

Please share your stories about how Open Access to this article benefits you.

Systematics and Paleoecology of a New
Peltaspermalean Seed Fern From the
Triassic Polar Vegetation of Gondwana

by Benjamin Bomfleur, Edith L. Taylor,
Thomas N. Taylor, Rudolph Serbet, Mi-
chael Krings, and Hans Kerp

2011

This is the published version of the article, made available with the permission of the publisher. The original published version can be found at the link below.

Bomfleur, B., Taylor, E., Taylor, T., Serbet, R., Krings, M., and Kerp, H. 2011. Systematics and Paleoecology of a New Peltaspermalean Seed Fern From the Triassic Polar Vegetation of Gondwana. *International Journal of Plant Sciences* 172(6): 807-835.

Published version: <http://dx.doi.org/10.1017/S0954102011000241>

Terms of Use: <http://www2.ku.edu/~scholar/docs/license.shtml>

SYSTEMATICS AND PALEOECOLOGY OF A NEW PELTASPERMALEAN SEED FERN FROM THE TRIASSIC POLAR VEGETATION OF GONDWANA

Benjamin Bomfleur,^{1,*} Edith L. Taylor,* Thomas N. Taylor,* Rudolph Serbet,* Michael Krings,† and Hans Kerp‡

*Department of Ecology and Evolutionary Biology, and Natural History Museum and Biodiversity Institute, University of Kansas, Lawrence, Kansas 66045; †Department für Geo- und Umweltwissenschaften, Paläontologie und Geobiologie, Ludwig-Maximilians-Universität, and Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333 Munich, Germany; and ‡Forschungsstelle für Paläobotanik am Institut für Geologie und Paläontologie, Westfälische Wilhelms-Universität Münster, Hindenburgplatz 57, 48143 Münster, Germany

A new Triassic seed fern is described on the basis of a large collection of well-preserved plant compressions from the Upper Triassic of Mt. Falla, Queen Alexandra Range, central Transantarctic Mountains. The foliage is simple entire-margined to pinnatifid to partly pinnate and is assigned to *Dejerseyia lobata* (Jones et de Jersey) Herbst emend. nov. Associated with these leaves occur two new reproductive structures. The ovulate organ *Matatiella dejerseyi* sp. nov. is a lax, conelike structure with primarily shield-shaped megasporophylls that are dissected into three to four narrow lobes, each bearing a single recurved, naked ovule. The pollen organ *Townrovia polaris* sp. nov. consists of a slender axis arising from a covered reproductive bud, bearing pinnately arranged, stalked, elongate receptacles each with ~20 unilocular, clavate pollen sacs; the pollen is bisaccate nontaeniate with an irregular longitudinal sulcus and coarse saccus endoreticulations, corresponding to the dispersed pollen *Falcisporites australis*. Similar pollen grains occur in the micropylar canals of seed cuticles of *M. dejerseyi*. Co-occurrence data indicate that the three taxa are probably different organs from one plant species. This new seed fern is assigned to the Matatiellaceae, which we place into the Peltaspermales because of structural similarities with vegetative and reproductive organs of other peltaspermalean seed ferns. It appears that several Triassic Gondwanan plant fossil taxa of currently uncertain affinities—such as *Pachydermophyllum*, *Linguifolium*, *Carpolithus mackayi*, and *Andersonia*—may belong to the Matatiellaceae as well. We suggest that the matatiellacean peltasperms were opportunistic, early successional plants that were particularly successful in colonizing stressed wetland environments in polar latitudes during the Triassic.

Keywords: *Dejerseyia*, *Matatiella*, *Townrovia*, Matatiellaceae, Antarctica, whole-plant reconstruction.

Introduction

The plant fossil record continues to yield evidence that the gymnosperms living today are only a small segment of the total diversity of gymnosperm lineages that existed before the rise of flowering plants during the Mesozoic (Taylor 1976; Anderson and Anderson 2003; Naugolnykh 2008; Gordenko 2010; Wang and Pfefferkorn 2010). Among the numerous extinct gymnosperm clades, the Peltaspermales was a particularly successful and diverse group of seed ferns that existed from the Late Carboniferous until the end of the Triassic (Taylor et al. 2006). Although long considered to be a typical Mesozoic group, peltasperms are now reported to have reached their greatest distribution and diversity during the Permian (Gomankov and Meyen 1979, 1986; Kerp 1982, 1988; Poort and Kerp 1990; Naugolnykh and Kerp 1996; Naugolnykh 2001, 2008; DiMichele et al. 2005; Booi et al. 2009). Thereafter, peltasperms appeared to be significant components mainly of Middle and Late Triassic floras of Eurasia (Harris 1931; Dobruskina 1975, 1988). Coeval vegeta-

tion in Gondwana, by contrast, was usually dominated by corystospermalean seed ferns (Anderson et al. 1999) and contained only subordinate proportions of peltasperms (Anderson and Anderson 1989; Holmes and Anderson 2005), even though the group as such was originally defined on material from South Africa (Thomas 1933).

During the Triassic, all major landmasses were united in the supercontinent Pangea, which extended almost from pole to pole. The Earth during that time was a greenhouse world; following climate warming during the Permian-Triassic transition, global temperatures were high overall and continental ice sheets were absent (Scotese et al. 1999; Kidder and Worsley 2004; Sellwood and Valdes 2006; Preto et al. 2010), which enabled vegetation to spread far into polar latitudes. Continental deposits of an extensive fluvial drainage basin in the high-latitude regions of southeastern Gondwana are today exposed in the Transantarctic Mountains. Plant fossil deposits associated with these sedimentary successions constitute an important source of information about the paleobiology and paleoecology of the past polar biotas of Gondwana (Taylor and Taylor 1990; Taylor et al. 2000).

This article reports on a well-preserved, parautochthonous plant fossil assemblage from the Late Triassic Falla Forma-

¹ Author for correspondence; e-mail: bbomfleur@ku.edu.

Manuscript received January 2011; revised manuscript received March 2011.

tion in the central Transantarctic Mountains. As a result of its unique local paleoenvironmental and depositional setting at a paleolatitude between 70° and 75°S (Lawver et al. 1998; Veevers 2004; Torsvik et al. 2008), this assemblage has an unusual floral composition that is unlike that of any other Gondwanan macroflora described to date. The assemblage is dominated by *Dejerseya lobata* (Jones et de Jersey) Herbst emend. nov., a seed fern leaf that has previously been known only from scattered occurrences in Australia (Jones and de Jersey 1947; Douglas 1969), South Africa (Anderson and Anderson 1989), and South America (Gnaedinger and Herbst 1998a, 2004). Associated with *Dejerseya* are well-preserved peltaspermean reproductive organs; other co-occurring fossils include various organs of a voltzialean conifer, a corystosperm, and a single filicalean fern.

This material allowed us to (1) clarify the problematic taxonomic status and delimitation of *Dejerseya* Herbst emend. nov. and its type species *D. lobata* (Jones et de Jersey) Herbst emend. nov.; (2) describe in detail the co-occurring reproductive organs, that is, the ovulate structure *Matatiella dejerseyi* sp. nov. and the pollen organ *Townrovia polaris* sp. nov.; (3) reconstruct these three taxa as belonging to a single plant; and (4) identify this plant and several other pteridosperm taxa from Gondwana as representatives of a particular, yet previously unrecognized group of Mesozoic peltasperms: the Matatiellaceae.

Material and Methods

The fossils were collected from the type section of the Falla Formation (Barrett 1969) on the northern flank of the western ridge of Mt. Falla (Queen Alexandra Range, central Transantarctic Mountains; 84°22'S, 164°55'E; fig. 1). At this locality, the Falla Formation unconformably overlies the Middle Triassic Fremouw Formation and is in turn capped by the volcanoclastic Lower Jurassic Hanson and Prebble formations (Elliot 1996). The Falla Formation is composed of sandstone

and carbonaceous shale developed in a series of 12 fining-upward cycles with a total thickness of 282 m (Barrett 1969; fig. 2). The formation represents deposits of a distal braided river system with a high proportion of paludal and lacustrine overbank fines (Barrett et al. 1986). The age of these strata is considered to be Carnian or Norian (early or middle Late Triassic) on the basis of palynological data (Kyle and Fasola 1978; Farabee et al. 1989).

The fossil plants from Mt. Falla were briefly described (Taylor and Taylor 1988; Taylor et al. 1992) and selected individual taxa already studied in detail (Boucher et al. 1993; Yao et al. 1993; Axsmith et al. 1998; Escapa et al. 2010; Bomfleur et al. 2011). The fossils were collected from a 16-m-thick interval ~140 m above the base of the Falla Formation (profile F2, level 14 of Barrett 1969; see Taylor and Taylor 1988) that is mainly composed of gray mudstones with a few intercalations of up to 1-m-thick coaly layers and thin sheets of light gray, fine-grained sandstones (Barrett 1969). The collection comprises 149 samples that consist mainly of large slabs of platy, medium gray to beige-colored, silty mudstone with yellow to orange weathering stains. Apart from more or less well-developed subhorizontal bedding, the specimens show no discernible sedimentary features.

The majority of plant fossils (901 specimens) are well-defined compressions of usually complete leaves or large leaf fragments. In most cases, leaves occur in variously concentrated accumulations, with some individual bedding surfaces almost entirely covered by mats of overlapping leaves; isolated leaves are comparatively rare. The state of preservation is variable, although often consistent among leaves on an individual bedding surface. For example, leaves on some surfaces consist of black compressions yielding well-preserved cuticles, whereas leaves on other bedding surfaces are partly degraded or skeletonized, leaving only light brown leaf outlines with an easily recognizable venation pattern. Accumulations of well-preserved, dispersed seeds occur sporadically.

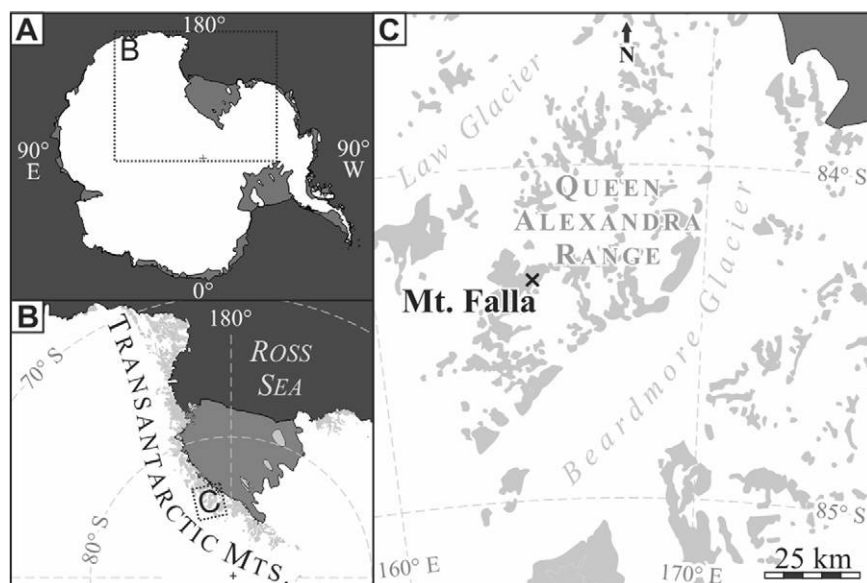


Fig. 1 Locality map of the fossil site at Mt. Falla in the Queen Alexandra Range, central Transantarctic Mountains, East Antarctica.

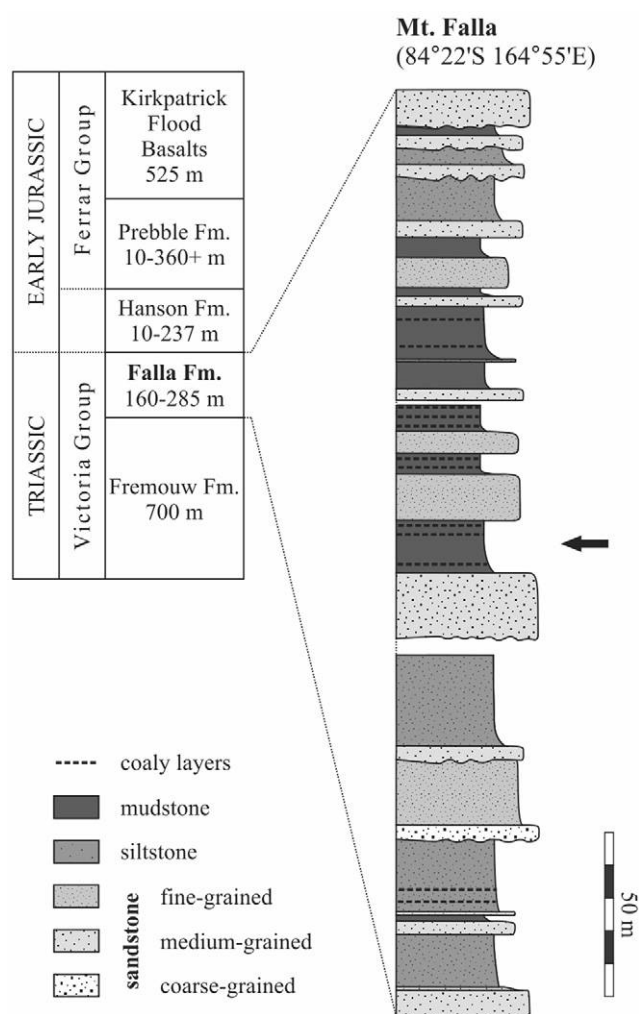


Fig. 2 Stratigraphy and main lithologies of the sedimentary section at Mt. Falla; arrow indicates the position of the plant-bearing horizon (stratigraphy after Elliot and Grimes 2011; lithological column after Barrett 1969).

Articulated reproductive organs are rare (17 specimens in total) and, in many cases, occur on surfaces that otherwise contain only few, if any, other aerial plant parts. Defoliated aerial axes of 1 to several centimeters in diameter are common, with some bearing conspicuous short shoots. In addition, most rock samples are penetrated by subvertically oriented, carbonized rooting structures up to 5 cm in diameter or contain horizontally spreading root compressions.

Large specimens were photographed with a Canon EOS 1000D digital single-lens reflex camera. Polarizing filters were used to enhance contrast, and in some cases, specimens were photographed under alcohol immersion to further enhance contrast. Surface details were analyzed using a Leica MZ 16 stereo dissecting microscope and photographed with a Leica DC500 digital camera. Selected specimens were further analyzed using a Zeiss Axioplan 2 UV epifluorescence microscope equipped with a Hamamatsu Orca-ER digital camera. Preparation of cuticles and in situ pollen were carried out following standard methods (Batten 1999; Kerp and Krings

1999). Selected specimens and bulk samples were treated with 48% hydrofluoric acid to isolate the fossils from the mineral matrix. Cuticles and pollen were further macerated using highly concentrated Schulze's reagent (40%–50% nitric acid [HNO₃] with a few crystals of potassium chlorate [KClO₃]) and cleaned and bleached using a 4% potassium hydroxide solution (KOH_{aq}) for a few seconds. After each step, the organic material was neutralized manually by careful decanting (or removing the solution with a pipette) and adding distilled water until the solution was neutral. Cuticles and pollen were finally dehydrated in glycerol and embedded on permanent microscope slides using glycerine jelly. Slides were analyzed using a Leica DM5000 compound microscope and photographed with a Leica DC500 digital microscope camera system.

The material is deposited in the Paleobotanical Collections of the Natural History Museum and Biodiversity Institute, University of Kansas, Lawrence, Kansas, under specimen accession numbers T5-38-146, T7-161-187, 194-0200, and T1852 and slide accession numbers 24042-24047 and 24049-24085.

Systematic Paleobotany

Order—Peltaspermales

Family—Matatiellaceae

Genus—*Dejerseya* Herbst emend. nov. *Bomfleur*,
E. Taylor, *T. Taylor*, *Serbet*, *Krings* et *Kerp*

Type. *Dejerseya lobata* (Jones et de Jersey) Herbst (selected by Herbst [1977]).

Basionym. *Rienitsia lobata* Jones et de Jersey.

Emended generic diagnosis. Petiolate or sessile, oblong to elliptical, straight to strongly curved, simple entire-margined to pinnatifid to partly pinnate leaves; degree of lobing usually decreasing toward the apex; midrib strong; secondary venation arising at acute angles, curving away from midrib, fan shaped to pinnate within lobes or pinnae, absent or dividing less frequently between lobes. Leaves amphistomatic with most stomata occurring in intercostal fields of abaxial leaf surface; stomata surrounded by 4–8 superficial, mostly papillate subsidiary cells; guard cells only moderately sunken.

Remarks. *Dejerseya* has a complex taxonomic history; the genus was established by Herbst (1977) for some species previously assigned to *Rienitsia* Walkom 1932, a genus for marattialean foliage. Jones and de Jersey (1947) described two species of *Rienitsia* with gymnosperm-like cuticles and emended the generic diagnosis of *Rienitsia* accordingly. Herbst (1977) recognized the need to separate the sporangia-bearing fern fronds described by Walkom (1932) from the gymnospermous leaves described by Jones and de Jersey (1947) and erected the genus *Dejerseya* for the latter. Herbst (1977) adopted the emended generic diagnosis of *Rienitsia* given by Jones and de Jersey (1947, p. 41). Because this latter diagnosis refers to both fern fronds with sporangia and gymnospermous leaves with cuticle (see appendix), a newly emended diagnosis is given here.

Although the sterile foliage may look superficially similar, *Rienitsia* and *Dejerseya* differ in the organization of the frond. *Dejerseya* has simple, pinnatifid to partly pinnate leaves, whereas *Rienitsia* has bipinnatifid to bipinnate fronds. This aspect was stressed by Jones and de Jersey (1947) in their de-

scription of the two new species of *Rienitsia* (now *Dejerseya*) from Australia and is further substantiated by collections of complete, simple *Dejerseya* leaves from South Africa (Anderson and Anderson 1983, 1989) and Antarctica (fig. 3A, 3B). The meager information that was available on epidermal anatomy has been used to suggest a cycadalean affinity for this leaf morphotype (“cuticle of the *Ctenis* type”; Jones and de Jersey 1947, p. 41). Information on epidermal and stomatal features in the emended diagnosis is given in descriptive terminology. The description of fertile features is omitted in the emended diagnosis.

Species—*Dejerseya lobata* (Jones et de Jersey) Herbst
emend. nov. Bomfleur, E. Taylor, T. Taylor,
Serbet, Krings et Kerp (Figs. 3, 4, 10B)

Basionym. *Rienitsia lobata* Jones et de Jersey. Jones and de Jersey 1947, p. 42; text figs. 33, 34; pl. 8, fig. 3; pl. 9, fig. 1.

Synonyms. *Rienitsia incisa* Jones et de Jersey. Jones et de Jersey 1947, p. 43; text figs. 35, 36; pl. 9, figs. 2, 3.

Dejerseya incisa (Jones et de Jersey) Herbst. Herbst 1977, p. 22.

Additional accepted records. *Rienitsia incisa* Jones et de Jersey. Hill et al. 1965, pl. 5, fig. 9.

Rienitsia ? *lobata* Jones et de Jersey. Douglas 1969, p. 18, figs. 1–3; p. 19, figs. 1, 4, 5; pl. 1, figs. 1–4.

Dejerseya lobata (Jones et de Jersey) Herbst. Anderson and Anderson 1983, pl. 16, figs. 1–4.

Dejerseya lobata (Jones et de Jersey) Herbst. Anderson and Anderson 1984, p. 55, figs. 5, 6.

Dejerseya lobata (Jones et de Jersey) Herbst. Anderson and Anderson 1985, pl. 198, figs. 5, 6.

Dejerseya lunensis (Johnston) Anderson et Anderson. Anderson and Anderson 1989, p. 257, figs. 1–35; p. 258, figs. 1–6; p. 259, figs. 1–8; pl. 139; pl. 140, figs. 1–7; pl. 141–154. (Anderson and Anderson [1989] published the combination *D. lunensis* [Johnston] Anderson et Anderson [see nomenclatural remarks on this name]. Anderson and Anderson [1989] assigned all *Dejerseya* specimens from the Triassic of South Africa to “*D. lunensis*.” On the basis of the arguments presented below, we regard these specimens as verified records of *D. lobata*.)

Dicroidium odontopteroides (Morris) Gothan. Boucher et al. 1993, figs. 2–4.

Dejerseya lunensis (Johnston) Anderson et Anderson. Anderson and Anderson 2003, p. 186, figs. 1–15; p. 187, figs. 1–6.

Dejerseya lunensis (Johnston) Anderson et Anderson. Gnaedinger and Herbst 2004, figs. 1, 4a–4c, 4e.

