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The Triassic seed cone *Telemachus* from Antarctica

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ABSTRACT

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The compressed conifer seed cone *Telemachus elongatus* is described from the Upper Triassic of Antarctica. The ovate cone measures up to 4.0 cm long and 4.0 cm wide, and contains helically arranged cone scale complexes. Each cone scale consists of an elongated bract fused to a 5-lobed ovuliferous scale. Two or three slightly reflexed ovules are borne on the adaxial surface of the ovuliferous scale. The cone scale cuticle is thin and possesses monocyclic stomata; cuticles are present on the ovules as well. These specimens represent the first record of an early conifer reproductive axis from the Triassic of Antarctica, and confirm that the early conifers were distributed southward to Antarctica by the early Mesozoic.

Introduction

To date three families of conifers (Araucariaceae, Podocarpaceae and Taxodiaceae), together with a number of other distinct late Paleozoic and Mesozoic taxa, have been described from Antarctica. The majority of these are based on foliage genera, with only a few known from reproductive organs (Stockey, 1990). No seed cones older than Jurassic have been reported from Antarctica; the Triassic seed cones known from Gondwana include *Voltziopsis* Potonié from South Africa and Australia (Townrow, 1967a; Gould, 1975), *Telemachus* Anderson from South Africa and New Zealand (Anderson, 1978; Retallack, 1981) and *Rissikia* Townrow from Madagascar, South Africa and Australia (Townrow, 1967b, 1969; Anderson and Anderson, 1985). Another seed cone described from South Africa (Anderson and Anderson, 1985) was referred to *Sewardistrobus* Anderson et Anderson and later transferred to *Voltziopsis* Potonié (Anderson and Anderson, 1989).

Recent collections of compressed plants from the Triassic of Antarctica include several specimens that we interpret as conifer seed cones. The specimens were collected from the Falla Formation on the north face of the western spur of Mt. Falla in the Queen Alexandra Range. This formation consists of sediments underlying the Prebble Conglomerate which is probably Lower Jurassic, and overlying the Fremouw Formation that is regarded as Lower–Middle Triassic (Farabee et al., 1989). The lower portion of the Falla Formation is characterized by sandstone to carbonaceous shales which contain abundant impression/compressions, some with well preserved cuticles. The upper part of the Falla Formation is predominately tuffaceous and lacks well preserved plants (Vavra, 1984). Based on pollen and spore assemblages, the plant containing beds are considered to be Late Triassic (Norian) (Farabee et al., 1989). The flora is dominated by several *Dicroidium* Gothan morphotypes, but also contains filicalean ferns, cycadophytes, ginkgophytes, and several other possible seed fern and conifer foliage genera (Barrett, 1969; Barrett et al., 1986; Taylor and Taylor, 1988). Also present are two reproductive organs (Taylor and Taylor, 1988). It is the intent

