan Hills and Mount Falla, *Heidiphyllum* forms a dominant component on many of the slabs. The intact *Switzianthus* cone from Allan Hills occurs on a slab that otherwise bears only *Heidiphyllum* leaves.

Conclusions

Taken together, the evidence leads us to the conclusion that *Switzianthus* is a voltzialean pollen cone that probably belonged to the same parent plants that produced the *Heidiphyllum* leaves and *Telemachus* seed cones of the Antarctic Triassic. Only a single morphospecies of *Heidiphyllum*, i.e. *H. elongatum*, is currently recognized in the Triassic of Antarctica and South Africa (Anderson & Anderson 2003). At the same time, however, at least five different species of voltzialean pollen cones have been described from the Molteno Formation, and possibly two further distinct taxa are known from the Triassic of Antarctica (Cantrill *et al*. 1995, Hermsen *et al*. 2007). If future studies should confirm that our interpretation of *Switzianthus* as yet another type of pollen cone to be affiliated with *H. elongatum* is accurate, this would indicate that a remarkable, yet previously unrecognized diversity and morphological disparity of natural conifer species may be hidden among the uniform morphology of voltzialean foliage and seed cones in the Triassic of Gondwana.

Acknowledgements

We wish to thank Ignacio Escapa (Trelew, Chubut, Argentina) and Hans Kerp (Münster, Germany) for valuable discussion, and gratefully acknowledge helpful comments and suggestions by Brian Axsmith (Mobile, AL, USA) and David Cantrill (Melbourne, Australia). Financial support has been provided by the Deutsche Forschungsgemeinschaft (DFG grant KE584/16-2) and in part by the National Science Foundation (NSF grant DPP 88-15976 to E.L.T. and T.N.T).

References

Anderson, H.M. 1978. *Podozamites* and associated cones and scales from the Upper Triassic Molteno Formation, Karoo Basin, South Africa. *Palaeontologia Africana*, **21**, 57–77.

Anderson, J.M. & Anderson, H.M. 1989. *Palaeoflora of southern Africa: Molteno Formation* (*Triassic*). Vol. 2. *Gymnosperms* (*excluding Dicroidium*). Rotterdam: Balkema, 567 pp.

Anderson, J.M. & Anderson, H.M. 2003. *Heyday of the gymnosperms: systematics and biodiversity of the Late Triassic Molteno fructifications*. Pretoria: National Botanical Institute, Strelitzia 15, 399 pp.

Arndt, S. 2002. Morphologie und Systematik ausgewählter Mesozoischer Koniferen. *Palaeontographica*, **B262**, 1–23.

Axsmith, B.J., Taylor, T.N. & Taylor, E.L. 1998. Anatomically preserved leaves of the conifer *Notophytum krauselii* (Podocarpaceae) from the Triassic of Antarctica. *American Journal of Botany*, **85**, 704–713.

Balme, B.E. 1995. Fossil *in situ* spores and pollen grains: an annotated catalogue. *Review of Palaeobotany and Palynology*, **87**, 81–323.

Barrett, P.J. 1969. *Stratigraphy and petrology of the mainly fluviatile Permian and Triassic Beacon rocks, Beardmore Glacier area, Antarctica*. Columbus, OH: Ohio State University Research Foundation, Institute of Polar Studies, Report No. 34, 132 pp.

Barrett, P.J., Elliot, D.H. & Lindsay, J.F. 1986. The Beacon Supergroup (Devonian–Triassic) and Ferrar Group (Jurassic) in the Beardmore Glacier area, Antarctica. *Antarctic Research Series*, **36**, 339–428.

Cantrill, D.J., Drinnan, A.N. & Webb, J.A. 1995. Late Triassic plant fossils from the Prince Charles Mountains, East Antarctica. *Antarctic Science*, **7**, 51–62.

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

Farabee, M.J., Taylor, T.N. & Taylor, E.L. 1989. Pollen and spore assemblages from the Falla Formation (Upper Triassic), central Transantarctic Mountains, Antarctica. *Review of Palaeobotany and Palynology*, **61**, 101–138.