Dejerseya lunensis (Johnston) Anderson et Anderson. Scott et al. 2004, fig. 2c.

Possible records requiring further study. The following specimens are potentially referable to *D. lobata*, although it is impossible to confirm or refute the identification on the basis of available evidence.

Pecopteris caudata Johnston. Johnston 1886, p. 373. (Not illustrated [see nomenclatural remarks].)

Pecopteris lunensis. Johnston 1894, pl. 1, figs. 5–7. (Identification remains doubtful because of the limited information

on macromorphology and cuticle features [see nomenclatural remarks].)

Pecopteris caudata Johnston. Johnston 1896, fig. 4. (Even though the lobed to serrated leaf appears superficially similar to some *Dejerseya* specimens, an assignment to *Dejerseya* remains questionable because of the lack of further information on macromorphology and cuticular details.)

Incertae sedis cf. *Hoegia antevsiana*. Gnaedinger and Herbst 1998a, fig. 13a, 13b. (These specimens may represent fragments of large *Dejerseya* leaves with asymmetrically subtriangular lobes and complex venation similar to some specimens figured here [figs. 3E, 3J, 5A].)

Dejerseya lobata (Jones et de Jersey) Herbst. Spalletti et al. 2007, fig. 6f. (The single specimen described is fragmented and poorly preserved and does not show sufficient features for a confident assignment on genus level.)

Excluded records. The following specimens are regarded as being distinct from *D. lobata*.

Dejerseya lunensis (Johnston) Anderson et Anderson. Anderson and Anderson 1989, pl. 140, figs. 8, 9. (We suggest that this specimen represents an entire-margined *Dicroidium* frond [Townrow 1967, figs. 1d, 2e, 3b].)

Dejerseya lobata (Jones et de Jersey) Herbst. Gnaedinger and Herbst 1998b, fig. 1; pl. 1, figs. a, b. (Specimens are pinnate to bipinnatifid and are therefore better interpreted as *Pachydermophyllum* leaves [e.g., *Pachydermophyllum praecordillerae* and *P. sp. indet.*: Retallack 1983], fragments of large-leaved *Dicroidium* fronds [e.g., *Dicroidium dubium*: see Retallack 1980], or sterile frond portions of *Rienitsia* [e.g., *Rienitsia arrondiana*: see Herbst 1977].)

Dejerseya lobata (Jones et de Jersey) Herbst. Gnaedinger and Herbst 2004, figs. 2, 4d, 4f–4g. (The figured fronds are pinnate, bipinnatifid to bipinnate; we suggest that this material more likely represents leaves of *Pachydermophyllum* [e.g., *P. praecordillerae* and *P. sp. indet.*: Retallack 1983], fragments of large-leaved *Dicroidium* fronds [e.g., *D. dubium*: see Retallack 1980], or sterile frond portions of *Rienitsia* [e.g., *R. arrondiana*: see Herbst 1977].)

Cf. *Dejerseya* sp. Gnaedinger and Herbst 2004, figs. 3a–3f, 5a–5d. (Specimens are pinnate to bipinnatifid with contracted pinna bases; we suggest this material likely represents sterile frond portions of marattialean fronds, such as *Rienitsia* [Herbst 1977] or *Symopteris* [Kustatscher et al. 2011].)

Emended specific diagnosis. Petiolate or sessile, oblong to elliptical, straight to strongly curved, simple entire-margined to pinnatifid to partly pinnate leaves of up to ~25 cm length; degree of lobing usually decreasing toward the apex; lobes rounded, asymmetrically subtriangular, or tongue shaped; secondary veins arising at acute angles, curving away from midrib; veins in each lobe forming a dense, fan-shaped to pinnate group; veins between lobes absent or inconspicuous and dividing less frequently. Leaves chartaceous with moderately thick cuticle; adaxial cell pattern more or less homogeneous; abaxial epidermis with costal fields of longitudinally aligned, elongated cells; cuticle smooth or with a single, small, solid papilla per cell. Leaves amphistomatic; most stomata occurring in intercostal fields of abaxial leaf surface; fewer stomata occurring above midrib and basal portions of secondary veins on adaxial leaf surface; stomata surrounded by an incomplete to complete ring of 4–8 superficial subsidi-

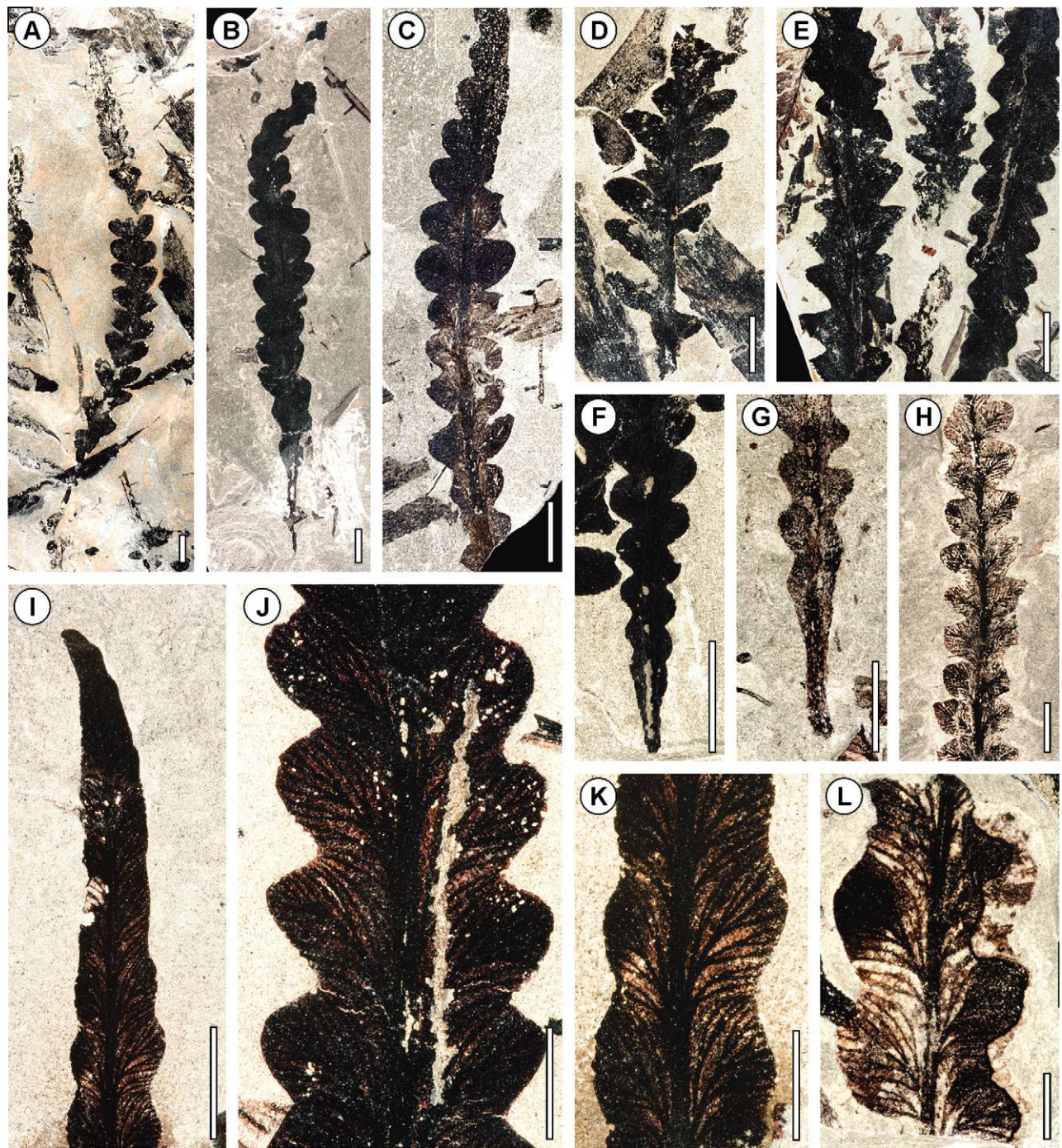


Fig. 3 Compressions of *Dejerseyia lobata* (Jones et de Jersey) Herbst emend. nov. from the Upper Triassic of Mt. Falla, Queen Alexandra Range, East Antarctica. *A*, Complete leaf showing the variation in the degree lobing across the leaf length. T5-74. *B*, Complete, irregularly lobed leaf with curved apical segment. T7-170. *C*, Basal to apical portion of a leaf; note prominent midrib. T5-41. *D*, Middle portion of a leaf with relatively wide lobes, resulting in a rather elliptical leaf shape. T5-112. *E*, Three leaves; note asymmetrically subtriangular lobes of the specimen on left. T7-175. *F*, Basal portion of a leaf with well-developed laminar wings fringing the basal part of the rachis. T5-101. *G*, Basal portion of a leaf with markedly swollen base. T7-162. *H*, Middle portion of a leaf; specimen figured by Boucher et al. (1993, fig. 2). T7-171. *I*, Apical leaf portion showing the decrease of lobing toward the apex. T5-122. *J*, Detail of a middle leaf portion under alcohol immersion to highlight the venation pattern; note pinnate to fan-shaped vein clusters in the lobes and weakly developed venation between the lobes. T7-175. *K*, Detail of a more apical leaf portion under alcohol immersion to highlight the venation pattern; note pinnate to fan-shaped vein clusters in the lobes and weakly developed venation between the lobes. T5-122. *L*, Partially degraded leaf fragment under alcohol immersion; note well-developed callus formations along margin-feeding traces on right-hand side. T5-46b. Scale bars = 1 cm (*A-I*), 5 mm (*J-L*).

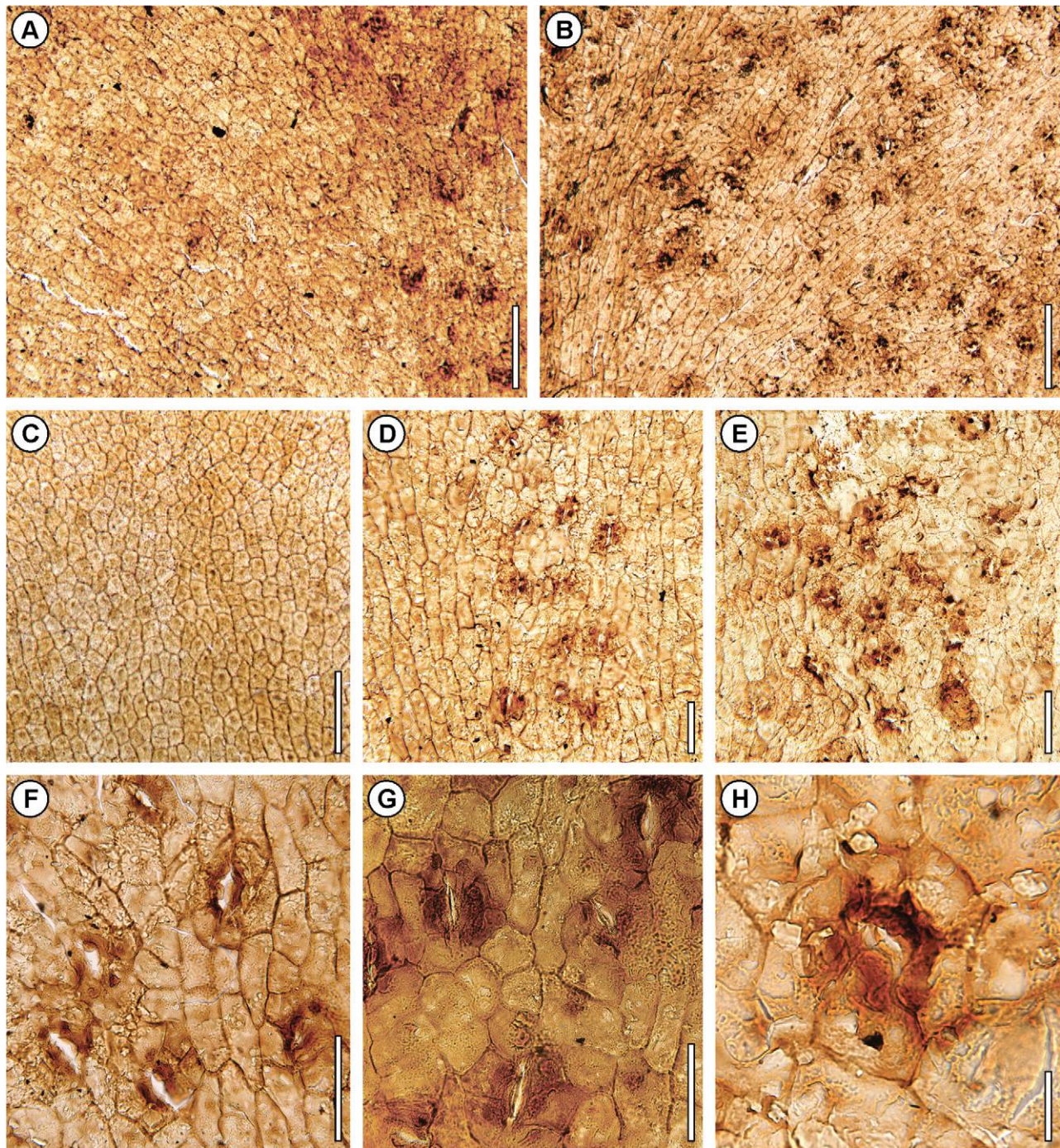


Fig. 4 Cuticles of *Dejerseyea lobata* (Jones et de Jersey) Herbst emend. nov. from the Upper Triassic of Mt. Falla, Queen Alexandra Range, East Antarctica. *A*, Cuticle of adaxial leaf surface showing a few stomata above midrib and basal portion of secondary veins (right). T5-145, slide 24066. *B*, Cuticle of abaxial surface of the same leaf portion, showing differentiation into costal fields below vein courses and intercostal fields with abundant stomata. T5-145, slide 24066. *C*, Detail of cuticle of adaxial leaf surface, showing the rather homogeneous cell pattern and papillae. T5-145, slide 24055. *D*, Detail of cuticle of abaxial leaf surface with longitudinally oriented stomata between two vein courses. T5-145, slide 24063. *E*, Detail showing a group of stomata in an intercostal field of the abaxial leaf surface. T5-145, slide 24070. *F*, Detail of stomata in intercostal field of the abaxial leaf surface. T5-145, slide 24056. *G*, Detail of stomata in intercostal field of the abaxial leaf surface. T5-145, slide 24053. *H*, Detail of a stomatal complex; note partially overarched, solid papillae on subsidiary cells. T5-145, slide 24063. Scale bars = 250 μm (*A-C*), 100 μm (*D, E*), 50 μm (*F, G*), 25 μm (*H*).

ary cells; subsidiary cells equally or more extensively cutinized than surrounding epidermal cells, generally with a single solid papilla positioned close to and in some cases overarch- ing the stomatal pit; guard cells moderately sunken, weakly cutinized, with prominent stomatal ledges.

Material. Four hundred and thirty-six specimens on the following 84 slabs: T5-38-42, 44-49, 52, 53, 55-58, 60-67, 69, 70, 74, 77, 81-84, 87-90, 92-97, 99, 100, 103, 104, 106, 107, 109, 110, 112, 114, 117-120, 122, 124, 129, 131, 133-135, 138, 143, T7-161, 162-168, 170, 171, 174, 175, 182, 185, 196, 197, 199.

Description. Simple to partly pinnate leaves, generally 12-20 cm, in some cases up to 25 cm long (fig. 3A-3C); generally of oblong shape and ~2 cm wide (length : width ratio ~12 : 1), in a few cases elliptical and up to ~5 cm wide (fig. 3D). Leaves straight or curved at an angle of up to 30° (fig. 3A). Leaf base swollen (fig. 3G); leaves either petiolate with petioles comprising about one-tenth of the leaf length (fig. 3A, 3B) or with the basal part of the rachis fringed by a narrow, decurrent laminar wing on each side (fig. 3F, 3G). Leaf margin generally entire to pinnatifid; most leaves in the present assemblage having alternate, rounded to asymmetrically subtriangular, more or less distinct lobes in basal and central leaf portions (fig. 3A-3C, 3E, 3H, 3J), progressively fusing toward the apex to form an undulating to eventually entire-margined, narrow tongue-shaped apical segment (fig. 3A, 3I); a few elliptical, partly pinnate leaves with particularly well-developed, long pinnae in central leaf portions (fig. 3D). Midrib prominent (fig. 3C, 3H, 3I-3L), projecting from abaxial leaf surface, dichotomizing shortly before reaching the leaf apex. Secondary veins generally departing at acute angles, curving away from midrib, dichotomizing repeatedly; in lobed leaf portions, secondary venation forming a fan-shaped to pinnate cluster in each lobe, and veins being less dense

and dividing less frequently between the lobes (figs. 3I-3L, 5A-5D). Leaves chartaceous, with lamina and cuticle being thicker than those of co-occurring fern fronds and about equally thick as those of co-occurring *Dicroidium* fronds and *Heidiphyllum* leaves.

Leaves amphistomatic (fig. 4A, 4B). Abaxial epidermal cell pattern differentiated into costal and intercostal fields (fig. 4B); adaxial epidermal cell pattern more or less homogeneous (fig. 4A, 4C). Costal fields with longitudinally aligned, elongate-rectangular to spindle-shaped epidermal cells oriented parallel to vein course (fig. 4B, 4D); intercostal fields with almost isodiametric-polygonal to elongate-rectangular cells (fig. 4B, 4E-4G). Anticlinal walls straight or slightly curved, with smooth, thin, and even cuticle flanges (fig. 4F-4H). Cuticle of periclinal walls of regular epidermal cells smooth (fig. 4G) or with a single papilla per cell (fig. 4A-4C, 4F); papillae positioned centrally or offset toward one end, solid, small, and 15-20 μm in diameter (fig. 4A-4C). Majority of stomata concentrated between vein courses on abaxial leaf surface (fig. 4B, 4D, 4G), with only a few stomata above midrib and secondary veins on adaxial surface (fig. 4A, right). Guard cells moderately sunken, weakly cutinized with well-developed stomatal ledges (fig. 4G, 4H), surrounded by an incomplete to complete ring of 4-8, usually 4-6, specialized subsidiary cells (fig. 4F-4H); subsidiary cells superficial, equally or more extensively cutinized than regular epidermal cells, and usually bearing a large, solid, cylindrical to clavate papilla close to and generally overarch- ing the stomatal pit (fig. 4F-4H). Stomatal pits oval to spindle shaped, in many cases oriented more or less parallel to adjacent vein courses (fig. 4D, 4F-4H).

Nomenclatural remarks. On the basis of several specimens from the Triassic of Tasmania that were originally described as *P. lunensis* Johnston (Johnston 1894), Anderson

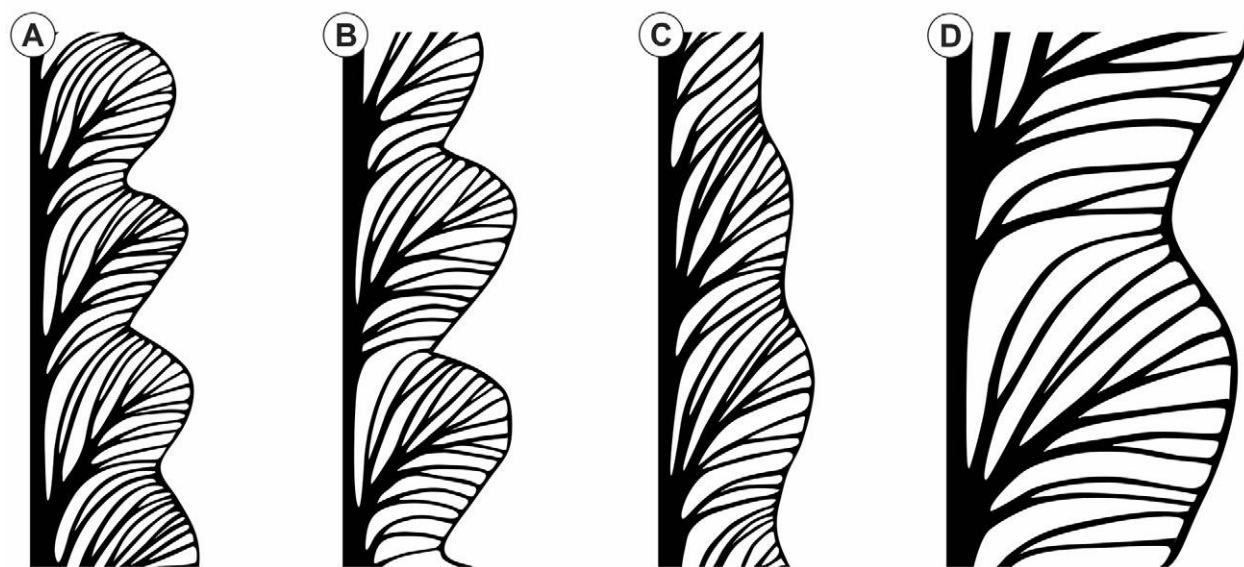


Fig. 5 Venation patterns in *Dejerseya lobata* (Jones et de Jersey) Herbst emend. nov. from the Upper Triassic of Mt. Falla, Queen Alexandra Range, East Antarctica. Note pinnate to fan-shaped vein clusters within the lobes and weakly developed venation between the lobes. A, Drawn after specimen T7-175 (fig. 3f). B, After specimen T5-124. C, After specimen T5-122 (fig. 3I, 3K). D, After specimen T5-46b.

and Anderson (1989) introduced the name *D. lunensis* (Johnston) Anderson et Anderson and considered *D. lobata* and *D. incisa* as junior synonyms of this taxon. The precise affinities of the leaves figured by Johnston (1894; pl. I, figs. 5–7) remain unknown, but the gross morphology appears to differ from *Dejerseyia* in several important aspects. The leaves are considerably smaller (~7–9 cm long), have entire, simple margins that are “never incised or lobed” (Johnston 1894, p. 170), and have rather abruptly tapering basal leaf portions. Epidermal and cuticular details, which could clarify the identification of this material, are not preserved. The individual specimens can therefore equally be interpreted as isolated *Rienitsia* pinnae (see Walkom 1932), *Linguifolium* leaves (see Retallack 1980 [figs. 7f–7h], 1981 [fig. 9a]), or entire-margined *Dicroidium* fronds (see Townrow 1967, figs. 1d, 2e, 3b). As a result, we consider *P. lunensis* Johnston and *D. lunensis* (Johnston) Anderson et Anderson to be nomina dubia and exclude them from consideration. Thus, the name *D. lobata* has priority and is adopted here for this species.