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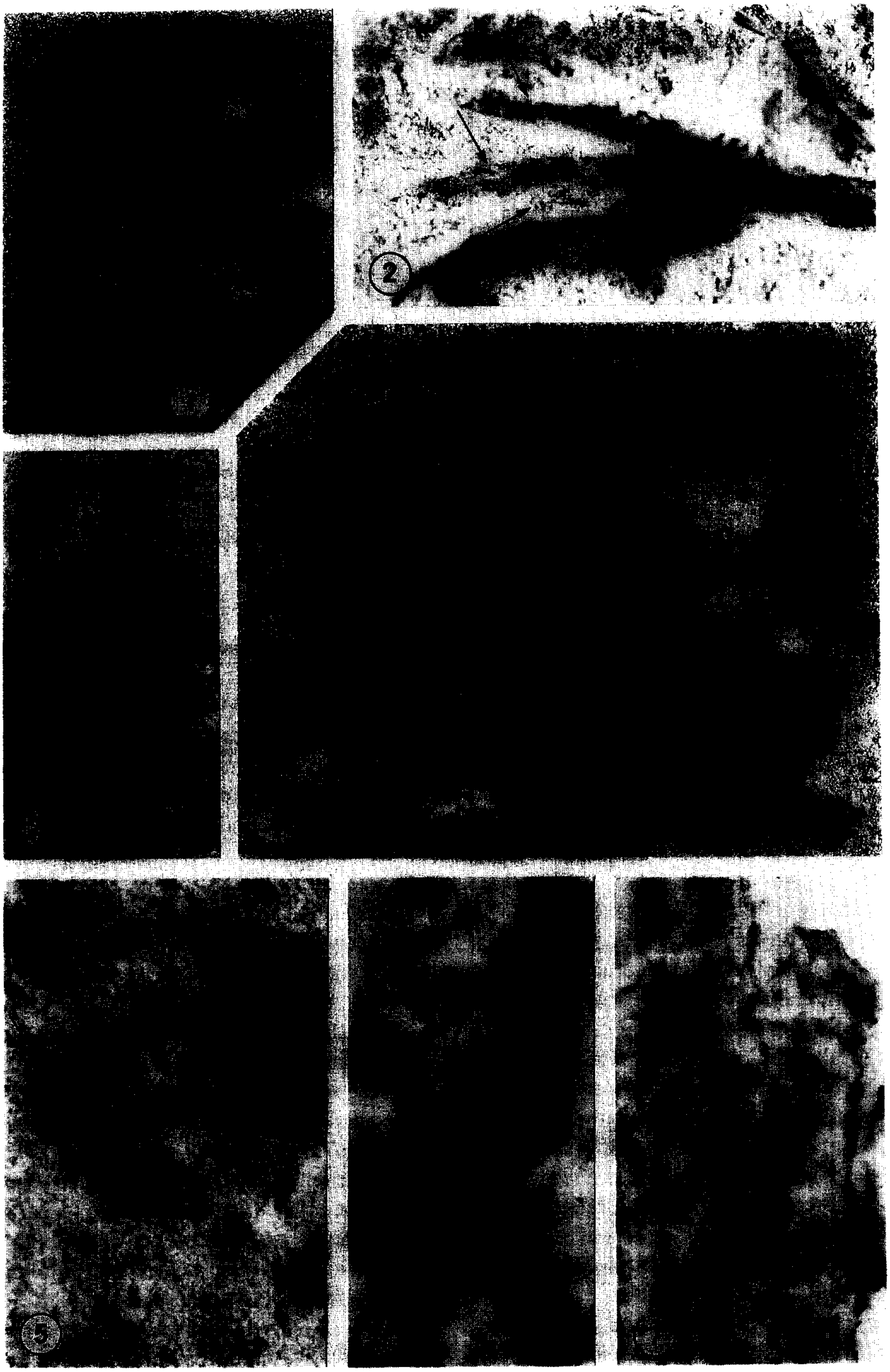
PLATE I



of this paper to describe a conifer seed cone based on compressed specimens collected from the Falla Formation.

Materials and methods

Two specimens were discovered in a fine-grained, medium to dark gray shale in the lower part of the Falla Formation [level 14 of Barrett's (1969) type section F2]. Cuticle fragments from the cone scales and ovules were macerated with nitric acid (90%) after cleaning with dilute hydrofluoric acid. Cuticles were subsequently mounted on standard microscope slides and examined with transmitted light; some fragments were attached to SEM stubs with silver paint for examination with the scanning electron microscope.