Feistmantel, O. 1889. Übersichtliche Darstellung der geologisch-palaeontologischen Verhältnisse Süd-Afrikas. I. Theil. Die Karoo-Formation und die dieselbe unterlagernden Schichten. *Abhandlungen der Königlichen Böhmischen Gesellschaft der Wissenschaften Mathematisch-Naturwissenschaftliche Klasse VII*, **3**, 1–89.

FLORIN, R. 1938–45. Die Koniferen des Oberkarbons und des unteren Perms, I–VII. *Palaeontographica*, **B85**, 1–729.

GRAUVOGEL-STAMM, L. 1978. La flore du Grès à Voltzia (Buntsandstein Supérieur) des Vosges du Nord (France). Morphologie, anatomie, interprétations phylogénique et paléogéographique. *Sciences Géologiques, Université Louis Pasteur de Strasbourg, Institut de Géologie, Mémoire*, **50**, 1–225.

GRAUVOGEL-STAMM, L. & SCHAARSCHMIDT, F. 1979. Zur Morphologie und Taxonomie von *Masculostrobus* Seward und anderen Formgattungen peltater männlicher Koniferenblüten. *Senckenbergiana Lethaea*, **60**, 1–37.

HERMSEN, E.J., TAYLOR, T.N. & TAYLOR, E.L. 2007. A voltzialean pollen cone from the Triassic of Antarctica. *Review of Palaeobotany and Palynology*, **144**, 113–122.

KYLE, R.A. & SCHOPF, J.M. 1982. Permian and Triassic palynostratigraphy of the Victoria Group, Transantarctic Mountains. *In* CRADDOCK, C., *ed. Antarctic geoscience*. Madison, WI: University of Wisconsin Press, 649–659.

MEYER-BERTHAUD, B. & TAYLOR, T.N. 1991. A probable conifer with podocarpaceous affinities from the Triassic of Antarctica. *Review of Palaeobotany and Palynology*, **67**, 179–198.

MILLER JR, C.N. 1977. Mesozoic conifers. *Botanical Review*, **43**, 218–280.

MORRIS, J. 1845. Fossil flora. *In* STRZELECKI, P.E., *ed. Physical descriptions of New South Wales and Van Diemens Land*. London: Brown, Green and Longmans, 245–250.

NIELSEN, S.N. 2005. The Triassic Santa Juana Formation at the lower Biobío River, south central Chile. *Journal of South American Earth Sciences*, **19**, 547–562.

RETALLACK, G.J. 1981. Middle Triassic megafossil plants from Long Gully, near Otematata, north Otago, New Zealand. *Journal of the Royal Society of New Zealand*, **11**, 167–200.

ROTHWELL, G.W. & MAPES, G. 2001. *Barthelia furcata* gen.et sp. nov., with a review of Palaeozoic coniferophytes and a discussion of coniferophyte phylogeny. *International Journal of Plant Sciences*, **162**, 637–667.

ROTHWELL, G.W., MAPES, G. & HERNANDEZ-CASTILLO, G.R. 2005. *Hanskerpia* gen. nov. and phylogenetic relationships among the most ancient conifers (Voltziales). *Taxon*, **54**, 733–750.

SCHWENDEMANN, A.B., TAYLOR, T.N., TAYLOR, E.L. & KRINGS, M. 2010. Organization, anatomy, and fungal endophytes of a Triassic conifer embryo. *American Journal of Botany*, **97**, 1873–1883.

TAYLOR, T.N., TAYLOR, E.L. & KRINGS, M. 2009. *Paleobotany: the biology and evolution of fossil plants*. London: Academic Press, 1230 pp.

YAO, X., TAYLOR, T.N. & TAYLOR, E.L. 1993. The Triassic seed cone *Telemachus* from Antarctica. *Review of Palaeobotany and Palynology*, **78**, 269–276.

YAO, X., TAYLOR, T.N. & TAYLOR, E.L. 1997. A taxodiaceous seed cone from the Triassic of Antarctica. *American Journal of Botany*, **84**, 343–354.