Another problematic name for possibly similar leaves is *P. caudata* Johnston (Johnston 1886, 1896). The species was poorly defined, and no illustrations were given in the original account (Johnston 1886). Although several of the described features are reminiscent of *Dejerseyia*, it remains unclear from the description whether these leaves are simple or forming part of bipinnatifid/bipinnate fronds. The subsequent illustration of an additional fragment from another Tasmanian locality is rather sketchy and shows little features apart from leaf outline (Johnston 1896). The material is no longer available for further study.

Comparisons. *Dejerseyia lobata* shares many individual characters with other foliage morphotaxa from the Mesozoic of the Southern Hemisphere, most notably with *Linguifolium* Arber emend. Retallack, *Pachydermophyllum* Thomas et Bose, and *Rintoulia* McLoughlin et Nagalingum (table 1). The combination of the simple to partly pinnate leaf morphology, weakly developed venation between lobes, and papillate subsidiary cells distinguishes *D. lobata* from these taxa.

Other Mesozoic gymnosperm leaves that are broadly similar to *Dejerseyia* belong to *Lepidopteris* Schimper emend. Townrow, *Scytophyllum* Bornemann, and *Kurtziana* Frenguelli emend. Petriella et Arrondo. The cuticles of certain *Lepidopteris* species—for example, *Lepidopteris stormbergensis* (Seward) Townrow and *Lepidopteris langlohisensis* Anderson et Anderson—appear to be almost identical to those of *Dejerseyia*, differing only in the more buttressed anticlinal walls or the more prominent development of papillae, respectively (Townrow 1960; Anderson and Anderson 1989; Bomfleur and Kerp 2010). Pinnatifid and partly pinnate *Dejerseyia* leaves may also bear a superficial resemblance to those representatives of the peltasperm leaf *Scytophyllum* that produce confluent pinna bases, such as *Scytophyllum apoldense* (Compter) Linnell, *Scytophyllum argentinum* (Frenguelli) Morel et al., *Scytophyllum austroafricanum* Anderson and Anderson, and *Scytophyllum pinnatum* (Sixtel) Dobruskina (Dobruskina 1969, 1975; Anderson and Anderson 1989; Kustatscher et al. 2007; Morel et al. 2010). Although the epidermal and cuticular features of *Dejerseyia* and *Scytophyllum* may in some cases be almost indistinguishable (Morel et al.

2010), however, *Scytophyllum* leaves are easily delimited by their characteristic venation, in which the secondary and tertiary veins do not reach the leaf margin but end blindly within the lamina (Dobruskina 1969, 1975; Morel et al. 2010). In general, *Kurtziana* can be well distinguished by its pinnate architecture and subcordate, more or less symmetrical pinna bases (Frenguelli 1942; Petriella and Arrondo 1982; Artabe et al. 1991; Artabe and Stevenson 1999). In addition, the guard cells in *Kurtziana* are deeply sunken in epistomatal chambers formed by multiple rows of neighboring cells (Artabe et al. 1991; Artabe and Stevenson 1999). In this context, it needs to be pointed out that the “*Kurtziana* generic concept” of Anderson and Anderson (2003) is somewhat misleading, since it encompasses fronds showing asymmetrical pinnae with contracted acroscopic margins and decurrent basicopic margins, all features that are instead typical of *Pachydermophyllum* (Artabe et al. 2007b).

Genus—*Matatiella* Anderson et Anderson emend. nov.
Bomfleur, E. Taylor, T. Taylor, Serbet, Krings et Kerp

Type. *Matatiella rosetta* Anderson et Anderson (selected in Anderson and Anderson 2003).

Emended generic diagnosis. Ovulate organ consisting of more or less straight central axis bearing pedunculate, primarily fan- to shield-shaped megasporophylls; megasporophyll lamina palmately divided into three to six radiating ovuliferous lobes, each lobe bearing a single ovule on lower (inner) surface; ovule free, anatropous, near-circular to ovate in compression, with up to three longitudinal ridges. Micropylar canal funnel shaped, more or less straight; nucellus attached only at chalazal end; seed unwinged.

Remarks. *Matatiella* was instituted on a limited number of compressions from the Upper Triassic Molteno Formation in South Africa (Anderson and Anderson 2003). Additional specimens, which were previously interpreted as peltasperm reproductive organs with some reservation, are known from New Zealand and Chile (Retallack 1981, 1983; Pole and Raine 1994; Nielsen 2005). The type species *M. rosetta* Anderson et Anderson has only recently been reported from the Upper Triassic of the Ischigualasto Basin, Argentina (Arce and Lutz 2010).

Interpretation of some of the features of *Matatiella*, including the arrangement and symmetry of megasporophylls and the position of the ovules, has remained problematic. The newly identified Antarctic material described here provides additional information that helps to clarify some of these aspects and allows us to emend the original generic diagnosis.

1. Megasporophyll arrangement in *Matatiella* was described as helical (Anderson and Anderson 2003), but it cannot be determined with certainty at present whether the arrangement is helical or pinnate, although the (sub)opposite position in many of the specimens may rather be indicative of a pinnate architecture (fig. 6A, 6E).

2. The megasporophyll lamina of *Matatiella* has been interpreted as being bilaterally symmetrical (Anderson and Anderson 2003). This is in contrast to some of the three-lobed specimens in the present collection that appear to show a radial symmetry (fig. 6F). We suggest that the apparent symmetry of these organs is of little diagnostic relevance and exclude this information in the proposed emendation.

Table 1

Comparison of *Dejerseya Herbst* emend. nov. with Selected Mesozoic Gymnosperm Leaf Morphogenera

	Leaf architecture	Leaf margins	Venation	Leaf substance	Stomata distribution	Papillae	Guard cells
<i>Dejerseya</i> Herbst emend. nov. ¹⁻⁴	Simple to partly pinnate	Entire, undulating to pinnately lobed to partly pinnate	Secondary venation fan shaped to pinnate within lobes or pinnae; absent or weakly developed between lobes	Chartaceous with moderately thick cuticle	Weakly amphistomatic; most stomata in intercostal fields of lower leaf surface; few stomata above midvein on upper leaf surface	Usually present on subsidiary cells; frequent on other epidermal cells	Moderately sunken
<i>Linguifolium</i> Arber emend. Retallack ^{3,5-7}	Simple	Entire	Lateral veins forking once, in few cases twice	Membranaceous with thin cuticle	Amphistomatic	Absent	Superficial
<i>Pachydermophyllum</i> Thomas et Bose ^{3,7-10}	Pinnate	Pinna margins entire, undulating to lobed, basally decurrent	Each pinna with a distinct midvein; lateral veins forking once, in few cases twice	Coriaceous with thick cuticle	Weakly amphistomatic; most stomata in intercostal fields of lower leaf surface	Usually present on subsidiary cells or encircling cells; common on other epidermal cells	Deeply sunken
<i>Rintoulia</i> McLoughlin et Nagalingum ^{2,10}	Pinnate	Pinnae fully sessile, with entire margins	Pinnate, with central vein extending about halfway into the lamina	Membranaceous with thin cuticle	Weakly amphistomatic; most stomata in intercostal fields of lower leaf surface	Prominent on subsidiary cells; otherwise absent	Deeply sunken
<i>Lepidopteris</i> Schimper emend. Townrow ^{3,11-13}	Pinnate to bipinnate, with intercalary pinnules	Pinna margins entire, undulating to lobed	Each pinnule with a distinct central vein and sparsely forking lateral veins	Chartaceous to coriaceous with moderately thick cuticle	Variably amphistomatic	Usually prominent on subsidiary cells; rare to common on other epidermal cells	Moderately sunken
<i>Scytophyllum</i> Bornemann emend. Linnell ^{3,14-16}	Pinnate to bipinnate	Pinna margins entire, undulating to lobed, pinnae cordate, basally decurrent, or confluent	Each pinna with a distinct midrib; higher-order venation pinnate with blindly ending veinlets	Coriaceous with thick cuticle	Weakly amphistomatic; most stomata in intercostal fields of lower leaf surface	Usually present on subsidiary cells; frequent on other epidermal cells	Deeply sunken
<i>Kurtziana</i> Frenguelli emend. Petriella et Arrondo ¹⁷⁻²⁰	Pinnate	Pinnae sessile with cordate base; pinna margins entire	Pinnae with distinct midrib; lateral veins forking repeatedly	Coriaceous with thick cuticle	Weakly amphistomatic; most stomata in intercostal fields of lower leaf surface	Subsidiary cells with or without papillae	Deeply sunken in epistomatal chambers

Sources. 1, Jones and de Jersey 1947; 2, Douglas 1969; 3, Anderson and Anderson 1989; 4, this study; 5, Arber 1917; 6, Retallack 1980; 7, Retallack 1983; 8, Thomas and Bose 1955; 9, Retallack 1981; 10, McLoughlin et al. 2002; 11, Thomas 1933; 12, Townrow 1960; 13, Stanislawsky 1976; 14, Dobruskina 1969; 15, Dobruskina 1975; 16, Morel et al. 2010; 17, Frenguelli 1942; 18, Petriella and Arrondo 1982; 19, Arrabe et al. 1991; 20, Arrabe and Stevenson 1999.

3. The number of ovuliferous lobes in *Matatiella* has previously been thought to be either four or six. The majority of the present specimens, however, bear three lobes.

4. Ovule attachment to the megasporophylls has been ambiguously interpreted as being either abaxial or adaxial; the type species, *M. rosetta*, was reconstructed with ovules borne on the upper (i.e., outer) surface (Anderson and Anderson 2003, p. 172, fig. 1). Lateral compressions in the present material and in some South African specimens (Anderson and Anderson 2003, pl. 50, fig. 1; pl. 51, fig. 1; pl. 52, fig. 3), however, clearly demonstrate that the ovules of *Matatiella* were borne on the lower (inner) surface of the ovuliferous lobes. This is further substantiated by isolated megasporophylls in dorsiventral compression; in these specimens, portions of the ovules lie below the partly dégaged lamina of the ovuliferous lobe (fig. 6F, 6H).

5. Cuticle preservation in the present material makes it possible to characterize the ovule and seed morphology of *Matatiella* in greater detail. The two features included in the emendation are the more or less straight, funnel-shaped micropylar canal and the nucellus-integument attachment only at the chalazal end.

Comparisons. The taxon that is most closely comparable to *Matatiella* is *Andersonia rastroensis* Arce et Lutz, an ovulate organ that was only recently described on the basis of a single specimen from the Upper Triassic of Argentina (Arce and Lutz 2010). The main differences between the two taxa are that the megasporophylls of *A. rastroensis* are reduced to just a single ovuliferous lobe and that the micropylar canal in *Andersonia* ovules is prominently elongated (Arce and Lutz 2010).

Matatiella is similar to the peltasperm ovulate organs *Peltaspermum* Harris emend. Townrow and *Autunia* Krasser emend. Kerp. In *Peltaspermum*, megasporophylls are usually peltate and radially symmetrical and bear a ring of five to possibly 25 pendant seeds (Townrow 1960; Gomankov and Meyen 1979; Naugolnykh and Kerp 1996; Naugolnykh 2001). *Autunia* differs from *Matatiella* in its usually fan-shaped, entire lamina and in bearing only two seeds per megasporophyll (Kerp 1982, 1988).

Superficially similar, coeval seed-fern ovulate organs—such as *Umkomasia* Thomas emend. Klavins et al., *Fanerotheca* Frenguelli, and *Petriella* Taylor et al.—can be readily distinguished from *Matatiella* in having ovules borne in more or less prominently developed cupulate structures (Holmes 1987; Anderson and Anderson 2003; Taylor and Taylor 2009). Moreover, corystosperm ovules and seeds, including *Feruglioa* Frenguelli and those of *Umkomasia*, differ from those of *Matatiella* in bearing typically curved, bifid micropylar extensions or prominent lateral wings (Klavins et al. 2002; Anderson and Anderson 2003; Artabe et al. 2007b; Barale et al. 2009).

Karibacarbon problematicum Lacey emend. Lacey is an enigmatic ovulate organ from the Triassic of Zimbabwe that consists of very large (up to 5.5 cm wide), stalked, fan-shaped and recurved, supposedly multiovulate megasporophylls (Lacey 1976). *Karibacarbon feistmantelii* Holmes et Ash, a much smaller species, was described from the Lower Triassic of the Lorne Basin, New South Wales (Holmes and Ash 1979). Isolated, empty cupules assigned to *Karibacarbon* are commonly split open, forming flattened star-shaped struc-

tures with 5–9 lobes that may bear superficial resemblance to isolated *Matatiella* megasporophylls (Walkom 1932, pl. 5, figs. 3–5; Holmes and Ash 1979, figs. 5, 6). Also, the co-occurring dispersed seeds of *K. feistmantelii* appear similar to those of *Matatiella* in many respects, although they are two to three times larger. The interpretation and the systematic placement of *Karibacarbon* remain uncertain at present; although both species were proposed to be transferred to *Umkomasia* Thomas emend. Holmes (Holmes 1987), several authors have noted that *Karibacarbon* may be better interpreted as a peltaspermalean organ (Retallack 1977, 1983; Klavins et al. 2002; Taylor et al. 2006) similar to *Autunia*.

Species—*Matatiella dejerseyi* Bomfleur, E. Taylor, T. Taylor, Serbet, Krings et Kerp sp. nov. (Figs. 6, 7)

1969 seeds: Douglas, p. 22; pl. 3, figs. 3, 4; text figs. 1, 8; 1, 10; 1, 11.

? 2005 *Antevsia* (?) sp.: Nielsen, p. 556, fig. 6 (2).

? 2006 *incertae sedis*: Barale et al., fig. 17.

Specific diagnosis. Ovulate organ composed of more or less straight central axis bearing pedunculate megasporophylls; megasporophyll laminae palmately dissected into 3–4 radiating, recurved ovuliferous lobes; each ovuliferous lobe obovate, oblanceolate, or spatulate with broadly rounded or truncated apex in dorsiventral view; widened distal portion of ovuliferous lobe with two longitudinal ribs, more or less convex, bearing a single recurved ovule on adaxial (inner) surface; ovule/seed free, anatropous, oblate-ellipsoid to flattened-ovoid, rounded or broadly truncated at chalazal end, tapering to conical apex, bearing 1–3 more or less prominent longitudinal ridges. Micropylar canal funnel shaped, short, more or less straight; chalaza slightly offset toward adaxial side; nucellus attached only at chalazal end.

Holotype (hic designatus). Specimen T5-63c in the University of Kansas Paleobotanical Collections.

Additional material. Six specimens on the following slabs: T5-56, T7-166, 182, 184, 185, 195, T-6139a; cuticle preparations on slides 24058–60, 24072, 24077, 24078, 24082, 24085.

Repository. Division of Paleobotany, Natural History Museum and Biodiversity Institute, University of Kansas, Lawrence.

Etymology. The specific epithet *dejerseyi* is chosen in honor of Noel J. de Jersey for his great contributions toward a better knowledge of Gondwanan paleobotany and palynology.

Type locality. Mount Falla, Queen Alexandra Range, central Transantarctic Mountains.

Stratigraphic occurrence. Middle part of the Falla Formation (profile F2, level 14 of Barrett 1969), Beacon Supergroup.

Age. Carnian or Norian (early or middle Late Triassic).

Description. Fragments of lax ovulate organs, presumably of narrow-ovate to narrow-lanceolate shape, at least 25 mm long and up to ~18 mm wide (fig. 6A, 6E). Central axis 1.5–2 mm wide, straight or slightly undulating, bearing pedunculate megasporophylls attached generally (sub)oppositely and at angles between 60° to almost 90° (fig. 6A–6E); megasporophyll peduncles 6–8 mm long, straight or slightly curving away from main axis (fig. 6A–6C, 6E); megasporo-

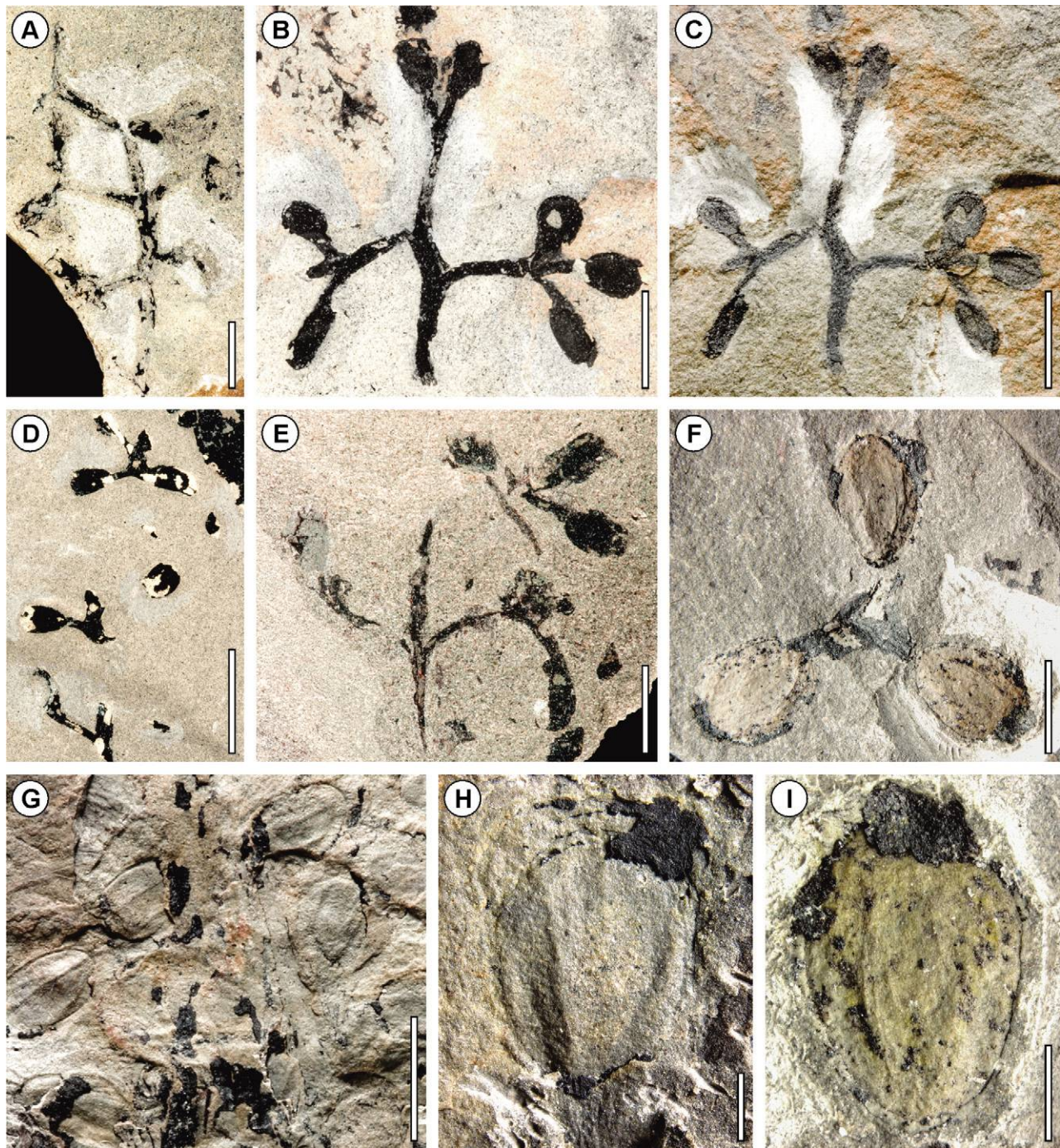


Fig. 6 *Matatiella dejerseyi* sp. nov. from the Upper Triassic of Mt. Falla, Queen Alexandra Range, East Antarctica. **A**, Fragmented ovulate organ showing (sub)opposite arrangement of at least six megasporophylls. T7-184b. **B**, Holotype specimen under alcohol immersion showing gross morphological features. T5-63a. **C**, Holotype specimen under oblique lighting showing three-dimensional features. T5-63a. **D**, Fragmented specimen consisting of linearly arranged, detached megasporophyll fragments. T7-166. **E**, Fragmented specimen showing opposite attachment of megasporophylls. T5-63c. **F**, External view of a detached, three-lobed megasporophyll with degauged ovules underneath the lobes. T-6139a. **G**, Cluster of isolated ovules/seeds with longitudinal ridges; note well-developed impression of outer sarcotesta in specimen at upper right. T5-056a. **H**, Recurved ovule with longitudinal ridges, partially degauged through lamina of the overlying ovuliferous lobe. T5-56. **I**, Recurved ovule with longitudinal ridges, partially degauged through lamina of the overlying ovuliferous lobe. T-6139a. Scale bars = 5 mm (A–C, E, G), 1 cm (D), 2.5 mm (F), 1 mm (H, I).

phylls heads measuring 8–12 mm in diameter, palmately dissected into usually three, in some cases four ovuliferous lobes (fig. 6B–6F); lobes obovate, oblanceolate, or spatulate with broadly rounded or truncated apices (fig. 6B–6F, 6H); widened distal portions of ovuliferous lobes more or less convex, usually with two prominent longitudinal ribs on abaxial (outer) surface (fig. 6C) and with a single, recurved ovule on adaxial (inner) surface (fig. 6C, 6E, 6F); ovule/seed free, anatropous, oblate-ellipsoid to flattened-ovoid, 3.5–5 mm long and 2.5–3.5 mm wide, rounded or broadly truncated at chalazal end, tapering to a conical apex, bearing 1–3 more or less prominent longitudinal ridges (fig. 6F–6I).