Systematics

Order CONIFERALES

Genus *Telemachus* Anderson, 1978

Species *Telemachus elongatus* Anderson, 1978

Diagnosis (emended): Ovate seed cone, 4.0–6.0 cm long and 4.0–6.0 cm wide, with helically arranged cone scales attached to axis up to 4 mm wide; cone scale up to 3.0 cm long, with bract and ovuliferous scale fused for about 1/2 length; bract elongate, extending beyond length of ovuliferous scale; scale 5-lobed at apex and bearing 2 or 3 slightly reflexed ovules below lobes, each ovule 1.5–2.0 mm in diameter; cuticle from basal part of cone scale thin (1 μm thick) with longitudinally elongate cells arranged in radial files; occasional monocyclic stomata with thickly cutinized and sunken guard cells surrounded by 5–6 subsidiary cells; cuticle from cone scale head thin, showing elongate hexagonal cells (75.0–106.0 × 7.2–9.6 μm), other cells irregular in outline; cuticle from outer integument of ovule thick, composed of rectangular to polygonal cells with strongly cutinized anticlinal walls, forming short, spine-like projections or flanges at cell corners; cuticle of inner integument lacking projections and less cutinized; nucellar cuticle showing hexagonal cell outline (15.0–18.7 μm) with straight anticlinal walls and granular surface.
Locality: Mount Falla, Queen Alexandra Range (84°21′S, 164°42′E), Buckley Island Quadrangle, Antarctica.
Stratigraphy: Lower Falla Formation. Level 14 of Barrett's type section (F2) (Barrett et al., 1986).
Age: Late Triassic.
Deposition of specimens: Specimen T-7-183, T-7-166 and slides deposited in the Paleobotanical Collections, Department of Plant Biology, The Ohio State University, Columbus, OH (slides include acquisition numbers 19,297–19,328).

Description

The following description is based on two cones: one is preserved longitudinally to reveal the cone axis and attachment of the cone scales (Plate I, 1), while the other specimen shows features of the cone surface (Plate I, 3). The cone is slightly

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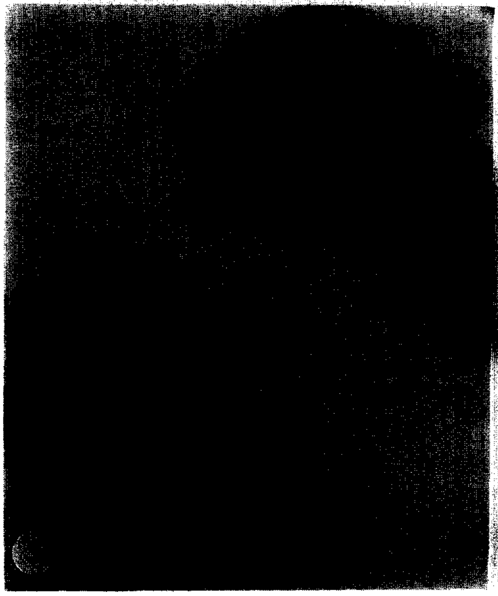
PLATE I

Telemachus elongatus.

1. Compressed cone showing axis and cone scale complexes with elongated bract (*B*) and lobed ovuliferous scale (*OS*). Arrow indicates scale illustrated in 2. T-7-183. × 1.6.
2. Exposed cone scale showing some ovuliferous scale lobes (arrows) and bract (arrow head). T-7-183. × 12.
3. Outer surface of cone showing helical phyllotaxy and expanded head of cone scales. Arrow indicates scale illustrated in 5. T-7-166. × 1.6.
4. Detail of cone in 1 showing attached ovules (arrows), micropyles (*m*), 5 lobes of ovuliferous scale (arrow heads) and bract (*B*). T-7-183. × 3.8.
5. One cone scale complex of cone in 3 showing impression of part of bract (*B*) and basal portion of 5 lobes of a ovuliferous scale (arrows). T-7-166. × 7.
6. Cuticle from stalk of cone scale showing epidermal cells and guard cells of stomatal complex. T-7-183. × 650.
7. Elongate epidermal cells from cone scale stalk. T-7-183. × 297.

PLATE II



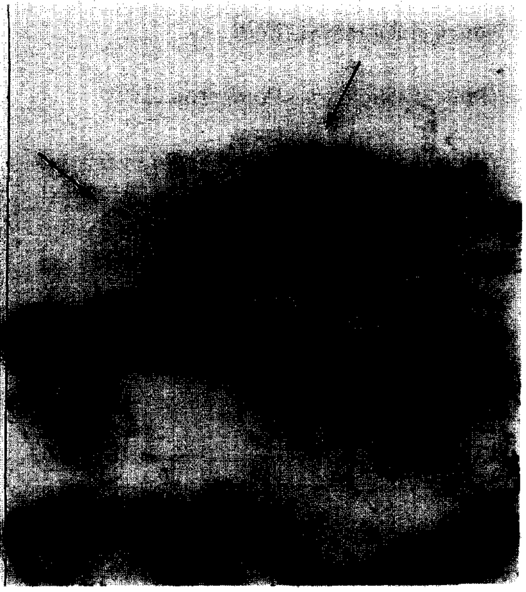


PLATE II

Telemachus elongatus.

1. Cuticle from expanded head of a cone scale. T-7-183. × 151.
2. Cuticle macerated from ovule. Arrows at left denote pollen grains; arrow at upper right shows spine-like flanges at corners of cells of outer integument. T-7-183. × 418.
3. Cuticle macerated from nucellus. T-7-183. × 650.
4. Cuticle macerated from ovule showing pollen grain (arrows indicate sacci). T-7-183. × 525.

oblong and measures 4.0 cm long and 4.0 cm in maximum diameter. Attached to the axis are numerous, helically arranged cone scales. The specimen illustrated in Plate I, 3 shows the distal ends of fourteen scales in an area of 2.4 cm^2. Cone scales range from 5 to 18 mm long depending on where they occur on the axis; the smallest ones occur at the distal end of the cone. Each cone scale consists of a bract and ovuliferous scale which are fused about 1/2 of their length. Where fused they form a pedicle-like structure that is approximately 1 mm thick and displays 12–15 longitudinal ridges. At the distal end where the ovuliferous scale and bract are free (Plate I, 2), the scale forms an expanded head characterized by a rhombic base (Plate I, 3, 5). The subtending bract is acute with the free portion extending past the ovuliferous scale about 3.0 mm (Plate I, 1). The distal end of the ovuliferous scale is divided into five lobes (Plate I, 4, 5). On the adaxial surface of each scale are 2 or 3 ovules, each reflexed approximately 50° (Plate I, 4). Ovules are nearly spherical and range from 1.5 to 2.0 mm in diameter (Plate I, 4). The micropylar end is slightly attenuated (Plate I, 4).

Several regions of the cone contained well preserved cuticles. Cuticle of the cone scale stalk is approximately 1.0 μm thick and shows outlines of elongate epidermal cells that are arranged in longitudinal files (Plate I, 7). Each epidermal cell is rectangular and measures 125–187 × 12–37 μm. The longitudinal wall is straight and approximately 1.3 μm thick, while the transverse wall is less conspicuous and often oblique. In some regions the wall appears unevenly thickened; however, this thickening may be the result of preservation of longitudinal folds. A few monocyclic stomata are present at some regions along the stalk. Each stomatal complex is elongate and consists of a pair of thickly cutinized guard cells, each 37.5–42.5 μm long by 5.0–11.3 μm wide (Plate I, 6), and 5–6 subsidiary cells which radially surround the guard cells. The cuticle at distal levels of the cone scale is thin and typically folded so that the outline of individual cells is often difficult to resolve (Plate II, 1). Some cell outlines are elongate and up to 106 μm long and range from 25 to 30 μm wide. No stomata have been observed.

Three distinct types of cuticles were recovered upon maceration of the ovules. Cuticle of the outer integument shows the outline of rectangular to polygonal cells 21.6–28.7 × 7.2–9.6 μm with short, spine-like projections forming pronounced flanges in the cell corners (Plate II, 2). The cuticle of the inner integument is thin and lacks flanges. Cuticle of the nucellus (Plate II, 3) is delicate and often shows the outline of hexagonal cells that vary from 15 to 18 μm in diameter. The anticlinal wall is straight; the surface of these cells shows a granular ornament.