Cuticle of inner integument well developed, enclosing an ovoid cavity with a blunt or rounded base (fig. 7A, 7B) and a short, generally straight micropylar canal at the distal end (fig. 7C); cuticle thin, smooth, with hexagonal and elongated cells $\sim 100 \mu\text{m}$ long (fig. 7A–7C); micropylar canal funnel shaped, at least 200 μm long, tapering to a width of $\sim 125 \mu\text{m}$ (fig. 7C), with irregularly thickened cuticle and indistinct cell outlines (fig. 7D); chalaza slightly laterally offset, being attached near the base of one side of the ovule (fig. 7A); nucellus free and attached only at the chalazal end, poorly preserved in the form of a more or less clearly delimited, circular to elliptical dark area containing granular organic material (fig. 7A, 7B).

Micropylar canal in some of the specimens containing clusters of pollen grains (fig. 7C, 7D); pollen bisaccate, between $70 \mu\text{m} \times 40 \mu\text{m}$ and $80 \mu\text{m} \times 50 \mu\text{m}$ (fig. 7D). Corpus outline more or less circular in equatorial view, about half as wide as the entire grain; cappa not markedly thickened; distal surface with a sharply defined, irregular longitudinal sulcus $\sim 10\text{--}15 \mu\text{m}$ wide (fig. 7D). Sacci elliptical to crescentic in polar view, with poorly preserved endoreticulations (fig. 7D).

Remarks. Douglas (1969) described undetermined seeds and seed cuticles from a deposit with abundant *D. lobata* in Victoria, Australia. The specimens agree in almost every respect with the present material; the only difference is that individual cells of the inner integument of the Australian cuticles may, in very few cases, each bear an isolated small, papilla-like projection. We regard this feature as being of only limited diagnostic significance and include the material figured and described by Douglas (1969) in *Matatiella dejerseyi*. A dispersed cuticle fragment of a four-lobed megasporophyll that we tentatively interpret as belonging to *M. dejerseyi* has been described from a cuticle-bearing peat deposit in the Upper Triassic of the Zambesi Valley, northern Zimbabwe (Barale et al. 2006). This specimen agrees in all observable features with the present material; stomatal organization has been described to be “identical to that of *Lepidopteris* sp.,” that is, with 5–6 papillate subsidiary cells surrounding a pair of sunken guard cells (Barale et al. 2006, p. 94).

In addition, an apparently three-lobed *Matatiella* megasporophyll comparable to those of *M. dejerseyi* has been reported as *Antevsia* (?) sp. from the Triassic Santa Juana Formation, Chile (Nielsen 2005). This specimen differs in its slightly larger size (diameter of $\sim 15 \text{mm}$) and in the less spreading and less divided ovuliferous lobes.

Comparisons. The main distinguishing characters of *M. dejerseyi* are the relatively large size of the ovules/seeds and the dissection of the megasporophyll laminae into three to

rarely four ovuliferous lobes. Five species of *Matatiella* have previously been described, that is, *M. rosetta* Anderson et Anderson, *Matatiella hemirosetta* Anderson et Anderson, *Matatiella sessilis* Anderson et Anderson, *Matatiella reducta* Anderson et Anderson, and *Matatiella courmanei* (Pole et Raine) Anderson et Anderson (Anderson and Anderson 2003). The number of specimens that these species are based on is very small, and it is difficult at present to estimate the reliability of diagnostic features in these taxa. We assume that problems have arisen mainly from incomplete knowledge about the natural variability and the developmental stages of these organs. Natural variability is most obviously manifested in the varying numbers of ovuliferous lobes per megasporophyll, even within an individual specimen. For instance, the type species of the genus, *M. rosetta*, has been described as bearing essentially six-lobed megasporophylls. By contrast, even the holotype specimen appears to bear at least two megasporophylls that are only four-lobed (Anderson and Anderson 2003, p. 174, fig. 2). Adding to this problem is that megasporophylls appear different in lateral preservation than in dorsiventral preservation; it is often difficult to determine the number of ovuliferous lobes when part of a laterally compressed megasporophyll may still be embedded in the matrix. Other diagnostic characters are largely dependent on the developmental stages of the organs. For instance, one of the discriminating features of *M. sessilis* is the presence of two aborted ovules, as seen in the holotype specimen (Anderson and Anderson 2003). It can be assumed, however, that this feature is of very limited diagnostic significance, since aborted ovules also occur commonly in other species (Anderson and Anderson 2003, p. 174, fig. 2).

As a result, we recognize only three groups of species that can be relatively well delimited from one another: (1) one group characterized by megasporophylls that are deeply dissected into generally six or (in fewer cases) four ovuliferous lobes, including *M. rosetta*, *M. courmanei*, and *M. reducta* from South Africa, New Zealand, and Argentina; (2) one group comprising megasporophylls that are only moderately divided into usually six ovuliferous lobes, including *M. hemirosetta* and *M. sessilis* from South Africa; and (3) one group with megasporophylls dissected into only three or rarely four lobes, being represented by *M. dejerseyi* from Antarctica. We suspect that this latter group may also include the undetermined megasporophylls that have been reported to occur with *Dejerseyia* in the Upper Triassic Ipswich Coal Measures, Queensland, Australia (Anderson and Anderson 1989 [p. 258, fig. 7], 2003 [p. 183, fig. 2]). Detailed comparisons, however, remain difficult, since this latter material has not yet been adequately described or figured.

If found dispersed, the bisaccate pollen grains in the micropyles of some *Matatiella* seed cuticles would probably be best accommodated in the dispersed pollen genus *Falcisporites* Leschik emend. Klaus, on the basis of the sharply delimited sulcus and the relatively coarse saccus reticulations (Balme 1970, 1995).

Genus—*Townrovia* Retallack

Type. *Townrovia petasata* (Townrow) Retallack (selected by Retallack [1981]).



Fig. 7 Seed cuticles of *Matatiella dejerseyi* sp. nov. from the Upper Triassic of Mt. Falla, Queen Alexandra Range, East Antarctica. *A*, Cuticle of inner integument with enclosed nucellus cuticle attached only at the base; note the chalaza being slightly displaced toward one side of the ovule. T5-145, slide 24059. *B*, Cuticle of inner integument with poorly preserved remains of nucellus cuticle inside. T5-145, slide 24072. *C*, Apical portion of inner integument cuticle with preserved micropylar canal containing pollen grains. T5-145, slide 24058. *D*, Detail of micropylar canal cuticle containing bisaccate, nontaeinate pollen grains with well-delimited distal longitudinal sulcus. T5-145, slide 24058. Scale bars = 500 μm (*A*–*C*), 50 μm (*D*).

Basionym. *Pteruchus petasatus* Townrow.

Remarks. The little-known genus *Townrovia* was erected for pinnate pollen organs with simple microsporophylls, each bearing ~20 unilocular, clavate pollen sacs attached in sev-

eral irregular rows along an elongate, median receptacle; stomata are sunken and overarched by subsidiary cell papillae, and the contained pollen is of the *Falcisporites* type (Retallack 1981; Balme 1995). In a taxonomic sense, the genus occupies

a small niche within a group of morphologically similar but largely unrelated late Paleozoic–Mesozoic pollen organs, including the peltasperm taxa *Permotheca* Zalessky and *Antevsia* Harris emend. Townrow, the corystosperm taxon *Pteruchus* Thomas emend. Townrow, and the ginkgoalean *Stachyopitys* Schenk emend. Kirchner et van Konijnenburg-van Cittert. On the basis of a combination of morphological features, epidermal anatomy, and pollen morphology, the genera can be reasonably well delimited from one another (table 2).

Species—*Townrovia polaris* Bomfleur, E. Taylor, T. Taylor, Serbet, Krings et Kerp sp. nov. (Figs. 8, 9)

Diagnosis. Pollen organ borne on a terminal, covered reproductive bud. Fertile axis straight or curved, smooth, slender, bearing simple microsporophylls composed of a straight peduncle and an elongate, enlarged terminal receptacle; ~15–20 pollen sacs attached to each receptacle in two or more irregular rows; pollen sacs ellipsoidal to clavate, unilocular, spreading in compression. Pollen sac cuticle membranaceous. Pollen grains bisaccate, nontaeinate; sacchi more or less inclined distally, narrow-elliptical to crescentic in polar view, with coarse reticulations; corpus outline circular to narrow-elliptical in polar view, about half as wide as the entire grain; distal surface with a broad longitudinal sulcus.

Holotype (hic designatus). Specimen T5-103b in the University of Kansas Paleobotanical Collections; counterparts of the holotype specimen preserved on fragments T5-103c–f; cuticle and pollen from the holotype material obtained from fragments T5-103c and d are prepared on microscope slides 24041–47.

Repository. Division of Paleobotany, Natural History Museum and Biodiversity Institute, University of Kansas, Lawrence.

Etymology. The specific epithet *polaris* (Latin *polus* = pole) refers to the paleogeographic occurrence in polar latitudes at 70°–75°S during the Triassic.

Type locality. Mt. Falla, Queen Alexandra Range, central Transantarctic Mountains.

Stratigraphic occurrence. Middle part of the Falla Formation (profile F2, level 14 of Barrett 1969), Beacon Supergroup.

Age. Carnian or Norian (early or middle Late Triassic).

Description. Pollen organ arising from a terminal reproductive bud borne on an ~2-mm-long lateral short shoot (fig. 8A–8D). Bud bulbous, 8 mm long and up to ~5 mm wide, with a scaly cover layer lacking cuticle and discernible venation (fig. 8D). Fertile axis apparently pinnate, 2 mm wide at the base and at least 27 mm long, gently curved, tapering only slightly toward the apex (fig. 8A, 8B), with a smooth surface and well-preserved cuticle showing strongly elongated, spindle-shaped epidermal cells with gently curved anticlinal walls; individual epidermal cells of fertile axis more than 300 μm long; stomata absent (fig. 8E). At least six simple microsporophylls attached irregularly to axis, opposite to alternate, at angles between 45° in the basal portion and 70° in the apical portion (fig. 8A, 8B); each microsporophyll composed of an up to 3-mm-long, straight peduncle with straight or helical striations and an elongate, enlarged, terminal receptacle up to 4 mm long (fig. 8A, 8B, 8F). Approximately 20 pollen sacs attached laterally to one surface

of each receptacle in two or more irregular rows, radiating to form an oval, stellate outline in dorsiventral compression (fig. 8F); pollen sacs unilocular, ellipsoidal to clavate, ~2 mm long by ~0.8 mm wide, with an evenly rounded apex and a small circular apical aperture (fig. 8F, 8G); surface of pollen sacs bearing faint, straight longitudinal striations (fig. 8G).

Pollen sacs with membranaceous cuticle showing longitudinal folds, containing clusters of pollen grains (fig. 9A). Pollen grains bisaccate, measuring between 70 μm \times 45 μm and 95 μm \times 65 μm in polar view (fig. 9B–9E). Corpus outline circular to narrow-elliptical in polar view, at least half as wide as the entire grain; cappa not markedly thickened; distal surface with a broad, irregular longitudinal sulcus (fig. 9B–9E). Sacchi narrow-elliptical to crescentic in polar view, with poorly preserved endoreticulations (fig. 9B–9E).

Remarks and comparisons. Pollen morphology in *T. polaris* is variable. The corpus outline ranges from circular to narrow-elliptical, and the outline of the sacchi may be either continuous (fig. 9E) or markedly discontinuous (fig. 9C, 9D) with the corpus outline. These morphologies correspond to the rather broadly defined dispersed taxon *Falcisporites australis* (de Jersey) Stevens (Balme 1970, 1995; Stevens 1981), which has also been documented to occur in other peltaspermalean (Retallack 2002) and corystospermalean pollen organs (Osborn and Taylor 1993; Balme 1995; Yao et al. 1995).

Townrovia polaris differs from the type species *T. petasata* primarily in having much smaller pollen sacs, that is, only up to 2 mm long as opposed to 3–4 mm long in *T. petasata* (Townrow 1965; Retallack 1981). On the basis of gross morphology, *T. polaris* is indistinguishable from *Stachyopitys lacrisporangia* Anderson et Anderson from the Triassic Molteno Formation, South Africa (Anderson and Anderson 2003). *Stachyopitys*, however, is a ginkgoalean pollen organ. Hence, it should be assumed that *S. lacrisporangia* contains simple, monocolpate ginkgoalean pollen referable to the dispersed genera *Cycadopites* Wodehouse, *Ginkgocycadophytus* Samoilovitch, or *Entylissa* Naumova emend. Potonié et Kremp (Balme 1995; Zhou 2009) and not bisaccate *Falcisporites*-type pollen, as in the present material. On the basis of the great similarity of the two pollen organs, however, we anticipate that in situ pollen analyses of the type material of *S. lacrisporangia* will demonstrate that it is also a peltasperm organ containing bisaccate pollen.

Co-occurring Gymnosperm Foliage

Order—*Voltziales*

Family—*Incertae sedis*

Species—*Heidiphyllum elongatum*
(Morris) Retallack (Fig. 10A, 10B)

Material. Three hundred and forty-six specimens on the following 75 slabs: T5-39–42, 44–53, 55–60, 63–67, 69–71, 74, 77, 80, 82, 85, 87, 88, 90, 93–97, 99, 100, 103, 105, 107, 109, 110, 112, 114, 118–120, 122, 124, 129, 130, 133–135, 138, 142, 143; T7-161, 163–166, 168, 174, 175, 179, 182, 199.

Description. Strap-shaped leaves exceeding 180 mm in length by up to 18 mm width; tapering evenly toward the base

Table 2

Comparison of *Townrovia* Retallack with Selected Permian and Triassic Pollen Organ Genera

	<i>Townrovia</i> Retallack ¹⁻³	<i>Pernotheca</i> Zalesky ⁴⁻⁹	<i>Antetisia</i> Harris emend. Townrow ^{5,10-15,26}	<i>Pteruchus</i> Thomas emend. Townrow ^{5,16-23}	<i>Stachyopitys</i> Schenk emend. Kirchner et van Konijnenburg-van Cittert ^{5,17,24-27}
Order	Peltaspermales	Peltaspermales	Peltaspermales	Corystospermales	Ginkgoales
Basal bud	Present	Absent	Absent or present ²⁶	Absent	Present (?)
Main axis	Slender, smooth	Thick, woody	With characteristic blisterlike swellings	Slender, smooth	Slender, smooth
Architecture	Simple, irregularly pinnate	Simple, microsporophylls arranged in single helix	Bipinnate with complex second-order branching	Variable; microsporophylls helically arranged	Irregular laterals with one to several orders of complex branching
No. pollen sacs	~20	4-9	3-12	~2.5-240	3-~10
Pollen sacs	Clavate	Fusiform	Fusiform	Fusiform	Fusiform to clavate
Pollen sacs attached to	Elongate receptacle	Pedicel	Pedicel	Flattened laminar head	Pedicel
Pollen sacs attached in	2-3 irregular rows	Fascicles	Fascicles	Multiple irregular rows	Fascicles
Pollen	Bisaccate monocolpate (<i>Falcisporites</i> type)	Bisaccate monocolpate (<i>Falcisporites</i> type)	Simple monocolpate (<i>Cycadopites</i> type)	Bisaccate monocolpate (<i>Falcisporites</i> type)	Simple monocolpate (<i>Cycadopites</i> type)
Subsidiary cells	Papillate	?	Papillate	Nonpapillate	?
Selected species	<i>T. petasata</i> (Townrow) Retallack <i>T. polaris</i> sp. nov.	<i>P. sardytkensis</i> Zalesky <i>P. disparis</i> (Zalesky) Naugolnykh <i>P. helbyi</i> Retallack	<i>A. zeilleri</i> (Nathorst) Harris <i>A. prynadae</i> Stanislavsky <i>A. mazenodensis</i> Anderson et Anderson ... (?) cf. <i>A. sp.</i> Retallack ²⁸	<i>P. africanus</i> Thomas emend. Townrow <i>P. dubius</i> Thomas emend. Townrow <i>P. foimstonii</i> (Feistmantel) Townrow <i>P. fremouuwensis</i> Yao et al. <i>P. barrealeensis</i> (Frenguelli) Holmes et Ash <i>P. septentrionalis</i> Kirchner et Mueller <i>P. sp.</i> Axsmith et al.	<i>S. preslii</i> Schenk <i>S. edwardsii</i> (Thomas) Townrow ^{18,19} <i>S. wettsteinii</i> (Krasser) Zhou ^{27,32} <i>S. anuboides</i> Frenguelli <i>S. venustus</i> Schweitzer et Kirchner <i>S. matatiranus</i> Anderson et Anderson <i>S. gypsianthus</i> Anderson et Anderson ... (?) <i>S. lacrisporangia</i> Anderson et Anderson ²⁶

Sources. 1, Townrow 1965; 2, Retallack 1981; 3, this study; 4, Zalesky 1929; 5, Balme 1995; 6, Naugolnykh and Kerp 1996; 7, Naugolnykh 1998; 8, Krassilov et al. 1999; 9, Retallack 2002; 10, Nathorst 1908; 11, Antevs 1914; 12, Harris 1932; 13, Harris 1937; 14, Townrow 1960; 15, Stanislavsky 1976; 16, Thomas 1933; 17, Townrow 1962; 18, Holmes and Ash 1979; 19, Holmes 1987; 20, Kirchner and Müller 1992; 21, Yao et al. 1995; 22, Axsmith et al. 2000; 23, Frenguelli 1944; 24, Kirchner and van Konijnenburg-van Cittert 1994; 25, Schweitzer and Kirchner 1995; 26, Anderson and Anderson 2003; 27, Zhou 2009; 28, Retallack 1985; 29, Shirley 1898; 30, Petriella 1980; 31, Jain and Delevoryas 1967; 32, Kräusel 1943.

Note. Selected species meeting all above-mentioned criteria are here considered as valid; other species, here considered of questionable generic placement, are marked by a question mark and are discussed in more detail in the text.

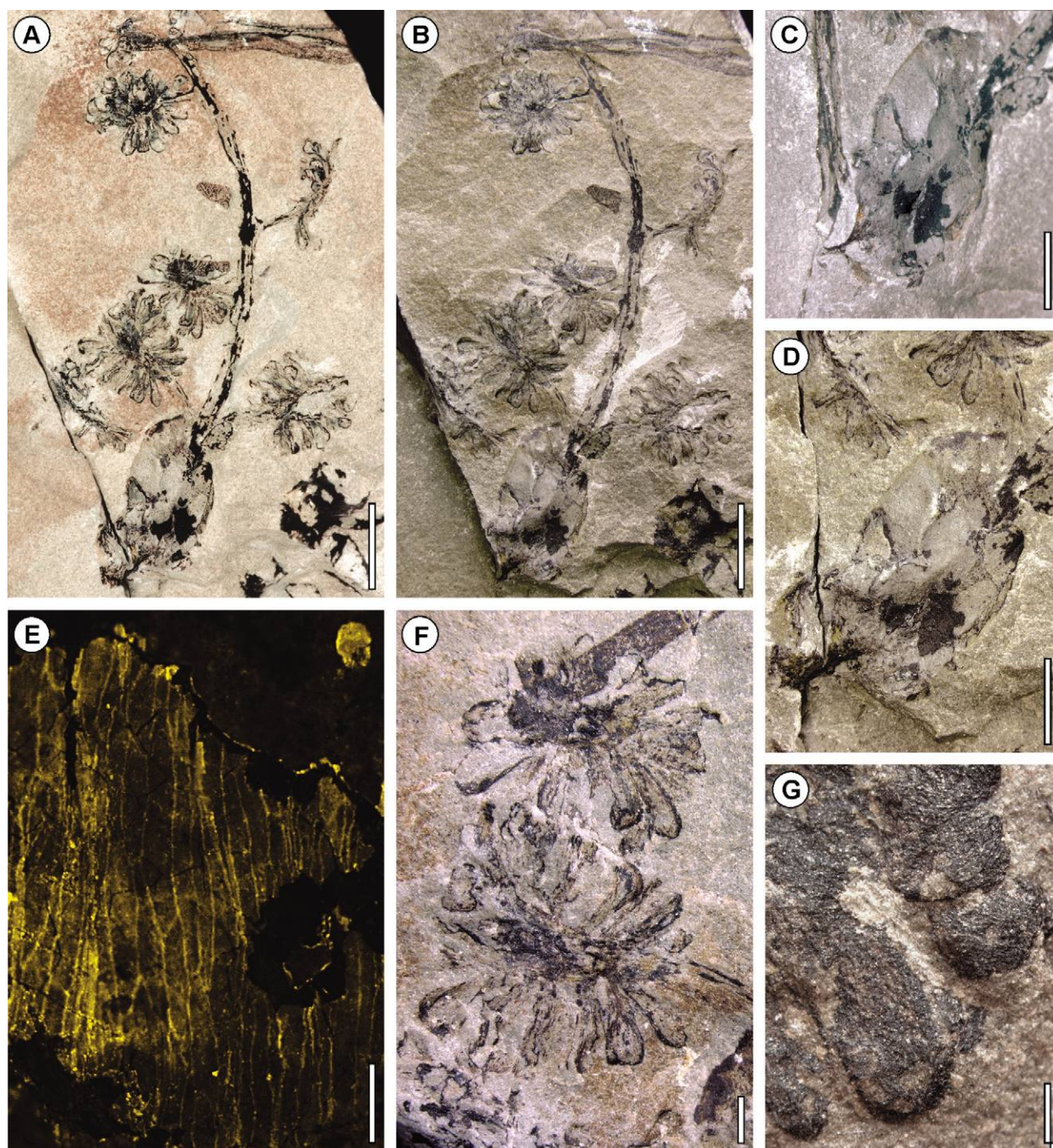


Fig. 8 *Townrovia polaris* sp. nov. from the Upper Triassic of Mt. Falla, Queen Alexandra Range, East Antarctica. Holotype specimen T5-103b. *A*, Specimen under alcohol immersion. T5-103b. *B*, Specimen under oblique lighting; note that the rock fragment in lower left of *A* is here removed, with the rock having split along the main axis to which the short shoot is attached. T5-103b. *C*, Oblique-angle detail showing connection between main axis (left) and short shoot (toward right). T5-103b. *D*, Detail of short shoot and terminal, covered reproductive bud. T5-103b. *E*, Cuticle of main axis of the pollen organ under UV epifluorescence, showing strongly elongated, spindle-shaped epidermal cells; note the dispersed bisaccate pollen grain in top right corner. T5-103b. *F*, Detail showing pollen sacs attached to an elongate median receptacle. T5-103b. *G*, Detail of pollen sacs with fine striations and porelike distal openings. T5-103c. Scale bars = 5 mm (*A*, *B*), 2.5 mm (*C*, *D*), 100 μ m (*E*), 1 mm (*F*), 500 μ m (*G*).

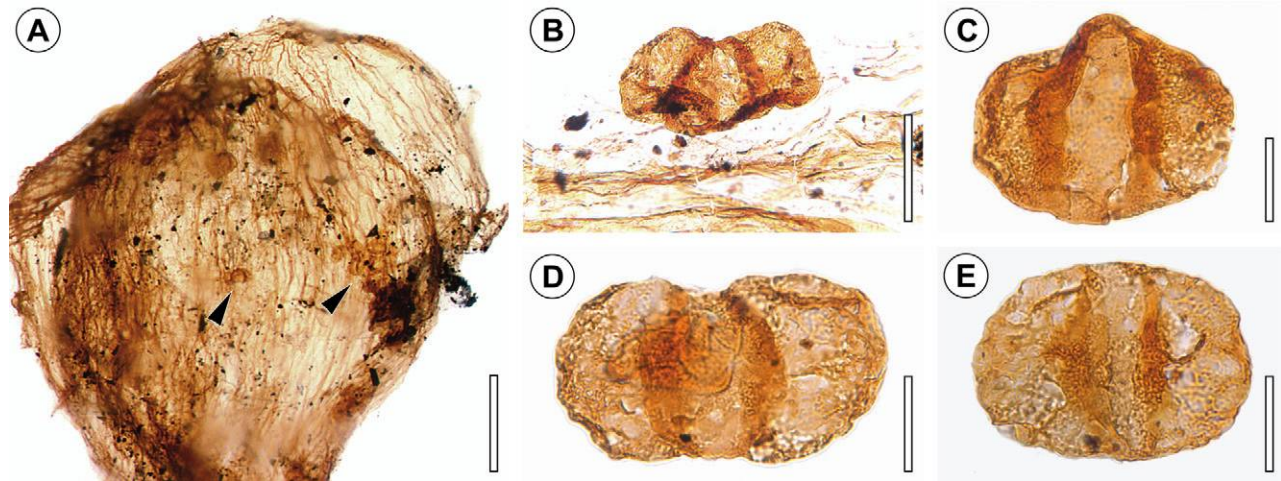


Fig. 9 Pollen sac cuticles and in situ pollen of *Townrovia polaris* nov. sp. from the Upper Triassic of Mt. Falla, Queen Alexandra Range, East Antarctica; material isolated from counterparts of the holotype specimen. *A*, Delicate pollen sac cuticle containing bisaccate pollen grains (arrowheads). T5-103c, slide 24047. *B*, Detail of a pollen grain attached to pollen sac cuticle. T5-103d, slide 24044. *C*, Isolated pollen grain showing well-delimited, irregular longitudinal distal sulcus. T5-103d, slide 24041. *D*, Isolated pollen grain with clearly demarcated saccus outlines in polar view. T5-103d, slide 24041. *E*, Isolated pollen grain with continuous, elliptical outline in polar view. T5-103d, slide 24041. Scale bars = 250 μm (*A*), 50 μm (*B*), 25 μm (*C*–*E*).

and more abruptly toward the apex; apex obtuse or rounded; several veins entering leaf base, dichotomizing within lower third, forming a total of 8–12 veins running parallel into leaf apex (fig. 10A, 10B).

Remarks. The material consists of accumulations of well-preserved, usually complete leaves covering individual bedding surfaces. Cuticles of some of the present specimens have been described by Axsmith et al. (1998).

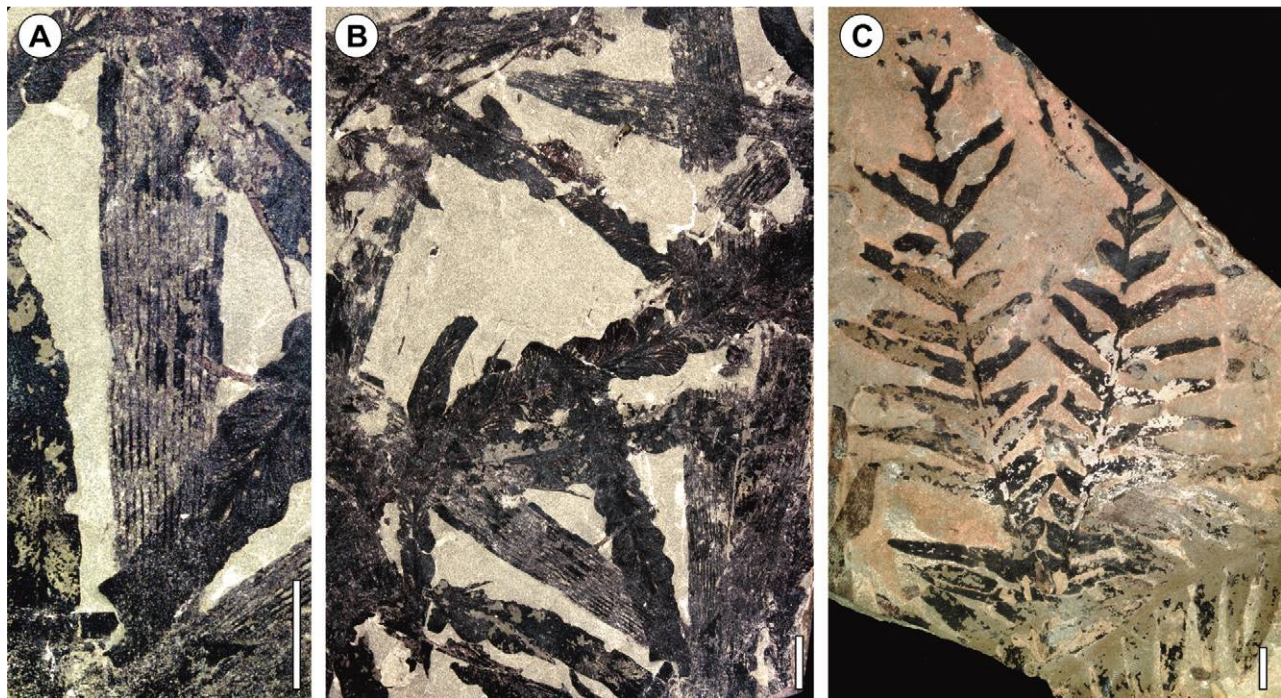


Fig. 10 Co-occurring gymnosperm foliage in the Late Triassic plant fossil assemblage from Mt. Falla, Queen Alexandra Range, East Antarctica. *A*, *Heidiphyllum elongatum* (Morris) Retallack. T5-58. *B*, Mat of partially overlapping leaves of *Heidiphyllum elongatum* (Morris) Retallack and *Dejerseya lobata* (Jones et de Jersey) Herbst emend. nov. T5-58. *C*, *Dicroidium lancifolium* (Morris) Gothan; parts of several individual fronds. T5-38.

Order—*Corystospermales*
 Family—*Corystospermaceae*
 Species—*Dicroidium lancifolium*
 (Morris) Gothan (Fig. 10C)

Material. One hundred and two specimens on the following 57 slabs: T5-38, 39, 42, 49–52, 56, 57, 61–64, 66, 69, 71, 72, 74–77, 79–81, 84, 87–98, 94, 103, 105, 108–110, 113, 114, 116, 120, 125, 127, 131, 139; T7-162, 163, 166, 167, 173, 174, 176, 178, 180, 182, 194, 197–199.

Description. Fronds up to ~25 cm long, pinnate, bifurcated within the basal portion at an angle between 15° and 55°; resulting frond portions asymmetrically lanceolate to elliptic (fig. 10C). Pinnules opposite to subopposite, sessile, separate, inserted at angles of ~80° in basal portion to down to ~30° near apex, elongate tongue shaped, up to 5 cm long and generally less than 1 cm wide, entire-margined, in few cases with weakly developed basal lobes; basal pinnules and interior pinnules above bifurcation less elongated or ear shaped; apical pinnules gradually fusing to form pinnatifid terminal segments (fig. 10C). Venation alethopteroid with prominent midvein persisting up to near pinnule apex; secondary veins dense, arising at acute angles between 25° and 45°, curving only slightly away from midvein, dichotomizing one to several times. Lamina chartaceous.

Remarks. The specimens were previously described by Boucher et al. (1993), including cuticle and epidermal features. Boucher et al. (1993) also recognized another species, *Dicroidium dubium* (Feistmantel) Gothan, in the Mt. Falla assemblage; this taxon has been described as differing from

D. lancifolium in having slightly lobed pinnules and less distinct subsidiary cells (Boucher et al. 1993). However, we regard these minor differences as falling within the range of intraspecific variability and consequently also include the few specimens with slightly lobed pinnule margins within *D. lancifolium*.

Several authors regard *D. lancifolium* as a synonym of either *Dicroidium odontopteroides* (Townrow 1957; Anderson and Anderson 1983) or *D. dubium* (Bomfleur and Kerp 2010). *Dicroidium odontopteroides* can be delimited from the present material on the basis of its smaller pinnules, odontopteroid venation, and characteristic papillae and trichomes (Townrow 1957; Bomfleur and Kerp 2010). We separate the present material from *D. dubium* because of the consistent frond morphology; all fronds of our material are characterized by slender, strongly elongate tongue-shaped pinnules and generally entire to only slightly lobed pinnule margins. By contrast, *D. dubium* generally has less elongate and more distinctly lobed pinnules (Anderson and Anderson 1983).

Discussion

Evidence for Reconstruction

We reconstruct the *Dejerseyia lobata* leaves, *Matatiella dejerseyi* ovulate organs, and the pollen organ *Tounrovia polaris* as belonging to one natural plant species (fig. 11). This is based mainly on the co-occurrence data in the present plant fossil assemblage. In general, caution should be taken when interpreting co-occurrences of plant fossils, because a variety of



Fig. 11 Suggested partial reconstruction of the new peltaspermalean pteridosperm from the Upper Triassic of Mt. Falla, Queen Alexandra Range, East Antarctica, including the ovulate organ *Matatiella dejerseyi* sp. nov. (left), a foliated axis with leaves of *Dejerseyia lobata* (Jones et de Jersey) Herbst emend. nov. (center), and the pollen organ *Tounrovia polaris* sp. nov. (right).

taphonomic biases may have affected the composition of plant fossil assemblages (Scheiing and Pfefferkorn 1984; Ferguson 1985; Greenwood 1991; Gastaldo 1992). Nevertheless, in the case of the present collection from Mt. Falla, we argue that there is good evidence to regard the co-occurrence data as reliable criteria for affiliating individual organs.

We interpret the plant fossil assemblage from Mt. Falla as a (par)autochthonous compression assemblage that formed under quiescent conditions mainly by accumulation of local leaf litter. This is evidenced by (1) high concentrations of overlapping, usually complete, petiolate gymnosperm leaves on individual bedding surfaces in the form of leaf mats; (2) commonly random horizontal orientation of leaves and axes; (3) similar degradational state of leaves on individual bedding surfaces; (4) the extremely low diversity of the assemblage; (5) the remarkable scarcity of cryptogams among foliage taxa (<2%); (6) the rarity of attached plant organs and of (intact) reproductive organs as a result of predominantly non-traumatic loss of plant parts; and (7) abundant occurrence of in situ rooting structures (Burnham 1990; Behrensmeyer and Hook 1992; Burnham et al. 1992; Gastaldo 1992; Ferguson et al. 1999; Ferguson 2005). In a few cases, minor transport may be indicated by a preferred directional orientation of some of the leaves and axes on certain bedding planes; sorting is evident only in the formation of small-scale seed accumulations on some sedimentary surfaces. Long-distance transport can be excluded, however, because the individual seeds are generally well preserved, with delicate micropylar extensions still intact (Ferguson 2005; Gee 2005).

The collection comprises a total of 901 leaves and 17 more or less intact reproductive organs (dispersed seeds not included). Given this comparatively large sample size and the parautochthonous character of the assemblage, we assume that the collection gives a fairly accurate depiction of the local vascular plant vegetation at this site during the time of deposition (see Burnham et al. 1992). The entire suite of recovered plant organs allows us to identify three natural gymnosperm taxa and one filicalean fern. The gymnosperms include (1) a pteridosperm represented by the *D. lobata* foliage, *M. dejerseyi* ovulate organs, and the pollen organ *T. polaris* described herein (fig. 11); (2) a voltzialean conifer with *Heidiphyllum elongatum* foliage, *Telemachus elongatus* Anderson emend. Escapa et al. seed cones, and *Switzianthus* sp. Bomfleur et al. pollen cones (Taylor and Taylor 1988; Yao et al. 1993; Axsmith et al. 1998; Escapa et al. 2010; Bomfleur et al. 2011); and (3) a corystosperm represented by *Dicroidium lancifolium* fronds, *Umkomasia* sp. ovulate organs, and dispersed seeds (Taylor and Taylor 1988; Boucher et al. 1993; this study).

The affiliation of *Matatiella* and *Townrovia* in particular is further supported by in situ pollen analyses, since the pollen grains occurring in the micropylar canals of *Matatiella* seed cuticles are similar to those extracted from *Townrovia* pollen sacs. This is no criterion for exclusion, however, because similar *Falcisporites*- and *Alisporites* s.l.-type pollen is known to have also been produced by a wide array of other Triassic gymnosperms, including corystosperms and voltzialean conifers (Yao et al. 1993; Balme 1995).

Some of the aerial axes in the collection bear short shoots of varying sizes. One particular type of short shoot bears

small, transverse-elliptical leaf scars of 1–2 mm diameter. These scars are distinctly smaller than the leaf bases of *D. lancifolium* and *H. elongatum* but correspond well with the morphology and dimensions of the leaf bases of *D. lobata*. Hence, there is some evidence that *Dejerseyia* leaves were borne on short shoots analogous to extant *Ginkgo biloba* L. or the Late Triassic *Dicroidium* plant from the Ipswich Coal Measures, Queensland, Australia (Anderson et al. 2008).

Assignment to the Peltaspermales

We assign the new pteridosperm plant from Mt. Falla to the Peltaspermales because each of the individual organs known so far shows the greatest correspondence with well-established peltasperm taxa.

Matatiella was assigned its order of seed ferns, the Matatiellales, by Anderson and Anderson (2003) on the basis of the assumption that *Matatiella* was fundamentally different from peltasperm organs in exhibiting bilateral symmetry. However, peltasperm ovulate structures, including *Peltaspermum*, may in some cases have bilaterally symmetrical megasporophylls (Harris 1937; Townrow 1960; Gomankov and Meyen 1979; Kerp 1982, 1988; Karasev 2009). Given the natural variation in the material studied, we suggest that the apparent symmetry should not be emphasized in classifying this group of ovulate organs. By contrast, we propose that the essential features characterizing *Matatiella* are the (1) primarily fan- to shield-shaped megasporophylls (depending on the point of attachment of the peduncle), (2) radiating arrangement of recurved ovules on the lower (inner) megasporophyll surface, and (3) freely developing ovules/seeds that are not enclosed in cupulate structures. With regard to these features, *Matatiella* is essentially similar to the peltasperm genera *Peltaspermum* and *Autunia*. In all three taxa, seeds are borne naked on the lower surface of pedunculate, variably lobed or dissected, fan- to shield-shaped megasporophylls that are attached to a main axis in either helical or pinnate arrangement to form a rather lax reproductive organ (Harris 1937; Townrow 1960; Kerp 1982; Naugolnykh and Kerp 1996; Anderson and Anderson 2003; Taylor et al. 2006). Moreover, the megasporophyll laminae in some *Peltaspermum* species—such as *Peltaspermum calycinum* Wang et Wang, *Peltaspermum incisum* Prynada emend. Stanislavsky, *Peltaspermum lobulatum* Wang et Wang, *Peltaspermum martinsii* (Kurtze) Poort et Kerp, and *Peltaspermum monodiscum* Anderson et Anderson—may be deeply lobed to incised (Solms-Laubach 1884; Stanislavsky 1976; Wang and Wang 1989; Anderson and Anderson 2003; Arce and Lutz 2010). Hence, the main characters distinguishing *Matatiella* from *Peltaspermum* are the further reduction of the megasporophyll lamina and the comparatively small number of ovules or seeds per megasporophyll.