Several bisaccate pollen grains were macerated from the cuticles of the cone scales and ovules (Plate II, 2, 4). Although none of these was found associated with the distal end of the nucellus in the region of the pollen chamber, the large number of these grains suggest that they were probably biologically associated with *Telemachus elongatus*. Individual grains range from 50 to 85 μm and consist of an oval corpus flanked by crescent-shaped sacci. The inner surface of the saccus is endoreticulate, while on the outer surface the exine is granulate. These grains compare favorably with *Alisporites* (Daugherty) Jansonius that is a common Triassic genus in Antarctica (Schopf and Askin, 1980).

Discussion

Numerous conifers have been described from the late Paleozoic to Mesozoic in both the Northern and Southern Hemispheres. In his detailed studies of late Paleozoic conifers and cordaites, Florin (1938–1945, 1951, 1954) recognized several important forms which were included in the family Lebachiaceae and Voltziaceae. Florin suggested that these early conifers were transitional forms between cordaites and modern conifers. More recently, Clement-Westerhof and her colleagues have augmented the classification of primitive conifers (Clement-Westerhof, 1984, 1987, 1988; Visscher et al., 1986; Kerp et al., 1990; Kerp and Clement-Westerhof, 1991) and established a new family, the Majonicaceae, while assigning others to Walchiaceae, Ullmanniaceae and several form genera. The most recent re-organization of fossil conifer families is that of Mapes and Rothwell

(1991) who combined some family names and created two new ones, Utrechtiaceae and Emporiaceae.

In contrast, Mesozoic conifers remain poorly known systematically. Although all the Mesozoic genera except those assigned to modern families and the Cheirolepidiaceae have been included in the family Voltziaceae, the family is represented by an assemblage of diverse fossil conifers (Townrow, 1967a; Clement-Westerhof, 1987). Among fossil conifer seed cones the specimens from Antarctica appear most similar to the genus *Telemachus* Anderson (Anderson, 1978; Retallack, 1981). In addition to the general morphology of the cone, the structure of the cone scale complex (flattened short shoots and partially fused bract and ovuliferous scale), elongated bract, number of ovuliferous scale lobes (5) and ovules (2 or 3) are features that suggest relationships with *Telemachus*.

Initially the affinities of *Telemachus* were unresolved (Anderson, 1978); however, the genus was subsequently placed in the Voltziaceae by Retallack (1981). In 1983, Anderson and Anderson modified this view by placing *Telemachus* in the Cycadocarpidiaceae, but later, based on the constant association with leaves of *Heidiphyllum*, included *Telemachus* in the Voltziaceae again. We agree that *Telemachus* shares a number of important features with those genera included in the Voltziaceae such as *Voltzia* and *Voltziopsis*. However, because the family includes such an array of cone types, this assignment is provisional.

Morphologically *Telemachus* is more or less similar to some Paleozoic and Mesozoic conifer seed cones that have been described from both the Southern and Northern Hemispheres. Retallack (1981) has discussed the similarities and differences between *Telemachus* and most closely related genera. The comparison of several selected genera considered most similar to *Telemachus* is summarized in Table I. As presently interpreted *Telemachus* includes two species, the type species *T. elongatus* Anderson, 1978, known from the Upper Triassic Molteno Formation (Carnian age) of South Africa (Anderson, 1978), and *T. lignosus* from the Middle Triassic Long Gully Formation (Ladinian age) of New Zealand (Retallack, 1981). The principal difference is the length of the bract in *T. elongatus*. The close correspondence between the Antarctic specimens and *T. elongatus*, especially concerning the distinctly long bract, suggests they are the same species. The slightly smaller size (4.0 cm long and 4.0 cm wide) of the Antarctic specimen compared to the South African cones (6.0 cm long and 6.0 cm wide) (Anderson, 1978) may simply represent natural variation or a developmental difference. Another difference is that the bract of the Antarctic specimen does not appear to be as reflexed at the base as those from South Africa. However, this difference seems minor and not sufficient to warrant segregation in a new species.