Further evidence for a peltasperm affinity of *Matatiella* comes from the affiliated foliage. Until now, the only leaf morphotaxon that has been related to *Matatiella* is *Pachydermophyllum* (Retallack 1981, 1983; Pole and Raine 1994), including the specimens referred to as *Kurtziana* by Anderson and Anderson (2003; see Artabe et al. 2007b). *Pachydermophyllum* has been interpreted as a peltasperm leaf based in part on leaf morphology and epidermal anatomy (Retallack

1977, 1981). The cuticle features of *Dejerseya* are also essentially similar to those of some well-known peltasperm leaves, especially to some representatives of *Lepidopteris* and *Scyto-phyllum* (Townrow 1960, 1965; Dobruskina 1969; Bomfleur and Kerp 2010; Morel et al. 2010; table 1).

Even though little is known about the pollen organs of this group of plants, the few specimens that have been found in association with *Matatiella* have been assigned to the peltasperm taxa *Townrovia* and *Anteusia* (Retallack 1981; Pole and Raine 1994). *Townrovia* has been interpreted as a peltaspermalean organ because it bears sunken stomata and a complete ring of papillate subsidiary cells; both features are typical for peltasperms and do not occur in the otherwise similar corytosperms (Retallack 1981). Furthermore, the type species *Townrovia petasata* occurs together exclusively with peltasperm leaves, that is, *Lepidopteris* and *Pachydermophyllum* (Townrow 1965; see Retallack 1981; Anderson and Anderson 1989).

This complement of evidence together with the affiliation in the present assemblage provides a solid basis to reconstruct *D. lobata*, *M. dejerseyi*, and *T. polaris* as a representative of a previously unrecognized group of peltasperms. We adopt the family name Matatiellaceae (Anderson and Anderson 2003) for these plants.

Paleoenvironment and Paleoecology of the Mt. Falla Assemblage

The present collection of plant fossils is characterized by an unusual composition that is so far unique among Gondwanan megafossil floras (fig. 12). Even though no detailed sedimentological data of the plant-bearing section at Mt. Falla are available, the description of Barrett (1969) together with the large sample size allow for a tentative reconstruction of the paleoenvironmental setting of this flora.

The fossiliferous interval at Mt. Falla (profile F2, level 14 of Barrett 1969) is a thick package of overbank mudstones that accumulated in a poorly drained flood basin under more or less constant, low-energy sediment input. Interbedded sandstone sheets likely represent punctual events of more proximal crevasse-splay sedimentation into the floodplain (Behrensmeyer and Hook 1992). The presence of coaly intercalations may reflect intervals of peat accumulation under water-logged conditions in a paludal or lacustrine environment (Behrensmeyer and Hook 1992). Notable soil formation and peat accumulation, however, occurred only sporadically. We speculate that this may have been due to constant, albeit low-energy input of fine-grained sediment, which probably hampered the establishment of more diversified plant communities.

The majority of fossils are abscised, complete gymnosperm leaves that were accumulated on individual bedding surfaces. Cryptogams account for only <2% of the foliar remains. These attributes are characteristic of an (par)autochthonous leaf litter assemblage that derived mainly from local deciduous vegetation (Burnham et al. 1992; Ferguson et al. 1999; Ferguson 2005). The foliage assemblage is dominated by *D. lobata* (48.4%), followed by *H. elongatum* (38.4%) and *D. lancifolium* (11.3%; fig. 12). *Dejerseya* and *Heidiphyllum* generally occur together in greater numbers, whereas *Dicroidium* fronds occur in many cases on bedding surfaces on which other taxa are rare or absent. This may indicate that

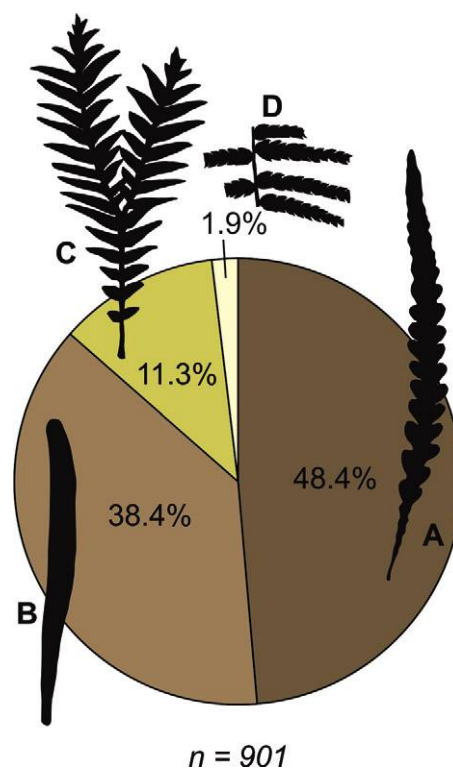


Fig. 12 Systematic composition of foliage taxa in the Late Triassic plant fossil assemblage from Mt. Falla, Queen Alexandra Range, East Antarctica. A, *Dejerseya lobata* (Jones et de Jersey) Herbst emend. nov. B, *Heidiphyllum elongatum* (Morris) Retallack. C, *Dicroidium lancifolium* (Morris) Gothan. D, Undetermined filicalean fern.

the leaf litter composition reflects small-scale vegetational patterns, with reduced intermixing of leaves from local sources (Burnham et al. 1992).

Heidiphyllum elongatum has been reconstructed as a shrubby conifer that commonly formed monodominant thickets in poorly drained, possibly peat-forming floodplain environments in southeastern Gondwana (Gabites 1985; Cairncross et al. 1995; Anderson et al. 1998; Bomfleur and Kerp 2010). A close association between *Heidiphyllum* and matatiellacean peltasperms has also been reported from the Molteno Formation, South Africa (Anderson and Anderson 2003), and the Tivoli Formation, eastern Australia (S. McLoughlin, personal communication, 2011). Although evidence for reconstructions is sparse, there is general agreement that many Triassic peltasperms were spreading, shrub- or small tree-sized understory plants (Townrow 1960; Retallack 1977; Anderson and Anderson 1989, 2003). The Middle Triassic Antarctic *Dicroidium* plants, by contrast, have been reconstructed as 20–30-m-tall forest trees with a *Ginkgo*-like habit based on anatomically preserved organs in Triassic permineralized peat deposits from Fremouw Peak (Taylor 1996; Taylor et al. 2006). Many Antarctic *Dicroidium* plants are supposed to have grown in better-drained floodplain areas or on levees fringing channel margins (Cúneo et al. 2003; Bomfleur and Kerp 2010). Taken together, we therefore envisage the Mt. Falla flora as a semimature, low-diversity wetland community that colonized a poorly drained floodplain

setting and consisted mainly of low-growing, deciduous peltasperms and voltzialean conifers, with some emergent *Dicroi-dium* trees on slightly elevated, better-drained spots and with a filiclean fern forming a monotonous herbaceous understory.

It is interesting to note that palynological samples from strata directly underlying the plant-bearing beds at Mt. Falla have yielded diverse microfloras with more than 40 taxa of dispersed spores and pollen (Kyle and Fasola 1978; Farabee et al. 1989). This indicates that the Mt. Falla plant fossil assemblage, with its low diversity and peculiar composition, probably represents only one particular subenvironment within an overall rich and diverse mosaic of plant communities in the basin.

Paleogeographic reconstructions indicate that the Mt. Falla flora flourished within South Polar latitudes during the Late Triassic (Lawver et al. 1998; Scotese 2004; Veevers 2004; Torsvik et al. 2008). The regional climate during that time is interpreted as having been mesothermal with high rainfall (Hammer et al. 1990; Parrish 1990; Scotese et al. 1999; Taylor et al. 2000; Cúneo et al. 2003; Bomfleur and Kerp 2010); there is no evidence for notable periods of frost or subzero temperatures (Taylor and Ryberg 2007; Hermsen et al. 2009). Nevertheless, the vegetation must have experienced strong seasonality in the form of the annual changes in solar radiation, with prolonged periods of polar twilight for up to several months during the winter. Some of the paleoecological characteristics of the Mt. Falla flora may be interpreted in the context of this strongly seasonal light regime.

Of particular interest are the apparent deciduous habit of all three gymnosperms and the formation of dormant reproductive buds in the newly identified peltasperm plant. Both phenomena appear to be analogous to the seasonal life cycles of many woody angiosperms in temperate to boreal vegetation today. In the Mt. Falla assemblage, synchronous leaf shedding at the end of the growth season is evidenced by the concentration of abscised leaves in distinct leaf mats and by the commonly uniform degradational state and size class of leaves on an individual bedding surface (Falcon-Lang and Cantrill 2001). The causes and consequences of the two contrasting main growth strategies in past polar forest vegetation—that is, an evergreen versus a deciduous habit—still remain poorly resolved and controversially discussed (Falcon-Lang and Cantrill 2001; Osborne et al. 2004; Brentnall et al. 2005). The deciduous growth of the different gymnosperms in the present assemblage, however, further corroborates the observation that deciduousness was a common and effective strategy in high-latitude vegetation of the Late Triassic greenhouse world (see Bomfleur and Kerp 2010).

The holotype of *T. polaris* became buried right after sprouting from a covered reproductive bud. The formation of such buds in fossil gymnosperms is an interesting phenomenon that has so far received comparatively little attention, even though buds similar to that of the present material have been reported in fossil gymnosperm pollen organs as early as the late nineteenth century (Shirley 1898). At present, we can only speculate about the function of these organs. Because the paleoclimatic setting of the Mt. Falla flora was presumably favorable throughout the year, however, it appears unlikely that bud formation served to increase cold hardiness like in many extant temperate plants. Instead, we assume that these dormant buds provided for a particularly early,

synchronous initiation of the reproductive cycle at the waning of the dark season in early spring. This can be well integrated into our interpretation of the paleoenvironmental setting and composition of the assemblage, which altogether characterize the Mt. Falla peltasperm as an early reproducing, opportunistic colonizer that formed a dominant component of rather early successional vegetation communities in disturbed wetland sites.

A further remarkable aspect of this plant assemblage is the sparse evidence for plant-insect interactions. In comparable plant fossil assemblages from the Molteno Formation of South Africa, up to 50% of *Heidiphyllum* leaves bear conspicuous insect damage, and ~50% to almost 100% of *Dejerseyia* leaves in individual assemblages show extensive continuous margin-feeding traces (Scott et al. 2004). By contrast, it appears that the proportion of leaves with insect damage in the present collection is very low (less than 5%; see fig. 3L). Some recent paleogeographic reconstructions indicate that the Molteno biome may have been situated in much lower latitudes than the Mt. Falla flora (Veevers 2004; Golonka 2007); we speculate that the remarkable difference in the amount of insect feeding may reflect a latitudinal gradient. It has only recently been suggested that increasing seasonality may provide a key explanation for the decrease in insect diversity toward higher latitudes (Archibald et al. 2010).

The Matatiellaceae: A Characteristic Group of High-Latitude Gondwanan Peltasperms?

The affiliation of *D. lobata*, *M. dejerseyi*, and *T. polaris* in the present assemblage renders it worth reconsidering several other Triassic seed-fern taxa from Gondwana in light of possible affinities with the matatiellacean peltasperms.

The Triassic Gondwanan species of *Pachydermophyllum* can confidently be included in the Matatiellaceae. A peltaspermalean affinity for these leaves has already been suggested on the basis of correspondences in leaf morphology and epidermal anatomy (Retallack 1981) and has since been further supported by the association with *Matatiella* in New Zealand (Retallack 1981; Pole and Raine 1994) and South Africa (Anderson and Anderson 2003). *Pachydermophyllum*, *Dejerseyia*, and the enigmatic leaf morphogenus *Linguifolium* form an intergrading series with respect to leaf morphology, venation pattern, lamina and cuticle thickness, development of papillae, and degree of stomatal protection (table 1; Jones and de Jersey 1947; Douglas 1969; Retallack 1977, 1980, 1981, 1983; Anderson and Anderson 1989, 2003). It is interesting to note that leaf and cuticle thickness, development of papillae, and degree of stomatal protection in some peltasperm leaves are known to vary along an ecological gradient even within a single species (Townrow 1960). Hence, there is good evidence to suggest that these taxa may be closely related and to envisage also *Linguifolium* as a possible member of the Matatiellaceae. This is further supported by the co-occurring dispersed seeds of *Carpolithus mackayi* Arber. These seeds have been described from several Middle Triassic deposits in New Zealand and occur exclusively in strata that also yield abundant *Linguifolium* leaves and few, if any, other gymnosperm foliage (Arber 1917; Retallack 1980, 1983). Apart from being considerably larger, *C. mackayi* is strongly similar to isolated seeds of *Matatiella*; both taxa are

characterized by (1) (assumed) anatropous attachment, (2) ellipsoid to ovoid form, (3) absence of wings or prominent micropylar protrusions, (4) usually two longitudinal ribs, (5) a well-developed sarcotesta (when found dispersed), (6) a nucellus attached to the integument only at the chalazal end, and (7) a prominent pollen chamber with (8) a small, straight, or slightly curved micropylar canal (Retallack 1980). Another ovulate organ that may be considered a member of the Matatiellaceae is *Andersonia rastruensis*, which differs from *Matatiella* merely in that each megasporophyll is reduced to just a single ovuliferous lobe (Arce and Lutz 2010).

There is little evidence for pollen organs to be affiliated with the Matatiellaceae. Apart from *T. polaris* described here, the only other reports include *T. petasata* and an *Antevsia*-like pollen organ, both co-occurring with *Pachydermophyllum* and *Matatiella* in Late Triassic assemblages of New Zealand (Retallack 1981; Pole and Raine 1994). We suggest, however, that the sparse evidence for pollen-organ fossils of this plant group may result from a characteristic reproductive cycle. Based on *T. polaris*, it appears reasonable to assume that the pollen organs were ephemeral, bursting out of a dormant bud at the beginning of the growth season and probably withering away shortly after pollen dispersal. Such short-lived and delicate organs are overall unlikely to enter the fossil record. Several problematic pollen organs from the Gondwanan Triassic, most of which are currently placed in the Corystospermales or the Ginkgoales, however, show some characters suggestive of a matatiellacean affinity. For instance, *Pteruchus simmondsii* (Shirley) Thomas emend. Townrow is characterized by a basal bud, a poorly developed or even absent microsporophyll lamina, a comparatively low number of pollen sacs per unit, and sunken stomata surrounded by a ring of usually papillate subsidiary cells (Shirley 1898; Thomas 1933; Townrow 1962); these features are more characteristic for *Townrowia* than for *Pteruchus* (table 2). Similarly, *Pteruchus rhaeticus* (Geinitz) Jain et Delevoryas from the Triassic of Argentina has relatively few, apparently clavate pollen sacs and lacks the flattened laminar head typical for *Pteruchus* (Jain and Delevoryas 1967). Also, a specimen tentatively referred to as *Antevsia* sp. from New Zealand may be better accommodated in *Townrowia*, on the basis of the slender peduncles and the rather large number of pollen sacs per unit (Retallack 1985). Six new species of *Stachyopitys* have been described from the Triassic Molteno Formation of South Africa (Anderson and Anderson 2003). Some of the figured specimens, however, appear quite unlike other well-established species of *Stachyopitys* because they lack the complex higher-order branching and bear comparatively large numbers of clavate pollen sacs that are attached along an elongate receptacle instead of forming a sessile fascicle (*Stachyopitys lacrisporangiata*; Anderson and Anderson 2003). Altogether, we anticipate that a detailed reevaluation, including in situ pollen analyses, will demonstrate that some of these problematic taxa may in fact belong to the Matatiellaceae.

Finally, a comparison of paleoenvironmental settings of those plant assemblages with a significant proportion of presumed matatiellacean seed ferns reveals an interesting pattern (table 3). The present assemblage, dominated by *Dejerseya*, is interpreted as a semimature wetland community colonizing a poorly drained flood basin environment in the high-latitude

continental interior of Gondwana. In the Molteno biome, matatiellacean seed ferns occurred in comparable settings along the periphery of *Heidiphyllum* thickets in areas of high water table (Cairncross et al. 1995; Anderson et al. 1998; Anderson and Anderson 2003). Along the very southern coastal margin of Gondwana in present-day New Zealand, *Pachydermophyllum-Matatiella* plants are interpreted to have formed monotonous mangrove-type vegetation fringing estuarine inlets at paleolatitudes of 80°–85°S (Retallack 1977, 1981; see Veevers 2004; Golonka 2007). Similar coastal lowlands during the Middle Triassic were inhabited by low-diversity communities strongly dominated by the *Linguifolium-C. mackayi* plants (Retallack 1977, 1980, 1981). Taken together, it appears that the matatiellacean peltasperms were opportunistic, probably early successional plants that were particularly successful in colonizing stressed wetland environments in very high southern latitudes during the Middle and Late Triassic.

Hypothesized Distribution Patterns among the Peltaspermales (Fig. 13)

The earliest records of the Peltaspermales are found in Pennsylvanian channel-fill and flood basin deposits (Remy 1975; Doubinger et al. 1995; Kerp et al. 2001; Boyarina 2010) that formed during glacial intervals under seasonally dry conditions (DiMichele et al. 2008, 2010; Falcon-Lang et al. 2009). It has therefore been suggested that the early, callipterid peltasperms were meso- to xerophilous plants that had originated in drier extrabasinal lowland settings of the Late Carboniferous paleotropical regions (Kerp et al. 2001; DiMichele et al. 2005) and then became more dominant and diverse as arid conditions became more widespread in the peri-Tethyan realm during the Permian (DiMichele et al. 2005; Booi et al. 2009). It appears that the Peltaspermales then spread northward into the cool-temperate Angaran biome, where they eventually formed the dominant, mostly endemic floral elements of the Late Permian high-latitude *Tatarina* flora (Gomankov and Meyen 1986). Remarkably, no peltaspermalean remains are so far known from the Permian high-latitude regions of Gondwana, maybe because those environments were almost invariably occupied by the ubiquitous and highly successful Glossopteridales (Pigg and Trivett 1994; Cúneo 1996). Immediately after the end-Permian biotic crisis, however, appeared the more modern *Lepidopteris*-type peltasperms in both hemispheres (McLoughlin et al. 1997; Retallack 2002). These plants later formed the typical *Lepidopteris* floras of the northern peri-Tethyan realm and mid- to high-latitude paratropics of Eurasia (Harris 1931; Dobruskina 1969, 1975; Krassilov and Karasev 2009). In the Middle and Upper Triassic of Gondwana, by contrast, the peltasperms have appeared to linger only as minor components in usually corystosperm-dominated floras (Anderson and Anderson 1989; Retallack 1995; Anderson et al. 1999; Holmes and Anderson 2005). Our interpretation of the Matatiellaceae as an endemic group of Gondwanan Peltaspermales suggests that the diversity and abundance of these seed ferns in the Triassic of Gondwana may have been much higher than previously thought.

It is assumed that the Peltaspermales disappeared at the end of the Triassic (Townrow 1960; Anderson et al. 1999). We hypothesize, however, that the presence of leaves such as *Rintoulia* and *Pachydermophyllum*, which are architecturally

Table 3

Geographic, Stratigraphic, and Paleoenvironmental Occurrences of *Matatiella* Anderson et Anderson emend. nov. and Presumably Allied Ovulate Organs with Co-occurring Foliage and Pollen Organ Taxa

Taxa		Occurrence				Vegetation and paleoenvironment
Ovulate organ	Associated foliage	Associated pollen organ	Locality	Stratigraphy	Age	
<i>Matatiella dejerseyi</i>	<i>Dejerseyia</i>	<i>Tounrovia polaris</i>	Mt. Falla, CTM	Falla Formation, Beacon Supergroup	Early to middle Late Triassic	Dominant with abundant <i>Heidiphyllum</i> in semimature woodland on poorly drained floodplain
<i>M. dejerseyi</i>	<i>Dejerseyia</i>		(?) Yandoit Hill, Victoria, Australia	Brassall Subgroup	Early Late Triassic	na
<i>Matatiella courmanei</i> <i>Matatiella rosetta</i> , <i>Andersonia raastroensis</i>	<i>Pachydermophyllum</i>	<i>Antevsia</i> sp.	Glenham, Southland, NZ	Murihiku Supergroup	(late Late?) Triassic	Near-coast delta environment
<i>Matatiella</i> spp.	<i>Pachydermophyllum</i> (= <i>Kurtziana</i> of Anderson and Anderson 2003)		Ischigualasto, San Juan Province, Argentina	Los Rastros Formation, Agua de la Peña Group	Early to middle Late Triassic	Lacustrine delta system
<i>Matatiella</i> sp.	<i>Pachydermophyllum</i>	<i>Tounrovia petasata</i>	Karoo Basin, South Africa	Molteno Formation, Karoo Supergroup	Early to middle Late Triassic	Abundant along <i>Heidiphyllum</i> -dominated backswamp vegetation in poorly drained floodplain
<i>Matatiella</i> sp.	<i>Pachydermophyllum</i>		Long Gully, Otago, NZ	Long Gully Formation, Corbies Creek Group	Middle Triassic	Dominant in mangrove-like vegetation along inland reaches of estuaries
<i>Matatiella</i> sp.	<i>Pachydermophyllum</i>		Benmore Dam, Canterbury, NZ	Black Jacks Congl., Otematata Group	Middle Triassic	Dominant in mangrove-like vegetation along inland reaches of estuaries
(?) <i>M. dejerseyi</i>	<i>Pachydermophyllum</i> , ? <i>Dejerseyia</i>		Manyima River, northern Zimbabwe	Angwa Sandstone Formation, Karoo Supergroup	Early Late Triassic	Allochthonous leaf litter accumulation in flood basin of meandering river system
(?) <i>M. dejerseyi</i>	<i>Pachydermophyllum</i> , ? <i>Dejerseyia</i>		Lower Biobío River, southern Chile	Santa Juana Formation	Late Triassic	na
(?) <i>Matatiella</i> sp.	<i>Dejerseyia</i>		Dinmore, Queensland, Australia	Ipswich Coal Measures	Early to middle Late Triassic	na
<i>Carpolithus mackayi</i>	<i>Linguiifolium</i>		Long Gully, Otago, NZ	Long Gully Formation, Corbies Creek Group	Middle Triassic	Dominant in coastal swamp woodlands
<i>C. mackayi</i>	<i>Linguiifolium</i>		Benmore Dam, Canterbury, NZ	Black Jacks Congl., Otematata Group	Middle Triassic	Dominant in coastal swamp woodlands
<i>C. mackayi</i>	<i>Linguiifolium</i>		Tank Gully, Canterbury, NZ	Tank Gully Formation, Mt. Potts Group	Middle Triassic	Dominant in coastal swamp woodlands

Sources. Douglas 1969; Retallack 1977, 1979, 1980, 1981, 1983; Anderson and Anderson 1989, 2003; Pole and Raine 1994; Nielsen 2005; Barale et al. 2006; Arce and Lutz 2010. Note. CTM, central Transantarctic Mountains; NZ, New Zealand; na, not applicable.

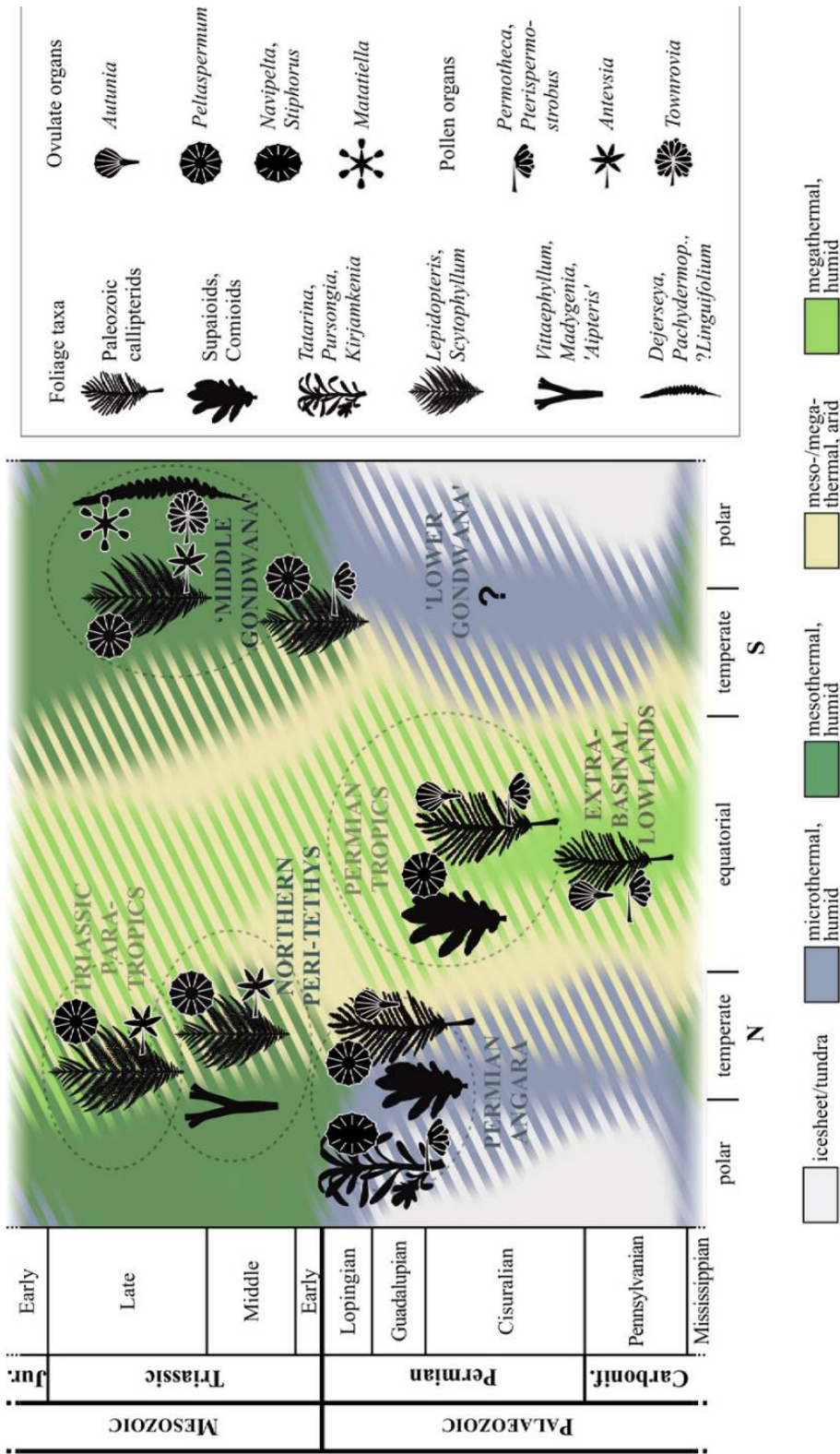


Fig. 13 Generalized distribution of peltaspermean seed-ferm taxa in a geochronological, paleogeographical, and paleoclimatological context. Peltaspermean occurrences after Townrow (1960), Dobruskina (1975, 1988), Gomanov and Meyen (1979, 1986), Retallack (1980, 1981, 1983, 2002), Kerp (1988), Anderson and Anderson (1989, 2003), Poort and Kerp (1990), Kerp et al. (2001), DiMichele et al. (2005), Arrabe et al. (2007a), Booi et al. (2009), Karasev (2009), and Boyarina (2010). Paleogeography and paleoclimate data based on PALEOMAP project data (Scorese 2002).

similar to matatiellacean foliage (Walkom 1921; Douglas 1969; McLoughlin et al. 2002), in the Jurassic and Lower Cretaceous might indicate that the peltasperm lineage persisted, albeit with a much narrower distribution, into later parts of the Mesozoic.

Acknowledgments

We thank Lisa Boucher, Ignacio Escapa, and Brian Axsmith for helpful discussion and Patrick Herendeen for valu-

able assistance in taxonomic and nomenclatural issues. The contribution has greatly benefited from detailed reviews and constructive comments by Stephen McLoughlin and William A. DiMichele. Technical assistance in fluorescence imaging by Heather Shinogle is gratefully acknowledged. Financial support has been provided in part by the Deutsche Forschungsgemeinschaft (grant KE584/16-1 to H. Kerp) and in part by the National Science Foundation (grant DPP 88-15976 to E. L. Taylor and T. N. Taylor).

Appendix

Original Diagnosis of *Dejerseya* Herbst emend. nov.

Original diagnosis (Herbst 1977, p. 22). “Como en Jones & de Jersey, 1947, Univ. Qld. Papers (Geol. Dept.) 3 (n.s.) No 3–4: 41.”

Corresponding emended diagnosis of Rienitsia given by Jones and de Jersey (1947, p. 41). “Pinnate (?) fronds bearing lobed pinnae each with a strong midrib; secondary veins at an acute angle to the midrib, curving away from the midrib; veins within each lobe arising from one strong secondary vein which by many divisions gives a fan-shaped group in each lobe; veins between the lobes absent or not so strong and dividing less frequently. Cuticle of the *Ctenis* type. Microsporophyll leaflike, the almost spherical microsporangia, being in groups on the (under ?) surface of the lamina. Megasporophyll unknown.”

Literature Cited

- Anderson HM, WBK Holmes, LA Fitness 2008 Stems with attached *Dicroidium* leaves from the Ipswich Coal Measures, Queensland, Australia. *Mem Queensl Mus* 52:1–12.
- Anderson JM, HM Anderson 1983 Palaeoflora of southern Africa: Molteno Formation (Triassic). Vol 1, pt 1. Introduction. Pt 2. *Dicroidium*. AA Balkema, Rotterdam.
- 1984 The fossil content of the Upper Triassic Molteno Formation, South Africa. *Palaeontol Afr* 25:39–59.
- 1985 Palaeoflora of southern Africa: prodromus of South African megaflores, Devonian to Lower Cretaceous. AA Balkema, Rotterdam.
- 1989 Palaeoflora of southern Africa: Molteno Formation (Triassic). Vol 2. Gymnosperms, excluding *Dicroidium*. AA Balkema, Rotterdam.
- 2003 Heyday of the gymnosperms: systematics and biodiversity of the Late Triassic Molteno fructifications. *Strelitzia* 15. National Botanical Institute, Pretoria.
- Anderson JM, HM Anderson, S Archangelsky, M Bamford, S Chandra, M Dettmann, R Hill, S McLoughlin, O Rösler 1999 Patterns of Gondwana plant colonisation and diversification. *J Afr Earth Sci* 28: 146–167.
- Anderson JM, HM Anderson, ARI Cruickshank 1998 Late Triassic ecosystems of the Molteno/lower Elliot biome of southern Africa. *Palaeontology* 41:387–421.
- Antevs E 1914 *Lepidopteris ottonis* (Göpp.) Schimp. and *Antholithus zeilleri* Nath. *K Sven Vetenskapsakad Handl* 51:1–18.
- Arber EAN 1917 The earlier Mesozoic floras of New Zealand. *N Z Geol Surv Paleontol Bull* 6:1–80.
- Arce FE, AI Lutz 2010 Fructificaciones de la Formación Los Rastros, Triásico Superior, Provincia de San Juan, Argentina. *Rev Mex Cienc Geol* 27:32–42.
- Archibald SB, WH Bossert, DR Greenwood, BD Farrell 2010 Seasonality, the latitudinal gradient of diversity, and Eocene insects. *Paleobiology* 36:374–398.
- Artabe AE, EM Morel, DG Ganuza 2007a Las floras triásicas de la Argentina. *Asoc Paleontol Argent Publ Espec* 11:75–86.
- Artabe AE, EM Morel, DG Ganuza, AM Zavattieri, LA Spalletti 2007b La paleoflora triásica de Potrerillos, provincia de Mendoza, Argentina. *Ameghiniana* 44:279–301.
- Artabe AE, DW Stevenson 1999 Fossil Cycadales of Argentina. *Bot Rev* 65:219–238.
- Artabe AE, AB Zamuner, S Archangelsky 1991 Estudios cuticulares en Cycadópsidas fósiles: el género *Kurtziana* Frenguelli 1942. *Ameghiniana* 28:365–374.
- Axsmith BJ, TN Taylor, EL Taylor 1998 Anatomically preserved leaves of the conifer *Notophytum krauselii* (Podocarpaceae) from the Triassic of Antarctica. *Am J Bot* 85:704–713.
- Axsmith BJ, EL Taylor, TN Taylor, NR Cúneo 2000 New perspectives on the Mesozoic seed fern order Corystospermales based on attached organs from the Triassic of Antarctica. *Am J Bot* 87:757–768.
- Balme BE 1970 Palynology of Permian and Triassic strata in the Salt Range and Surghar Range, West Pakistan. Pages 305–453 in B Kummel, C Teichert, eds. *Stratigraphic boundary problems: Permian and Triassic of West Pakistan*. University Press of Kansas, Lawrence.
- 1995 Fossil in situ spores and pollen grains: an annotated catalogue. *Rev Palaeobot Palynol* 87:81–323.
- Barale G, MK Bamford, B Gomez, TJ Broderick, MA Raath, A Cadman 2006 A fossil peat deposit from the Late Triassic (Carnian) of Zimbabwe with preserved cuticle of Pteridospermopsida and Ginkgoales, and its geological setting. *Palaeontol Afr* 41: 89–100.
- Barale G, G Guignard, MK Bamford 2009 Structure of corystospermaceous ovules from the Upper Triassic of Zimbabwe. *Botany* 87: 854–863.
- Barrett PJ 1969 Stratigraphy and petrology of the mainly fluvial Permian and Triassic Beacon rocks, Beardmore Glacier area, Antarctica. *Institute of Polar Studies Report* 34. Ohio State University Research Foundation, Columbus.
- Barrett PJ, DH Elliot, JF Lindsay 1986 The Beacon Supergroup (Devonian-Triassic) and Ferrar Group (Jurassic) in the Beardmore Glacier area, Antarctica. *Antarct Res Ser* 36:339–428.
- Batten DJ 1999 Small palynomorphs. Pages 15–19 in TP Jones, NP

- Rowe, eds. Fossil plants and spores: modern techniques. Geological Society, London.
- Behrensmeyer AK, RW Hook 1992 Paleoenvironmental contexts and taphonomic modes. Pages 15–136 in AK Behrensmeyer, JD Damuth, WA DiMichele, R Potts, H-D Sues, SL Wing, eds. Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals. University of Chicago Press, Chicago.
- Bomfleur B, H Kerp 2010 *Dicroidium* diversity in the Upper Triassic of north Victoria Land, East Antarctica. *Rev Palaeobot Palynol* 160: 67–101.
- Bomfleur B, R Serbet, EL Taylor, TN Taylor 2011 The possible pollen cone of the Late Triassic conifer *Heidiphyllum/Telemachus* (Voltziales) from Antarctica. *Antarct Sci*, doi:10.1017/S0954102011000241.
- Booi M, IM van Waveren, JHA van Konijnenburg-van Cittert 2009 *Comia* and *Rhachiphyllum* from the early Permian of Sumatra, Indonesia. *Rev Palaeobot Palynol* 156:418–435.
- Boucher LD, EL Taylor, TN Taylor 1993 *Dicroidium* from the Triassic of Antarctica. Pages 39–46 in SG Lucas, M Morales, eds. The non-marine Triassic. *N M Mus Nat Hist Sci Bull* 3.
- Boyarina N 2010 Late Gzhelian pteridosperms with callipterid foliage of the Donets Basin, Ukraine. *Acta Palaeontol Pol* 55:343–359.
- Brentnall SJ, DJ Beerling, CP Osborne, M Harland, JE Francis, PJ Valdes, VE Wittig 2005 Climatic and ecological determinants of leaf lifespan in polar forests of the high CO₂ Cretaceous “greenhouse” world. *Glob Change Biol* 11:2177–2195.
- Burnham RJ 1990 Some Late Eocene depositional environments of the coal-bearing Puget Group of western Washington State, U.S.A. *Int J Coal Geol* 15:27–51.
- Burnham RJ, WL Wing, GG Parker 1992 The reflection of deciduous forest communities in leaf litter: implications for autochthonous litter assemblages from the fossil record. *Paleobiology* 18:30–49.
- Cairncross B, JM Anderson, HM Anderson 1995 Palaeoecology of the Triassic Molteno Formation, Karoo Basin, South Africa: sedimentological and palaeontological evidence. *S Afr J Geol* 98: 452–478.
- Cúneo NR 1996 Permian phytogeography in Gondwana. *Palaeogeogr Palaeoclimatol Palaeoecol* 125:75–104.
- Cúneo NR, EL Taylor, TN Taylor, M Krings 2003 In situ fossil forest from the upper Fremouw Formation (Triassic) of Antarctica: paleoenvironmental setting and paleoclimate analysis. *Palaeogeogr Palaeoclimatol Palaeoecol* 197:239–261.
- DiMichele WA, CB Cecil, IP Montañez, HJ Falcon-Lang 2010 Cyclic changes in Pennsylvanian paleoclimate and effects on floristic dynamics in tropical Pangaea. *Int J Coal Geol* 83:329–344.
- DiMichele WA, H Kerp, M Krings, DS Chaney 2005 The Permian peltasperm radiation: evidence from the southwestern United States. Pages 67–79 in SG Lucas, KE Zeigler, eds. The nonmarine Permian. *N M Mus Nat Hist Sci Bull* 30.
- DiMichele WA, H Kerp, NJ Tabor, CV Looy 2008 The so-called “Paleophytic-Mesophytic” transition in equatorial Pangea: multiple biomes and vegetational tracking of climate change through geological time. *Palaeogeogr Palaeoclimatol Palaeoecol* 268:152–163.
- Dobruskina IA 1969 Genus *Scytophyllum* (morphology, epidermal structure and systematical position). Pages 35–58 in SV Meyen, ed. Pteridosperms of the Upper Palaeozoic and the Mesozoic. Nauka, Moscow.
- 1975 The role of peltaspermacean pteridosperms in Late Permian and Triassic floras. *Paleontol J* 4:536–549.
- 1988 The history of land plants in the Northern Hemisphere during the Triassic with special reference to the floras of Eurasia. *Geol Paläont Mitt Innsbruck* 15:1–12.
- Doubinger J, P Vetter, J Langiaux, J Galtier, J Broutin 1995 La flore fossile du bassin houiller de Saint-Étienne. *Mem Mus Natl Hist Nat* 164:1–355.
- Douglas JG 1969 The Mesozoic floras of Victoria. Pts 1, 2. *Geol Surv Vic Mem* 28. 310 p.
- Elliot DH 1996 The Hanson Formation: a new stratigraphical unit in the Transantarctic Mountains, Antarctica. *Antarct Sci* 8:389–394.
- Elliot DH, CG Grimes 2011 Triassic and Jurassic strata at Coombs Hills, south Victoria Land: stratigraphy, petrology and cross-cutting breccia pipes. *Antarct Sci*, doi:10.1017/S0954102010000994.
- Escapa IH, A-L Decombeix, EL Taylor, TN Taylor 2010 Evolution and relationships of the conifer seed cone *Telemachus*: evidence from the Triassic of Antarctica. *Int J Plant Sci* 171:560–573.
- Falcon-Lang HJ, DJ Cantrill 2001 Leaf phenology of some mid-Cretaceous polar forests, Alexander Island, Antarctica. *Geol Mag* 138:39–52.
- Falcon-Lang HJ, WJ Nelson, S Elrick, CV Looy, PR Ames, WA DiMichele 2009 Incised channel fills containing conifers indicate that seasonally dry vegetation dominated Pennsylvanian tropical lowlands. *Geology* 37:923–926.
- Farabee MJ, TN Taylor, EL Taylor 1989 Pollen and spore assemblages from the Falla Formation (Upper Triassic), Central Transantarctic Mountains, Antarctica. *Rev Palaeobot Palynol* 61: 101–138.
- Ferguson DK 1985 The origin of leaf assemblages: new light on an old problem. *Rev Palaeobot Palynol* 46:117–188.
- 2005 Plant taphonomy: ruminations on the past, the present, and the future. *Palaios* 20:418–428.
- Ferguson DK, C-C Hofmann, T Denk 1999 Taphonomy: field techniques in modern environments. Pages 210–213 in TP Jones, NP Rowe, eds. Fossil plants and spores: modern techniques. Geological Society, London.
- Frenquelli J 1942 Contribución al conocimiento de la Flora del Gondwana superior en la Argentina. IX. *Kurtzia cacheutensis* Kurtz sp., n. gen. et n. comb. *Notas Mus La Plata Paleontol* 50:331–339.
- 1944 Contribuciones al conocimiento de la Flora del Gondwana superior en la Argentina. XVII. *Stachyopitys anthoides* n. sp. *Notas Mus La Plata Paleontol* 65:385–392.
- Gabites HI 1985 Triassic paleoecology of the Lashly Formation, Transantarctic Mountains, Antarctica. MSc thesis. Victoria University, Wellington.
- Gastaldo RA 1992 Taphonomic considerations for plant evolutionary investigations. *Palaeobotanist* 41:211–223.
- Gee CT 2005 The genesis of mass carpological deposits (bedload carpodeposits) in the Tertiary of the Lower Rhine Basin, Germany. *Palaios* 20:463–478.
- Gnaedinger S, R Herbst 1998a La flora triásica del Grupo El Tranquilo, provincia de Santa Cruz (Patagonia). IV. Pteridospermae. *Ameghiniana* 35:33–52.
- 1998b La flora triásica del Grupo El Tranquilo, provincia de Santa Cruz (Patagonia). V. Pteridophylla. *Ameghiniana* 35:53–66.
- 2004 Pteridophylla triásicas del Norte de Chile. II. Géneros *Dejerseya* Herbst, *Linguifolium* (Arber) Retallack y *Yabeiella* Oishi. *Rev Mus Argent Cienc Nat*, NS, 6:49–59.
- Golonka J 2007 Late Triassic and Early Jurassic palaeogeography of the world. *Palaeogeogr Palaeoclimatol Palaeoecol* 244:297–307.
- Gomankov AV, SV Meyen 1979 Members of the family Peltaspermaceae from the Permian of the Russian Platform. *Paleontol J* 2: 240–254.
- 1986 *Tatarina* flora (taxonomic composition and distribution in the Late Permian of Eurasia). *Proc Geol Inst Acad Sci USSR* 401: 1–174. (In Russian.)
- Gordenko NV 2010 Vladimariales ordo nov. (Gymnospermae) from the Middle Jurassic deposits of the Mikhailovskii rudnik locality (Kursk Region, European Russia). *Paleontol J* 44:1281–1307.
- Greenwood DR 1991 The taphonomy of plant macrofossils. Pages