Although the *Alisporites* grains found associated with *T. elongatus* were only associated with cone scales and ovule cuticles, the high percentage of these grains suggests a potential biological relationship between the pollen and seed cone. *Sporae dispersae* grains of *Alisporites australis* de Jersey have been reported from the same shale lenses as those containing the cone (Kyle and Fasola, 1978; Farabee et al., 1989). Another interesting biological association involves the numerous strap-shaped leaves with parallel venation found together with *Telemachus* in the Falla Formation. These leaves are morphologically similar to those of *Heidiphyllum* (Taylor and Taylor, 1988). The association of *Telemachus* and *Heidiphyllum* has also been reported from South Africa and New Zealand (Anderson, 1978; Retallack, 1981). Cuticle of *H. elongatum* from South Africa is well known (Anderson, 1978; Retallack, 1981; Anderson and Anderson, 1983, 1989) and shows some features that are also found in the Antarctic *Telemachus* cones, including the stoma with 5–6 subsidiary cells, but differ in that the guard cells of *Heidiphyllum* are not as strongly cutinized as those of *Telemachus*, and the subsidiary cells of *Telemachus* have some thickening adjacent to guard cells but lack papillae or the cutin lappet found in *Heidiphyllum*. It is too early to conclusively state that these two genera are parts of the same plant.

Based on the study of plant microfossils, Balme (1963) suggested that some members of the Triassic Gondwana flora migrated south from the Northern

TABLE I

Comparison of the seed cone of *Telemachus* and several selected genera

Character	Genus					
	Telemachus	*Voltziopsis*	*Rissikia*	*Voltzia*	*Glyptolepis*	*Pseudovoltzia*
Short shoot	Flattened	Flattened	Flattened	Flattened	Flattened	Less flattened
Fusion of bract and scale	Partially fused	?	?	?	?	Partially fused
Bract	Elongated, non-forked	Bifurcate	Trifid	Non-forked	Non-forked	Non-forked
Ovuliferous scale lobes	5	5 (rarely 6)	3	5	5 to 6	5
No. of ovules per scale	2 or 3	5	2–6 (1 or 2 when mature)	2 or 3	2	3
Ovule	Recurved	Recurved	Recurved	Recurved	Recurved	Recurved
Ovule position	Adaxial, below lobes	Adaxial, stalked, extended up to lobes	Adaxial, stalked, extended up to lobes	Adaxial, stalked, extended up to lobes	Lateral, stalked	2 marginal ovules slightly lateral, non-stalked
References	Anderson, 1978; Retallack, 1981; Yao et al., this paper	Townrow, 1967a	Townrow, 1967b, 1969	Florin, 1951; Miller, 1977	Florin, 1951; Miller, 1977	Schweitzer, 1963; Clement-Westerhof, 1987
Age	Triassic	Permian–Triassic	Triassic	Triassic	Permian–Triassic	Permian
Locality	Southern Hemisphere (South Africa; New Zealand; Antarctica)	Southern Hemisphere (Africa; Australia)	Southern Hemisphere (Madagascar; South Africa; Australia)	Northern Hemisphere	Northern Hemisphere	Northern Hemisphere

Hemisphere during the Late Permian. Townrow (1967a) supported this suggestion based on the analysis of pollen associated with *Voltziopsis wolganensis* Townrow from the Triassic of Australia as well as the distribution of pollen associated with *Rissikia* Townrow. The biogeography of the Triassic Antarctic flora can be further tested as additional floral components are described and illustrated. The discovery of *T. elongatus* from Antarctica provides perhaps the first evidence of a reproductive axis that suggests that the early conifers migrated south to Antarctica already in the Triassic as a component of the Gondwana flora.

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