- 141–169 in SK Donovan, ed. The processes of fossilization. Columbia University Press, New York.
- Hammer WR, JW Collinson, WJ Ryan III 1990 A new Triassic vertebrate fauna from Antarctica and its depositional setting. *Antarct Sci* 2:163–167.
- Harris TM 1931 Rhaetic floras. *Biol Rev* 6:133–162.
- 1932 The fossil flora of Scoresby Sound East Greenland. 2. Description of seed plants *incertae sedis* together with a discussion of certain cycadophyte cuticles. *Medd Gronl* 85:1–114.
- 1937 The fossil flora of Scoresby Sound East Greenland. 5. Stratigraphic relations of the plant beds. *Medd Gronl* 112:1–114
- Herbst R 1977 Sobre Marattiales (Filicopsidae) Triásicas de Argentina y Australia. II. Los géneros *Danaeopsis* y *Rienitsia*. *Ameghiniana* 16:19–32.
- Hermesen EJ, EL Taylor, TN Taylor 2009 Morphology and ecology of the *Antarcticycas* plant. *Rev Palaeobot Palynol* 153:108–123.
- Hill D, G Playford, JT Woods 1965 Triassic fossils of Queensland. Queensland Palaeontographical Society, Brisbane.
- Holmes WBK 1987 New corystosperm ovulate fructifications from the Middle Triassic of eastern Australia. *Alcheringa* 11:165–173.
- Holmes WBK, HM Anderson 2005 The Middle Triassic megafossil flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales. 5. The genera *Lepidopteris*, *Kurtziana*, *Rochipteris* and *Walkomiopteris*. *Proc Linn Soc N S W* 126:39–79.
- Holmes WBK, SR Ash 1979 An Early Triassic megafossil flora from the Lorne Basin, New South Wales. *Proc Linn Soc N S W* 103:47–70.
- Jain RK, T Delevoryas 1967 A Middle Triassic flora from the Cacheuta Formation, Minas de Petroleo, Argentina. *Palaeontology* 10:564–589.
- Johnston RM 1886 General observations regarding the classification of the upper Palaeozoic and Mesozoic rocks of Tasmania, together with a full description of all the known Tasmanian coal plants, including a considerable number of new species. *Pap Proc R Soc Tasman* 1885:343–387.
- 1894 Further contributions to the fossil flora of Tasmania. I. *Pap Proc R Soc Tasman* 1893:170–178.
- 1896 Further contributions to the fossil flora of Tasmania. II. *Pap Proc R Soc Tasman* 1894/1895:57–63.
- Jones OA, NJ de Jersey 1947 The flora of the Ipswich Coal Measures: morphology and floral succession. *Univ Qld Pap Dept Geol, NS*, 3:1–88.
- Karasev EV 2009 A new genus *Navipelta* (Peltaspermales, Pteridospermales) from the Permian/Triassic boundary deposits of the Moscow Syncline. *Paleontol J* 43:1262–1271.
- Kerp H, J Broutin, S Lausberg, H Aassoumi 2001 Discovery of Latest Carboniferous–Early Permian radially symmetrical peltaspermaeous megasporophylls from Europe and North Africa. *C R Acad Sci Ser II A* 332:513–519.
- Kerp H, M Krings 1999 Light microscopy of cuticles. Pages 52–56 in TP Jones, NP Rowe, eds. *Fossil plants and spores: modern techniques*. Geological Society, London.
- Kerp JHF 1982 Aspects of Permian palaeobotany and palynology. II. On the presence of the ovuliferous organ *Autunia milleryensis* (Renault) Krasser (Peltaspermales) in the Lower Permian of the Nahe area (F.G.R.) and its relationship to *Callipteris conferta* (Sternberg) Brongniart. *Acta Bot Neerl* 31:417–427.
- 1988 Aspects of Permian palaeobotany and palynology. X. The West- and Central European species of the genus *Autunia* Krasser emend. Kerp (Peltaspermales) and the form-genus *Rhachiphyllum* Kerp (callipterid foliage). *Rev Palaeobot Palynol* 54:249–360.
- Kidder DL, TR Worsley 2004 Causes and consequences of extreme Permo-Triassic warming to globally equable climate and relation to Permo-Triassic extinction and recovery. *Palaeogeogr Palaeoclimatol Palaeoecol* 203:207–237.
- Kirchner M, A Müller 1992 *Umkomasia franconica* n. sp. und *Pteruchus septentrionalis* n. sp., Fruktifikationen von *Thinnfelida* Ettingshausen. *Palaeontographica B* 224:63–73.
- Kirchner M, JHA van Konijnenburg-van Cittert 1994 *Schmeissneria microstachys* (Presl, 1833) Kirchner et Van Konijnenburg-van Cittert, comb. nov. and *Karkenienia hauptmannii* Kirchner et Van Konijnenburg-van Cittert, sp. nov., plants with ginkgoalean affinities from the Liassic of Germany. *Rev Palaeobot Palynol* 83:199–216.
- Klavins SD, TN Taylor, EL Taylor 2002 Anatomy of *Umkomasia* (Corystospermales) from the Triassic of Antarctica. *Am J Bot* 98:664–676.
- Krassilov VA, SA Afonin, SV Naugolnykh 1999 *Permotheca* with in situ pollen grains from the Lower Permian of the Urals. *Palaeobotanist* 48:19–25.
- Krassilov VA, E Karasev 2009 Paleofloristic evidence of climate change near and beyond the Permian–Triassic boundary. *Palaeogeogr Palaeoclimatol Palaeoecol* 284:326–336.
- Kräusel R 1943 Untersuchungen zur Mesozoischen Floren-Geschichte des alpinen und süddeutschen Raumes. II. Die Ginkgo-phyten der Trias von Lunz in Nieder-Österreich und von Neuwelt bei Basel. *Palaeontographica B* 137:60–93.
- Kustatscher E, C Pott, JHA van Konijnenburg-van Cittert 2011 A contribution to the knowledge of the Triassic fern genus *Symopteris*. *Rev Palaeobot Palynol* 165:41–60, doi:10.1016/j.revpalbo.2011.02.006.
- Kustatscher E, M Wachtler, JHA van Konijnenburg-van Cittert 2007 Horsetails and seed ferns from the Middle Triassic (Anisian) locality Kühwiesenkopf (Monte Prà della Vacca), Dolomites, northern Italy. *Palaeontology* 50:1277–1298.
- Kyle RA, A Fasola 1978 Triassic palynology of the Beardmore Glacier area of Antarctica. *Palinologia* 1:313–319.
- Lacey WS 1976 Further observations on the Molteno flora of Rhodesia. *Arnoldia (Rhod)* 7:1–14.
- Lawver LA, LM Gahagan, IWD Dalziel 1998 A tight-fit Early Mesozoic Gondwana: a plate reconstruction perspective. Pages 214–229 in Y Motoyoshi, K Shiraiishi, eds. *Proceedings of the International Symposium “Origin and Evolution of Continents.”* Mem Nat Inst Polar Res Spec Issue 53.
- McLoughlin S, S Lindström, AN Drinnan 1997 Gondwanan floristic and sedimentological trends during the Permian-Triassic transition: new evidence from the Amery Group, northern Prince Charles Mountains, East Antarctica. *Antarct Sci* 9:281–298.
- McLoughlin S, A-MP Tosolini, NS Nagalingum, AN Drinnan 2002 Early Cretaceous (Neocomian) flora and fauna of the lower Strzelecki Group, Gippsland Basin, Victoria. *Assoc Aust Palaeontol Mem* 26:1–144.
- Morel EM, AE Artabe, DG Ganuza, A Zúñiga 2010 La paleoflora triásica del cerro Cacheuta, provincia de Mendoza, Argentina. Bryopsida, Lycopsida, Sphenopsida, Filicopsida y Gymnospermopsida (Corystospermales y Peltaspermales). *Ameghiniana* 47:3–23.
- Nathorst AG 1908 Paläobotanische Mitteilungen. 6. *Antholithus zeilleri* n. sp. mit noch erhaltenen Pollenkörnern aus den rhätischen Ablagerungen Schonens. *K Sven Vetenskapsakad Handl* 43:20–24.
- Naugolnykh SV 1998 Flora of Kungurian Stage of the Middle Fore-Urals. *Proc Geol Inst Russ Acad Sci* 509. GEOS, Moscow. (In Russian.)
- 2001 A new peltaspermaeous pteridosperm from the Upper Permian of the Russian Platform. *Palaeobotanist* 50:189–205.
- 2008 A new gymnosperm *Sylvocarpus armatus* gen. et sp. nov. from the Lower Permian of the Ural Mountains. *Paleontol J* 42:431–439.
- Naugolnykh SV, H Kerp 1996 Aspects of Permian palaeobotany and

- palynology. XV. On the oldest known peltasperms with radially symmetrical ovuliferous discs from the Kungurian (uppermost Lower Permian) of the Fore-Urals (Russia). *Rev Palaeobot Palynol* 91:35–62.
- Nielsen SN 2005 The Triassic Santa Juana Formation at the lower Biobío River, south central Chile. *J S Am Earth Sci* 19:547–562.
- Osborn JM, TN Taylor 1993 Pollen morphology and ultrastructure of the *Corystospermales*: permineralized in situ grains from the Triassic of Antarctica. *Rev Palaeobot Palynol* 79:205–219.
- Osborne CP, DL Royer, DJ Beerling 2004 Adaptive role of leaf habit in extinct polar forests. *Int For Rev* 6:181–186.
- Parrish JT 1990 Gondwanan paleogeography and paleoclimatology. Pages 15–26 in TN Taylor, EL Taylor, eds. *Antarctic paleobiology: its role in the reconstruction of Gondwana*. Springer, New York.
- Petriella B 1980 Sinopsis de las *Corystospermaceae* (*Corystospermales*, *Pteridospermyta*) de Argentina. II. Estructuras fértiles. *Ameghiniana* 17:168–180.
- Petriella B, OG Arrondo 1982 El género *Kurtzia* Frenguelli: su morfología y vinculaciones. *Ameghiniana* 19:209–215.
- Pigg KB, ML Trivett 1994 Evolution of the glossopterid gymnosperms from Permian Gondwana. *J Plant Res* 107:461–477.
- Pole MS, JS Raine 1994 Triassic plant fossils from Pollock Road, Southland, New Zealand. *Alcheringa* 18:147–159.
- Poort RJ, JHF Kerp 1990 Aspects of Permian palaeobotany and palynology. XI. On the recognition of true peltasperms in the Upper Permian of West and Central Europe and a reclassification of the species formerly assigned to *Peltaspermum* Harris. *Rev Palaeobot Palynol* 63:197–225.
- Preto N, E Kustatscher, PB Wignall 2010 Triassic climates: state of the art and perspectives. *Palaeogeogr Palaeoclimatol Palaeoecol* 290:1–10.
- Remy W 1975 The floral changes at the Carboniferous-Permian boundary in Europe and North America. Pages 305–352 in JA Barlow, ed. *The age of the Dunkard*. Proceedings of the First I. C. White Memorial Symposium. West Virginia Geological and Economic Survey, Morgantown.
- Retallack GJ 1977 Reconstructing Triassic vegetation of eastern Australasia: a new approach for the biostratigraphy of Gondwanaland. *Alcheringa* 1:247–277.
- 1979 Middle Triassic coastal outwash plain deposits in Tank Gully, Canterbury, New Zealand. *J R Soc N Z* 9:397–414.
- 1980 Middle Triassic megafossil plants and trace fossils from Tank Gully, Canterbury, New Zealand. *J R Soc N Z* 10:31–63.
- 1981 Middle Triassic megafossil plants from Long Gully, near Otematata, north Otago, New Zealand. *J R Soc N Z* 11:167–200.
- 1983 Middle Triassic megafossil marine algae and land plants from near Benmore Dam, southern Canterbury, New Zealand. *J R Soc N Z* 13:129–154.
- 1985 Triassic fossil plant fragments from shallow marine rocks of the Murihiku Supergroup, New Zealand. *J R Soc N Z* 15:1–26.
- 1995 An early Triassic fossil flora from Culvida Soak, Canning Basin, Western Australia. *J R Soc West Aust* 78:57–66.
- 2002 *Lepidopteris callipteroides*, an earliest Triassic seed fern from the Sydney Basin, southeastern Australia. *Alcheringa* 26:475–500.
- Scheiuing MH, HW Pfefferkorn 1984 The taphonomy of land plants in the Orinoco Delta: a model for the incorporation of plant parts in clastic sediments of Late Carboniferous age of Euramerica. *Rev Palaeobot Palynol* 41:205–240.
- Schweitzer H-J, M Kirchner 1995 Die rhäro-jurassischen Floren des Iran und Afghanistans. 8. Ginkgophyta. *Palaeontographica B* 237:1–58.
- Scotese CR 2002 PALEOMAP project. <http://www.scotese.com>.
- 2004 A continental drift flipbook. *J Geol* 112:729–741.
- Scotese CR, AJ Boucot, WS McKerrow 1999 Gondwanan palaeogeography and palaeoclimatology. *J S Afr Earth Sci* 28:99–114.
- Scott AC, JM Anderson, HM Anderson 2004 Evidence for plant–insect interactions in the Upper Triassic Molteno Formation of South Africa. *J Geol Soc Lond* 161:401–410.
- Sellwood BW, PJ Valdes 2006 Mesozoic climates: general circulation models and the rock record. *Sediment Geol* 190:269–287.
- Shirley JS 1898 Additions to the fossil flora of Queensland, mainly from the Ipswich Formation, Trias-Jura System. *Qld Dept Mines Geol Surv Bull* 7:1–25.
- Solms-Laubach H 1884 Die Koniferenformen des deutschen Kupferschiefers und Zechsteins. *Palaeontol Abh* 2:82–116.
- Spalletti LA, EM Morel, JR Franzese, AE Artabe, DG Ganuza, A Zúñiga 2007 Contribución al conocimiento sedimentológico y paleobotánico de la Formación El Freno (Jurásico Temprano) en el valle superior del río Atuel, Mendoza, Argentina. *Ameghiniana* 44:367–386.
- Stanislavsky FA 1976 The Middle Keuper flora of the Donetz Basin. *Naukova Dumka*, Kiev.
- Stevens J 1981 Palynology of the Callide Basin, east-central Queensland. *Pap Dept Geol Qld* 9:1–35.
- Taylor EL 1996 Enigmatic gymnosperms? structurally preserved Permian and Triassic seed ferns from Antarctica. *Rev Palaeobot Palynol* 90:303–318.
- Taylor EL, LD Boucher, TN Taylor 1992 *Dicroidium* foliage from Mount Falla, central Transantarctic Mountains. *Antarct J U S* 27:2–3.
- Taylor EL, PE Ryberg 2007 Tree growth at polar latitudes based on fossil tree ring analysis. *Palaeogeogr Palaeoclimatol Palaeoecol* 255:246–264.
- Taylor EL, TN Taylor 1988 Late Triassic flora from Mount Falla, Queen Alexandra Range. *Antarct J U S* 23:2–3.
- 2009 Seed ferns from the late Paleozoic and Mesozoic: any angiosperm ancestors lurking there? *Am J Bot* 96:237–251.
- Taylor EL, TN Taylor, NR Cúneo 2000 Permian and Triassic high-latitude paleoclimates: evidence from fossil biotas. Pages 321–350 in BT Huber, KG MacLeod, SL Wing, eds. *Warm climates in earth history*. Cambridge University Press, Cambridge.
- Taylor EL, TN Taylor, H Kerp, EJ Hermsen 2006 Mesozoic seed ferns: old paradigms, new discoveries. *J Torr Bot Soc* 133:62–82.
- Taylor TN 1976 Patterns in gymnosperm evolution. *Rev Palaeobot Palynol* 21:1–3.
- Taylor TN, EL Taylor 1990 *Antarctic paleobiology: its role in the reconstruction of Gondwana*. Springer, New York.
- Thomas HH 1933 On some pteridospermous plants from the Mesozoic rocks of South Africa. *Philos Trans R Soc B* 222:193–256.
- Thomas HH, MN Bose 1955 *Pachydermophyllum papillosum* gen. et sp. nov. from the Yorkshire Jurassic. *Ann Mag Nat Hist* 12:535–543.
- Torsvik TH, C Gaina, TF Redfield 2008 Antarctica and global paleogeography: from Rodinia, through Gondwanaland and Pangea, to the birth of the Southern Ocean and the opening of gateways. Pages 125–140 in AK Cooper, PJ Barrett, H Stagg, B Storey, E Stump, W Wise, 10th ISAES editorial team, eds. *Antarctica: a keystone in a changing world*. Proceedings of the 10th International Symposium on Antarctic Earth Sciences. National Academies Press, Washington, DC.
- Townrow JA 1957 On *Dicroidium*, probably a pteridospermous leaf, and other leaves now removed from this genus. *Trans Geol Soc S Afr* 60:21–56.
- 1960 The *Peltaspermaceae*, a pteridosperm family of Permian and Triassic age. *Palaeontology* 3:333–361.
- 1962 On *Pteruchus* a microsporophyll of the *Corystospermaceae*. *Bull Br Mus (Nat Hist) Geol* 6:289–320.

- 1965 A new member of the Corystospermaceae Thomas. *Ann Bot, NS*, 29:495–511.
- 1967 Fossil plants from Allan and Carapace nunataks, and from the upper Mill and Shackleton glaciers, Antarctica. *N Z J Geol Geophys* 10:456–473.
- Veevers JJ 2004 Gondwanaland from 650–500 Ma assembly through 320 Ma merger in Pangea to 185–100 Ma breakup: supercontinental tectonics via stratigraphy and radiometric dating. *Earth Sci Rev* 68:1–132.
- Walkom AB 1921 Mesozoic floras of New South Wales. I. Fossil plants from Cockabutta Mountain and Talbragar. *Mem Geol Surv N S W Palaeontol* 12:1–21.
- 1932 Fossil plants from Mount Piddington and Clarence Siding. *Proc Linn Soc N S W* 57:123–126.
- Wang J, H Pfefferkorn 2010 Nystroemiaceae, a new family of Permian gymnosperms from China with an unusual combination features. *Proc R Soc B* 277:301–309.
- Wang Z, L Wang 1989 Earlier Early Triassic fossil plants in the Shiqianfeng Group in North China. *Shanxi Geol* 4:23–40. (In Chinese.)
- Yao X, TN Taylor, EL Taylor 1993 The Triassic seed cone *Telemachus* from Antarctica. *Rev Palaeobot Palynol* 78:269–276.
- 1995 The corystosperm pollen organ *Pteruchus* from the Triassic of Antarctica. *Am J Bot* 82:535–546.
- Zalessky 1929 Sur des débris de nouvelles plantes permiennees. *Bull Acad Sci URSS* 77:677–689.
- Zhou Z-Y 2009 An overview of fossil Ginkgoales. *Palaeoworld* 18: 1–22.